

THE ECOLOGY OF SMALL RODENTS IN THE GRASSLAND
COMMUNITY OF THE QUEEN ELIZABETH NATIONAL PARK,
UGANDA.

by

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FACULTY OF SCIENCE

ZOOLOGY

Doctor of Philosophy

THE ECOLOGY OF SMALL RODENTS IN THE GRASSLAND COMMUNITY
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by Brian Richard Neal

During the period April 1965 to May 1966 a total of 2,390 small mammals, representing 14 species of rodents and various species of Insectivora, were collected in four grassland areas of the Queen Elizabeth National Park, Uganda. Two areas were trapped throughout a complete year and the main seasonal changes occurring in the grassland were recorded.

In one area the distribution of the different rodent species was studied with respect to the major plant communities. Each species was found to have a slightly different distribution. In general those species with more specialized feeding habits had restricted distributions compared with the omnivorous species.

The distribution and habitat preferences of the rodents were found to be profoundly modified by burning in the grassland. At first the number of animals and species present in the burnt areas were reduced, apparently by emigration to the unburnt areas. Some species were more effected by the burn than others. Trapping in the burnt

and unburnt areas during the ten months after the fire showed that preferences for the two areas changed markedly during this period.

A study of the breeding biology revealed that all rodent species were breeding at a maximum during or towards the end of the two rainy seasons each year, although different species varied in their breeding patterns. There was a marked loss in weight of the testes, epididymides and seminal vesicles in some species during the dry season, and some males appeared to be in anoestrus during the dry seasons like the females.

A study of changes in the age structure of the population throughout the year, supported the cycle of breeding activity already established.

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I. INTRODUCTION

The Order Rodentia has been classified in various ways by Thomas (1896), Tullberg (1899), Miller and Gidley (1918), Winge (1924), Weber (1928), Ellerman (1940) and Simpson (1945). These classifications have been discussed by Ellerman (1940, 1949) and Simpson (1945) and in the following account Simpson's subdivision of the Order has been followed. All the small rodents collected in the present study have been included by Simpson in the Families Cricetidae and Muridae. These two families form the nucleus of the Muroidea, which is a superfamily of the myomorph rodents.

According to Simpson, members of the Muroidea probably evolved from the sciuromorphs in the late Eocene. The most primitive members are the cricetids which first appeared in the Oligocene of North America, Europe and Asia. They mainly evolved in Holarctica, occasionally extending southwards as geographic conditions allowed. In various areas, such as Madagascar, these southern migrants were insulated from the later murid invasion, radiated and became the dominant small ground rodents. Where they were not so insulated, such as in southern Asia and Africa, they became subordinate to the dominant murids.

The murids probably evolved from the cricetids in the Old World tropical zones of Africa, southern Asia, East Indies and Australia. In these regions they have radiated and become the

dominant small ground rodents, and a few have migrated into the Palaearctic region. They have been introduced into the New World by man so that, in the present day, the family has a worldwide distribution.

Typically, however, the murids are found in the tropical and subtropical regions of the Old World, and the cricetids in the New World and Palaearctic regions. It is generally true to say that the biology of these animals is only well known for those occurring in North America and the Palaearctic region, with the result that for most murids and many cricetids very little is known.

The paucity of scientific study and the importance of studying the mammals of Africa has been emphasized by Matthews (1954) and Meester (1954). Matthews stressed the importance of big game studies, whilst Meester suggested that the study of small mammals was equally important because of the scientific and economic problems they present.

The numerous scientific expeditions that have visited Africa, such as those reported by Thomas and Wroughton (1909-10), Hollister (1919), Allen and Lawrence (1936), Frechkop (1938, 1943, 1954), Hatt (1940), Sanderson (1940), Allen and Loveridge (1942), Lawrence and Loveridge (1953), Loveridge (1953) and Happold (1966a) have collected much incidental information about the Muroidea. However, as Matthews (1954) has remarked, the main object of most expeditions has been to collect dead specimens for

museums rather than to study the animals in the field. Consequently, most of the material collected can only be used for taxonomic studies.

General accounts for small african rodents have been given for South West Africa* by Shortridge (1934), South Africa by Fitzsimons (1920) and Roberts (1951), for Zambia by Ansell (1960), for what was then French Equatorial Africa, French West Africa, Algeria and neighbouring French Territories by Dekeyser (1955), for West Africa by Booth (1960), for the Congo by Schouteden (1944-6, 1948) and Eastern Congo by Curry-Lindahl (1956, 1960), for Kenya by Copley (1950), for Eastern Uganda by Watson (1950), and for Uganda by Delany and Neal (1966) and Hopkins (undated manuscript). These all list the species known to occur in these territories, and then describe what is known about their ecology and biology. All these works admirably illustrate how little is known about african small rodents.

The first detailed general ecological study on small african rodents appears to have been made by Sanderson (1940) in the North Cameroons forest area. This excellent study was primarily designed to test the effects of ecological conditions on variation at the specific and subspecific levels. The habitats where each species occurred were accurately described, and breeding

*This area, together with place names mentioned subsequently in the text, may be found in fig. 1.

records and general aspects of their biology were also noted.

Most of the early ecological studies on small african rodents were made in the Congo. Wanson, Richard and Toubac (1947) made a general survey of the small mammals occurring around Leopoldville. Their object was to describe the ecology of the various species so that a useful relationship with bubonic plague or the murine typhus, which they harbour, could be established. They made notes on the habitats, diets and biology of the various species, and then recorded the ectoparasites each species carried, and what part they played in different diseases.

Pirlot and van den Bulcke (1952) made a collection of small rodents in Katanga, initially for a taxonomic study, but decided to study their ecology instead. They described their trapping techniques and compared them with those used in Britain and America. They estimated the density of the populations occurring in a variety of major habitats, and concluded that the relict patches of forest contained an exceptionally high population density compared with any other area studied. They also considered climatic influences on the populations, and regular changes in the sex ratio over the year. Their results suggested that the small mammal behaviour varied according to the species and sex.

Pirlot (1953) went on to describe the ecological distribution of the small rodents in Katanga using the same material that was collected in the previous study. The study was not very detailed because the rodents were only identified as far as genera

and the habitats in which they occurred were classified into only four main types. He largely discussed the problem, suggesting factors which may affect the distribution, rather than being able to say precisely what the distribution was. Later, Pirlot (1957b) went on to study the ecology of small rodents occurring in Ruanda Urundi and the adjoining area of the Congo to the west of Lake Kivu. The study was as vague and hypothetical as his previous one. He compared his results with those obtained from Katanga and noted that the faunas of the two areas were quite different. He related this difference to the differences in habitat and altitude.

The same general area of the Congo to the west of Lake Kivu was studied in more detail by Rahm and Christiaensen (1963). They trapped all the major habitats in the area, which they accurately described, and related the distribution of most small mammals to the type of habitat. Most species were found to be quite specific in their choice of habitat. They also made notes on the diet, biology and breeding of the various species.

Misonne (1963) made a study of the rodents occurring about 150 miles to the north of the last study area, around the Ruwenzori Mountains in the Albert National Park. He described the general characteristics of the area, including the topography, climate and vegetation, and then described the distribution giving notes on their biology of the various species collected. In this way the work was very similar and compared well with the previous

studies. Misonne went on to discuss the inter-relationships of the various species, how the distribution of one affected another, and the associations of the different species within the various habitats studied. He also considered the distribution of relict species associated with mountains and tropical rain forest throughout the whole of Africa. The invasion of East and Central Africa by Rattus rattus (Linnaeus), and the competition between Rattus rattus and Mastomys natalensis Smith, was also discussed.

The distribution of rodents in high forest in Uganda was investigated in more detail by Southern and Hook (1963a). They found a large number of species which showed some habitat specialisation in this complex major habitat. Different species preferred wet or dry forest and ground or shrub layers.

Delany (1964a) studied the ecology and breeding of the small mammals in Uganda during the last six months of 1961. All the major habitat types in Uganda were trapped, using a variety of traps in an attempt to capture the whole size range of these animals. Most habitats were found to contain a large number of species, many of which were specific to one type of habitat. There was very little breeding in most species which suggested a limited breeding season which may coincide with the rains. In contrast a few species were breeding when caught, which suggests either that they breed throughout the year, or that the different species do not breed simultaneously. Different species were also found to vary in their activity during the day. Later, Delany

(1964b) went on to study the small mammals occurring in the Queen Elizabeth National Park in western Uganda. Five localities were trapped intensively, ranging from grassland through scrub to semi-deciduous forest. The species collected and their abundance varied according to the habitat. They appeared to be at a maximum in thick grassland where numbers of large game animals were low. When their feeding habits were studied, some rodents were found to be purely insectivorous, others herbivorous, and the rest omnivorous. There was little reproductive activity during the three month study (July - September), but the population structure of the most abundant species indicated a limited breeding season. He concluded that the distribution and abundance of small mammals was accounted for by the nature of the vegetation, through the food and cover it provides, and how this is modified by large mammals and fire. Hatt (1963) made a live-trap study of the small mammals in Rhodesia for a period of four weeks in July and August 1961. He attempted to find the habitat preferences, distribution and relative abundance of the various species, and also performed homing experiments. The homing ability of the various species varied considerably, and the results were compared with those of similar experiments in America.

The distribution and biology of most of the small rodents found in Malawi have been studied by Hanney (1965). He related their distribution to the habitat and the rainfall. The morphometrics and variation in coat colour have been described for

many species. In most species sufficiently studied the reproductive activity was at a maximum during the wet season or early part of the dry season. There was evidence that in some species the males also showed seasonal variation in their reproductive activity. The influence of burning in the grassland was also studied.

A general survey of the small rodents in the Serengeti National Park in northern Tanzania was carried out by Misonne and Verchuren (1966). Ecological notes were given for each species together with a general survey of the different biotopes. The density of the population in various habitats was estimated and mortality factors discussed. They concluded, like Delany (1964b), that they were most abundant in little-grazed grassland where there were no trees. They found two important causes of mortality, predation by birds, and sudden flooding.

Instead of studying the general ecology of all the small rodents occurring in a particular area, other workers have studied the biology of just one animal, or one particular aspect of the biology of the different rodents.

The most prolonged and detailed research on african rodents has been to determine what part they play in the transmission of bubonic plague. Roberts (1939) and Heisch, et al (1953) in Kenya, Hopkins (1949) in Uganda, Davis (1946, 1948, 1953) in South Africa, Devignat (1946, 1949) and Misonne (1959) in the Congo, have all made considerable contributions to this study.

Whilst Roberts (1939) and Hopkins (1949) found no evidence for the alleged relation of field-rodents with plague in East Africa, the improved techniques employed by Heisch et al (1953) showed conclusively that wild rodents did form a plague reservoir in Kenya. Similarly, other workers have found in their territories that the plague-causing bacillus can be present in sylvatic rodents, domestic rodents, as well as in man. It is transmitted from one animal to another by certain specific fleas. In Africa the domestic rodents, most important in the transmission of plague to man, are Mastomys natalensis and to a lesser extent the introduced Rattus rattus. In certain areas in the east of the Congo there are peridomestic rodents, principally Arvicanthis and, to a lesser extent, Mus minutoides Smith, which are intermediate between the sylvatic and domestic rodents and which play an important role in the transmission of plague between these two communities. The sylvatic rodents, which are most important as reservoirs of bubonic plague, are different in different parts of Africa. The most important in the eastern Congo are Arvicanthis, Otomys irroratus (Brants), and Lophuromys flavopunctatus Thomas, in Kenya are Arvicanthis, Mastomys and Otomys species, and in South Africa are Tatera brantsi (A. Smith) and Tatera afra (Fray).

The biology of some of the rodents which play an important role in the transmission of bubonic plague to man has been well studied, particularly the domestic rat Mastomys natalensis.

The breeding of this rodent has been studied in Sierra Leone by Brambell and Davis (1941), In Tanzania by Chapman, Chapman and Robertson (1959), in the Transvaal by Coetzee (1965), and in the laboratory by Oliff (1953) and Johnson and Oliff (1954). These studies have shown that there is seasonal fluctuation in the breeding of this animal, with maximum reproductive activity at the end of the rains. The animal is a prolific breeder with tremendous powers of increase. Davis and Oettle (1958) have shown that it is very suitable for use in the laboratory. The early post natal development of this animal in the laboratory has been studied by Meester (1960), and the growth and sexual maturity in the wild by Pirlot (1957c). Its behaviour has been studied by Veenstra (1958), and the occurrence, structure and the homology of the prostrate glands in the adult female has been studied by Brambell and Davis (1940).

The growth and reproduction of the two gerbils, Tatera brantsi and Tatera afra has been studied by Measroch (1954) for the females, and by Allanson (1958) for the males. They found that breeding was seasonal for both species, Tatera brantsi breeding at a reduced rate for part of the year, and Tatera afra having a definite breeding season with no breeding at other times.

Petter, Chippaux and Monmignaut (1964) studied the growth and biology of reproduction and activity of Lemniscomys striatus (Linnaeus) in the laboratory. They established growth curves for the weight and body length, the gestation period,

average litter size, and average duration of the oestrous cycle. Trapping in the region at Bangui in the Central African Republic showed that breeding was seasonal and at a maximum in the two rainy seasons.

Pirlot (1954, 1957a) studied the breeding of a variety of rodents from Katanga and the eastern Congo. The results suggested seasonal breeding for some species, but for others no seasonal breeding was indicated. However, his results are open to question as he makes no attempt to identify the rodents further than the generic level, relying on the species distribution established by Schouteden (1947) for the identification of the species. Furthermore, his criteria for determining juveniles and adults are very arbitrary.

Southern and Hook (1963b) also studied the breeding of a variety of rodents in Uganda and Kenya. They had too little data, and the study was too short (three months), for any firm conclusions to be drawn. However, there did appear to be differences in the breeding rates of the different species.

A similar general breeding study of small rodents was made by Happold (1966b) in the northern Sudan. Although the limited information prevented any firm statements being made, the results suggested that the desert species breed at the end of the rainy season, whilst the species found along the Nile and in the houses probably breed throughout the year.

The ecology, breeding and pre- and postnatal development of Acomys cahirinus dimidiatus Cretzschmar and A. c. minous Bate have been well studied by Dieterlen (1961, 1962, 1963a, b). In Malawi, the biology of the giant rat Cricetomys has been studied by Morris (1963), and the pouched rat Beamys major Dollman by Hanney and Morris (1962). Hanney (1964) made a further study of the harsh-furred rat, Lophuromys flavopunctatus.

This introduction to the work published on african Muridae and Cricetidae covers most of the major studies. It is evident that considerable variety exists in the ecology of the different species; which enables this group to exploit the majority of the resources of all types of habitat. Compared with temperate regions most habitats contain a large number of species, and in many areas of Africa this group may be of considerable importance to man.

The study of small african rodents, however, has been carried out in a few stereotyped ways which have imposed certain limitations on our knowledge of the group. Most studies have been very general, and usually concerned with relating the distribution of the animals to the major habitats. Any other information about these rodents has been largely accidental in such studies, with the result that only a few notes on the biology are available for most species. Where one aspect, such as breeding, has been studied in more detail for a large number of species, there have been limitations of time, lack of material, or an inadequate

analysis of the available material. The only detailed studies have been on single, isolated species, which limits the comparisons that can be made between different species because of the different conditions in which they live. These studies have often been carried out in the laboratory, far removed from field conditions. When material has been collected in the field, the seasonal changes observed have seldom been accurately related to seasonal changes in the climate and vegetation, because the relevant observations were not made. In general, most studies, have either been so broad as to find out little about any one species, or so specific that few comparisons can be made.

The aim of the present study has been to investigate certain aspects of the ecology of small rodents in one of the more simple habitats, open grassland, over the seasonal cycle of the year. This habitat was chosen because Delany (1964b) found that it contained a large number of species in great abundance. Consequently, a comparison of the biology of a few species was possible, to see how differently they behaved in similar conditions. The distribution of the various species within the grassland in relation to the different plant communities in the area has been analysed, and the effect of burning in the grassland on the different rodents has also been studied. The main emphasis of the study has been on the breeding cycles of the various species, in relation to the seasonal changes in the grassland. Changes in the age-structure of the population throughout the year have been studied, to find out more about the question of seasonal breeding.

II. MATERIALS AND METHODS

(A) Trapping Methods

(1) Traps

(a) Break-back Traps

One of the features of the small mammal fauna of Africa is that it includes a large number of species which have a considerable size range. Pirlot and Van den Bulcke (1952) and Delany (1964a,b) have stressed the importance of using different sized traps to capture the whole size range of these animals. To achieve this, three different traps were used in the present study. The Museum Special break-back trap, used by Delany (1964a,b) and Happold (1966a), was used for the smaller species. For the larger species two commercially produced break-back traps, the Reporter and Giljotin, were used. The first of these two traps, used by Delany (1964b), was made of metal with a large raised platform which released the action of the trap when depressed, whilst the other was made of wood with a small raised platform of metal which activated the trap when depressed.

The trap selection for two of the traps, the Reporter and Museum Special, has been analysed in an Appendix to this section. The results suggest that the traps are not entirely satisfactory as each species is apparently sampled in a different way.

(b) Live-Traps

The only trap available for the live-trap study was the smallest model Havahart live trap, used by Southern and Hock

(1963a), Delany (1964a) and Happold (1966). This trap was unsatisfactory for a general live-trap study because Delany (1964a) demonstrated that it selectively caught the smaller individuals.

(2) Bait

For the first two and a half months no bait was used, but after June 4 all traps were baited with a mixture of banana and maize meal. The two substances were mixed together into a firm paste and then left to ferment in a closed jar for at least a day until it smelt strongly of alcohol. The bait was originally chosen because it was cheap and readily available throughout the year. It appears to be the first time such a bait has been used.

A variety of baits have been used by other workers in Africa. Pirlot and Van den Bulcke (1952) used ^{dry} smoken bacon, fresh cassava, maize, carrots, palm nuts, groundnuts and wild fruits. Hanney (1965) used groundnuts smeared with peanut butter and Happold (1966) used dates and peanut butter. There is little information about bait preferences. Pirlot and Van den Bulcke (1952) suggested that Crocidura preferred meat and Aethomys and Cricetomys preferred palm nuts. They also suggested that animals would only enter traps if the bait was palatable and the bait smell was therefore unimportant. This last suggestion was not supported by the results of the live-trap study. The two Mus species were often caught but rarely ate the bait in the trap.

In the present study, the baited traps caught a greater variety of species, and three to four times as many animals as the unbaited traps. No species appeared to avoid the baited traps, because all the species that were caught in the unbaited traps were also caught in baited traps. The baited traps apparently attracted some species more than others, especially Lemniscomys striatus.

(3) Trap Placings

(a) Break-back Traps

Throughout the study in the Crater Track, Royal Circuit, and Katwe Count area, the traps were set in lines on the ground with a ten pace interval between each trap and each trap line approximately 50 yards apart. A similar arrangement of traps has been used by Pirlot and Van den Bulcke (1952), Delany (1964a, b) and Hanney (1965). The traps were visited every morning, the catches removed, and the traps then moved and set in another trap line. The trap lines were marked out by the wheel-tracks of a landrover. The traps were usually set about two yards from the trap-line, but if a bush was near, the traps were always set underneath it. After a trap had been set, the grass was tied in a knot over it to mark its position, and to help prevent the trap from being 'sprung' by heavy rain.

The Museum Special and Reporter traps were usually used in these areas (see Table 1), and were set in alternate positions and approximately equal numbers.

On Mweya Peninsula, the traps were set in the Arvicanthis runs around the houses, or set in the houses near to any holes in the floor or wall. The Reporter and Giljotin traps were generally used, although a number of Museum Special traps were also set.

Trapping was carried out every month from April 1965 to May 1966 in the Crater Track Area; from April 1965 to March 1966 on Mweya Peninsula; in June 1965 in the Royal Circuit Area; and in July 1965 in the Katwe Count Area. The total number of traps set in each locality is indicated in Table 1.

(b) Live-Traps

Live trapping was only carried out in the Crater Track Area. As there were only 64 traps available, a 20 yard grid covering an area 140 yards by 300 yards was used. This gave each trap two grid placings. When set, each trap was wired to two metal stakes set in the ground to prevent the trap being dragged away by small carnivores, such as mongoose. Each trap was covered with a sheet of polythene to keep the occupants dry during rain, and also by a layer of grass which shielded the trap from the sun.

The traps were set in alternate lines of the grid, and after prebaiting for one or two days, were set for three days. They were then moved to the unoccupied trap lines where they were set for two days more. The traps were visited between 8 and 10 o'clock in the morning, and 5.30 to 6.30 in the evenings. A

total of 5,808 trap days and nights were used. Trapping took place from June 1965 and was continued for every month except December, until April 1966.

(B) Material Collected

(1) Animals Caught

The number of animals of each sex and species has been summarized in Table 1. In a total of about 15,708 trap nights, 2,390 small mammals, representing 14 species of rats and various insectivores, were collected. The species of rats were identified using the keys in Delany and Neal (1966). These identifications were subsequently confirmed by comparison with the collections in the British Museum (Natural History).

(2) Treatment of Dead Material

Each animal collected was weighed to the nearest gram, and the head-and-body length; tail length; hind foot; and ear were measured. The head-and-body length was taken as the distance from the tip of the nose to the posterior edge of the pelvic girdle, and the tail length the distance from the latter point to the tip of the tail, excluding the end hairs. In practice these measurements were taken by placing the animal supine alongside a ruler, sliding a pair of forceps along the tail until the pelvic girdle was met, depressing the chin so that the head was flattened into the horizontal plane, and then reading off the measurements directly from the ruler. These measurements closely correspond to those described by Corbet (1964) and discussed by Jewell and Fullager (1966). The hind foot was taken as the distance from the heel to the tip of the longest toe, excluding the claw, and

the ear was measured from the notch to the tip. All measurements were made in millimetres.

The gut (from the lower oesophagus to the rectum) was removed and weighed to the nearest gram so that the clean body weight could be calculated. The skull was kept for ageing purposes and to confirm the species identification. In the females, the imperforate or perforate condition of the vagina, and whether they were lactating or not was recorded.

Every animal was dissected and where possible the reproductive material and stomachs were fixed in Bouin's fluid and kept for further study.

From the males the paired testes, vesiculae seminales, caudae epididymides and the penes were dissected out and kept. Testes lengths were measured and a sperm smear taken from each cauda epididymis. The relative abundance of sperms in the smears was determined microscopically. Four classes of abundance were recognised; absent (0); with only a few sperm present amongst fat globules ($\frac{1}{4}$ or $\frac{1}{2}$); more sperm but still scattered ($\frac{3}{4}$); or sperm very abundant with hardly any other recognisable material (1). These correspond to the classes described by Coetzee (1965).

From the females the paired ovaries, fallopian tubes, uteri, and the upper vaginae were dissected out in one piece and kept. The uteri were examined and the animals classified as; immature if unvascularized, small and thin; in oestrous, if extended and filled with a translucent or blood-red fluid;

sexually mature with active uterus, if slightly swollen and vascularized; pregnant, if visibly pregnant; parous, where placental sites were present; and in anoestrous, if the animal was obviously mature but the uteri were thin and apparently inactive.

The number of live and resorbing embryos in each limb of the uterus was recorded for the pregnant animals. The placental scars were classified as: very recent if large and still distending the uterus; recent if somewhat smaller and yellow in colour; and old where black in colour and very small. The presence of a sperm plug in the vagina was also recorded when found.

The collected material when returned to England, was transferred to 70% alcohol. The paired testes, epididymides, and vesiculae seminales (with the anterior lobe of the prostate dissected off), were lightly dried and weighed to the nearest 10 milligrams. The embryos were dissected from the pregnant females, weighed to the nearest 10 milligrams, and then had their head-rump length measured to the nearest 0.1 millimetre, using a pair of callipers. The small embryos were also drawn to assist their arrangement in order according to the stage of gestation.

(3) Treatment of Live-Trapped Animals

Each animal caught was identified, sexed and weighed to the nearest gram. The imperforate or perforate condition of the

vagina, and the condition of the mammary glands was also noted for the females. They were then marked by a system of toe clipping. Fullager and Jewell (1965) found this to be the best method of marking animals for long-term study.

(C) Ageing

The animals have been aged using the eruption and subsequent wear of the upper molars as a criterion. The skulls were cleaned using Dermestes beetles and the teeth were then scraped free of bait or any other material covering the surface.

In the following description of age-classes, the numbering of the cusps follows Miller (1912 - p.801), with the exception of m^3 because the remaining cusps in this tooth could not be related to the complete pattern. For this tooth, the remaining cusps have been numbered in order from front to back and from the internal to external sides. Two cusps have been classed as joined when a blunt seeker could be pushed along the dentine from one to the other without touching the enamel. Sometimes it was found that the teeth of the left and right sides had different degrees of wear, in which case a mean was taken of the two. The cusp-sets or sets of cusps, subsequently referred to in the text, may be composed of a single cusp or several cusps which have joined.

(1) Arvicanthis niloticus

In this species 12 age-classes have been recognised and are described below. The distribution of the cusps is shown in fig. 2.

Class I Only m^1 and m^2 present, or m^3 fully erupted but cusps unworn.

Class II The three molars fully erupted, the cusps no longer sharp and beginning to show slight wear.

III Cusps, particularly of m^3 more worn. No cusps joined but the dentine becoming continuous between some cusps of m^1 and m^2 .

IV One or two sets of cusps joined. Usually T8 and 9 of m^1 , and/or two of T4, 5 and 6 of m^2 . Number of separate cusp-sets 15 or 16.

V Three to five sets of cusps joined so number of separate cusp-sets is 12 to 14. Great variation in which cusps have joined. Usually cusps T4, 5 and 6, and at least two of T1, 2 and 3 of m^1 remain separate.

VI Eleven remaining cusp-sets.

VII Ten remaining cusp-sets.

VIII Nine remaining cusp-sets called laminae. Laminae made up of cusps T1, 2, 3; T4, 5, 6; T8, 9 of m^1 ; T1, T4, T5, T6, T9, T8 of m^2 ; and T1, T2, T3 of m^3 .

IX One or two laminae joined, so only 7 or 8 separate laminae left.

X Three or four laminae joined, so only 5 or 6 separate laminae.

XI Only 4 separate laminae.

XII Teeth worn smooth.

It should be noted that Crater Track and Mweya Peninsula animals in the same age-groups may not be of the same age, because the teeth appear to be very different between the two populations.

(2) Lemniscomys striatus

In this species 14 age-groups have been recognised and are described below. The cusp pattern of this species differs from Arvicanthis in that T3 of m^2 is present (i.e. better developed), and is shown in fig. 2.

Class I m^3 still not fully erupted.

II m^3 just fully erupted, almost unworn. Last laminae of m^1 and m^2 projecting backwards so that cutting surface cannot be seen from above.

III All 18 cusps distinctly separate. Dentine showing on T8 of m^2 . The last laminae of m^1 and m^2 now vertical and not angled backwards.

IV One or two sets of cusps joined so only 16 or 17 cusp-sets left. Usually T2 and T3 of m^3 are the first to join.

V Thirteen to 15 separate cusp-sets. Great variation in which cusps have joined.

VI Eleven to 12 separate cusp-sets.

VII Ten separate cusp-sets.

VIII Nine separate cusp-sets called laminae. T1 and T3 of m^2 are still separate, and T2 and T3

of m^3 are joined. Otherwise the cusp composition of the laminae is the same as for Arvicanthis.

Class IX	Eight laminae present.
X	Seven laminae present.
XI	Six laminae present.
XII	Five laminae present.
XIII	Four laminae present.
XIV	Teeth worn smooth.

(3) Lophuromys sikapusi

Six age-classes have been recognised in this species.

The arrangement of cusps is similar to Lemniscomys except that m^3 has only two cusps, and is shown in fig. 2.

Class I	m^3 not yet erupted or only just erupted. Cusps all sharp. Dentine of T2 of m^1 cannot be seen as the cutting edge of the first lamina is vertical. T8 and T9 of m^1 joined. Dentine not visible yet in T8 and T9 of m^2 .
II	Cusps more worn. First lamina of m^1 no longer vertical but at an angle or nearly flat. No cusps joined in m^2 or T4, T5 and T6 just starting to join. Dentine visible in T8 and T9 of m^2 .
III	Cusps T4, T5 and T6 of m^2 now joined and T8 and T9 beginning to join. First lamina of m^1 now flat.

Class IV T8 and T9 of m^2 now joined. Dentine exposed in m^3 . Nine cusp-sets left called laminae.

V One or two laminae join. Usually last two laminae of m^2 join first. Seven or eight laminae left.

VI Three or more sets of laminae have joined so that there are six laminae left or less.

(4) Mastomys natalensis

Thirteen age-classes have been recognised in this species.

The arrangement of the cusps, shown in fig. 3, is the same as in Lemniscomys, except that T8 and T9 of m^1 usually joined.

Class I m^3 still not erupted to the level of the other teeth.

II m^3 fully erupted and all teeth have very sharp cusps. The first lamina of m^1 is vertical and the second lamina of m^1 slopes backwards at an angle. T8 and T9 of m^1 joined and the dentine sometimes continuous between T4, T5 and T6 of m^1 and m^2 , although they are not yet considered as joined. If the dentine is continuous between these cusps no dentine is yet visible in the cusps of m^3 .

III Dentine beginning to appear in T2 of m^3 . First lamina of m^1 still nearly vertical and the second lamina of m^1 still at an angle. The dentine is

continuous but the cusps are still not joined of T_4 , T_5 and T_6 of m^1 and m^2 . Number of cusps is 17.

Class IV As for class 3 but two sets of cusps joined out of T_4 , T_5 and T_6 of m^1 and m^2 so that there are only 15 or 16 separate cusp-sets. Dentine now well visible in T_2 of m^3 but the cusps in this tooth are still sharp.

V Cusps of m^3 worn and flat. Only 14 cusp-sets left. Often T_8 and T_9 of m^2 join. First lamina of m^1 no longer vertical but at an angle to the vertical. Dentine of its cusps just visible from above.

VI First lamina at about 45° to the vertical. Its dentine clearly visible from above. Only 13 cusp-sets left. T_8 and T_9 of m^2 nearly always joined.

VII First lamina nearly flat. Twelve sets of cusps left. T_8 and T_9 of m^2 always joined.

VIII First lamina nearly flat. Two cusps of T_1 , T_2 , and T_3 of m^1 now joined. Eleven cusp-sets left.

IX First lamina flat. T_1 , T_2 and T_3 of m^3 all joined. Ten sets of cusps left, called laminae. The cusp composition of the laminae is the same as for Lemniscomys except that T_2 and T_3 of m^3

are still separate.

Class X Usually the second two laminae of m^3 join so that only 9 laminae remain. All cusps are very flat.

XI Eight laminae left. Usually m^3 is worn completely smooth.

XII Six or 7 laminae left.

XIII Five or less laminae remain.

(5) Mus triton

In this species 8 age-classes have been recognised.

The cusp pattern is similar to that of Lemniscomys except that all the cusps of m^3 are joined (see fig. 3).

Class I m^3 not yet erupted or just erupted. All 16 cusps separate although T8 and T9 of m^1 are only just so.

II One or two sets of cusps joined so that only 14 or 15 cusp-sets are left. Usually T8 and T9 of m^1 and m^2 are the first cusps to join.

III A further one or two sets of cusps joined so only 12 or 13 separate sets of cusps are left. Usually one or two of T1, T2 and T3 or T4, T5 and T6 join. m^3 more worn.

IV Nine to 11 sets of separate cusps remain. Usually T4, T5 and T6 of m^2 remain separate and are the last cusps within a lamina to join.

Class V Only seven or eight sets of cusps called
 laminae remain.

VI Six laminae remain.

VII Five laminae remain.

VIII Four laminae left or teeth worn smooth.

(6) Mylomys

In this species 9 age-classes have been recognised.

The cusp pattern, shown in fig. 3, is similar to Lemniscomys
except that there is an extra cusp in m^3 .

Class I m^3 not erupted or only just erupted. All cusps
 clearly separate. Dentine not showing in T9
 of m^1 and m^2 . Enamel of the anterior border
 of all median cusps projecting upwards into a
 spike.

II T2, T3 and T4 of m^3 close together but dentine
 still separate. All 19 cusps are still separate.
 Anterior border of enamel of median cusps now
 smooth.

III Two cusps of T2, T3, T4 of m^3 usually join.
 Eighteen sets of cusps left.

IV Seventeen sets of cusps left.

V Fifteen to 16 sets of cusps remain.

VI Thirteen to 14 sets of cusps remain.

VII Ten to 12 sets of cusps remain.

Class VIII Seven to nine sets of cusps remain.

IX Six sets of cusps remain or less.

(7) Tatera valida

In this species 8 age-classes have been recognised.

As it is a member of the Family Cricetidae, there are only two rows of cusps in the upper molars, instead of three (see fig. 4).

Each row of cusps is referred to here as a lamina.

Class I m^3 not erupted or just erupted. If erupted laminae can be seen to be composed of two cusps.

II All laminae separate. None divided into two cusps.

III Enamel of the two laminae of m^3 joining.

IV Dentine of the two laminae of m^3 just becoming continuous, but constricted where the two laminae join.

V Dentine of the two laminae of m^3 joined and not constricted where the two laminae join.

VI Enamel of first two laminae of m^1 joining.
Dentine of the two laminae of m^3 no longer T-shaped.

VII Two or three laminae of m^1 joined. Only the two laminae of m^2 remain separate.

VIII Two laminae of m^2 joined. All teeth worn flat.

It should be noted that this method does not give an exact age determination because of differential wear due to individual and environmental variation and the rate of wear is not known. This method is in part subjective, but is useful in separating the population into different groups born in different breeding seasons.

III. STUDY AREAS

(A) Introduction

The Queen Elizabeth National Park is situated in Western Uganda, in the Western Rift Valley around the shores of Lake Edward and Albert, (fig.5). The Park is long and narrow, and covers an area of 764 square miles. The equator traverses its northern sector, such that about one fifth of the Park lies in the northern hemisphere. The altitude of the Park is approximately 3,200 feet above sea level. The average annual rainfall varies in different areas of the Park from 30 to 55 inches. There are two rainy seasons, in March - May and in August - November, McCallum (1962), though the exact dates vary slightly from year to year. The vegetation consists largely of short grass savanna (less than 4 feet high), which is associated with semi-deciduous thicket in certain places. In the central region is a moist semi-deciduous forest, the Maramagambo, which is fringed by an area of dense thicket. In the north-east around the shores of Lake Albert, and in the south-west around the shores of Lake Edward are areas of aquatic grassland and herb swamp. Langdale-Brown (1962), Langdale-Brown, Osmaston and Wilson (1964) and Pratt, Greenway and Gwynne (1966).

All the areas trapped were in the northern area of the Park, and were between 5 and 13 miles South of the Equator, (fig. 6).

(B) Crater Track Area

This area lies above the general level of the Park, the areas trapped lying between 3,300 feet and 3,600 feet. Most of the area consists of a whole series of explosion craters, formed less than 7,000 years ago in a very violent outburst of volcanic activity of short duration. During these explosions huge clouds of ash were blown from the craters, which have settled as a deep layer, not only in this area, but also in the other areas trapped. The soils so produced are very fertile, but are limited in productivity by lack of rainfall. The areas trapped were either the gentle sloping valleys leading from the craters, or the flat bottoms of the explosion craters, (fig. 7).

The vegetation of this area is grassland with few bushes or trees. There are three major grass communities dominated by Imperata cylindrica, Cymbopogon afronardus, and Themeda triandra. There were also a few isolated patches dominated by Hyparrhenia filipendula. These grass communities formed a dense cover of a general height of three to four feet, (fig. 17). The community dominated by Cymbopogon was usually found at the bottom of the valleys, or the foot of slopes, or in any situation where the soil was deep and the area wet. Imperata dominated most of the area trapped. This community was usually interposed between the Cymbopogon and Themeda communities in deep soil. Themeda was mostly confined to the poorer soils around the crater

edges, or in other areas where the soil layer was thin and little weathered. These major grass communities would often intergrade, usually the Themeda with the Imperata, and the Imperata with the Cymbopogon. The areas dominated by Hyparrhenia filipendula were found both with the Themeda and Imperata communities. Other grasses occurring in the area were Panicum maximum, usually found in Cymbopogon, taller patches of Imperata, or around bushes; Brachiaria brizanthum, usually found in Cymbopogon but also in Imperata; Sporobolus stapfianus and Michrochloa kunthii, usually found in Imperata and Themeda communities; Sporobolus pyramidalis, Bothriochloa sp, Chloris gayana, and Heteropogon contortus were less frequently found, mainly occurring with Themeda but also present in Imperata; Digitaria diagonalis was found occasionally in all grass communities; Hyparrhenia dissoluta was occasionally found in small isolated patches in the Themeda and Hyparrhenia filipendula communities; and Setaria sphacelata was found occasionally in both Imperata and Cymbopogon. There were few other herbs occurring in the area. Legumes were the most frequent herbs found, especially Indigofera species, of which Indigofera paniculata and I. simplicifolia were the most common. Vigna ambacensis was also frequently found. Immediately after the burn in the area, many annual herbs grew, flowered, seeded and then died, but these were not identified. The few bushes occurring in the area were Capparis species, and the trees were Acacia species and Euphorbia candelabrum (figs. 12-17).

Rainfall for the area was recorded in a simple storage gauge and is shown in fig. 8. The effective periods of the rains during the study were April-May and August-December 1965, and late February-April 1966. Dry months were June and July 1965, and January 1966. Variation in light and temperature over the year may be ignored as both are very constant.

All the seasonal changes which occur in the grassland appear to result directly or indirectly from the pattern of rainfall which the area receives. The two rainy seasons stimulate the flowering and seeding of all grasses except Imperata which flowers after burning. During the rains most of the active growth takes place. At these times the waterholes fill up and large game animals, particularly elephant and buffalo migrate into the area. During the long dry season, the parched grass is usually burnt, after which Imperata flowers and many annual herbs grow up. Large herds of game animals, including buffalo, Uganda kob, and waterbuck, migrate into these burnt areas feeding on the succulent shoots of grass that sprout. During the rains the grass in the burnt areas grows faster than it can be eaten by the game animals, so that eventually the grass is tall and thick and the game animals move out of the area.

(C) Mweya Peninsula

The area trapped was on gently sloping or flat ground, mostly within 100 yards of the houses on the Peninsula, which are about 3,100 feet above sea level. The most abundant grasses in the area were Sporobolus pyramidalis, Chloris gayana, C. pycnothrix, and Cenchrus ciliaris. Eragrostis tenuifolia, Aristida adscensionis Sporobolus festivus and Michrochloa Kunthii were also common. The bush, Capparis sp., was very common with Urochloa panicoides and Commelina sp. present underneath. However, close to the houses the vegetation was considerably modified, Cyanodon dactylon dominated many of the areas trapped, and Panicum maximum was also common in various areas.

The rainfall in the area was seasonal, like in the Crater Track Area, (fig. 8). The seasons were not very marked in the year of study, but July 1965 was a particularly dry month.

All the grasses seeded during the rains, as in the Crater Track Area, and became very dry during the dryer months. During the day there was no grazing by large game animals, but at night much of the area was regularly grazed by buffalo, elephant and waterbuck. The intensity of grazing was probably little affected by the seasons.

(D) Royal Circuit Area

This was an area of flat grassland at an altitude of 3,200 feet, (figs. 6 and 7). The general appearance of the grassland was similar to the Crater Track Area, except that no Cymbopogon afronardus was present. There were two major grass communities, dominated by Imperata cylindrica, and a mixture of Themeda triandra, Bothriochloa sp., Sporobolus pyramidalis, and Hyparrhenia filipendula. The other grass species occurring in the Crater Track Area also occurred, and Cyanodon dactylon and Erogrostis tenuifolia were also present.

The rainfall in the area had a similar pattern to the Crater Track Area, (fig. 8), and the seasonal effects it produced were very similar. The area had not been burnt prior to trapping for at least two years, however, and grazing by large game animals was far more extensive and not so seasonal.

(E) Katwe Count Area

This was a gently sloping area, lying between 3,000 and 3,200 feet. It was subjected to very heavy hippopotamus grazing, which resulted in extensive bare patches, or patches of very closely grazed vegetation, lying between patches of very thick bush. The plants occurring in the closely grazed areas were Eragrostis tenuifolia, Chloris pycnothrix, Brachiaria brizanthum, Cyanodon dactylon, Portulacca sp., Amaranthus sp., and Indigofera sp. Where the vegetation was not so grazed Sporobolus pyramidalis and Cenchrus ciliaris were the commoner species of grass. The patches of bush often included Euphorbia candelabrum trees.

The area received less effective rainfall than the other study areas, as there was a lot of 'run-off' after heavy storms. This was because the soil was so hard and compacted, and there was little vegetation to hold the water. The rainfall was seasonal as in the other areas studied.

The area was not subjected to burning as fire cannot spread through the extensive bare patches. The grasses grow up during the rains, and some even seed, but mostly they are kept to a low level because of the heavy grazing pressure. Besides hippopotamus, the grass was heavily grazed by buffalo, and elephant. Uganda kob and waterbuck also migrate through the area when watering at Lake Edward.

IV. HABITAT PREFERENCES IN CRATER TRACK AREA

(A) Introduction

Previous investigations of the distribution of small rodents in Africa have largely been concerned with relating their distribution to that of the major habitat types. The various species have been said to occur in grassland, montane forest, swamp, and so on, but little or no attempt has been made to find out if there are any habitat specialisations within these complex major habitats. A few such specialisations have been noted by Pirlot and Van den Bulcke (1952), Rahm and Christiaensen (1963) and Southern and Hook (1963 a), but even these are of a general nature.

In view of the large number of species caught in the Crater Track Area and the presence of a few well-defined and distinct vegetation types, it appeared that this area would offer an ideal situation for examining micro distributions in detail. To facilitate this the dominant species of vegetation was recorded at each trap placing from July 1965 onwards. The results are summarised in figs. 9, 10 and 11, and table 2.

(B) Results

Interpretation of the results is hampered owing to the considerable effects of burning in the grassland. In certain species one grassland community may be favoured in burnt areas, whilst it is avoided in unburnt areas. Such effects of burning will be discussed in section V.

Aethomys nyikae showed a marked preference for bush. It was also found, though in comparatively low numbers in Imperata cylindrica, Themeda triandra and Hyparrhenia fillipendula. It was never found in Cymbopogon afronardus, (fig. 9 and table 2).

Arvicanthis niloticus was found most frequently in the Themeda and Hyparrhenia communities, and to a lesser extent in bush and Imperata in the unburnt areas. In the burnt areas, however, it was most frequently found in bush, followed by Imperata and then Themeda. Like Aethomys it was never recorded in the Cymbopogon community (fig. 9 and table 2).

Dendromus sp. was only caught twice, once in Imperata and once in Themeda (table 2).

Lemniscomys striatus was found in large numbers in all types of vegetation. In the unburnt areas it was found in much the same numbers in all communities, perhaps showing a slight preference for Themeda and Hyparrhenia, and occurring in the highest numbers under bushes. In the burnt areas, however, it seemed to prefer Cymbopogon, at least for the first eight months

after burning, although it occurred in high numbers in the other grasses and bush as well. For the first few months after burning the unburnt areas were preferred to the burnt areas, but after six months there was a marked preference for the burnt areas (fig. 9 and table 2).

Lophuromys sikapusi preferred the Imperata community, but was also found in Themeda and Cymbopogon. It was never found by bushes in this area (fig. 10 and table 2).

Mastomys natalensis, like Lemniscomys, was found in all vegetation types. There was a marked preference for bushes in all areas, and more were found in the burnt than unburnt areas. There appeared to be little or no preference between the different grass communities, except that it was seldom caught in Cymbopogon in the unburnt areas (fig. 10 and table 2).

Mus minutoides was caught too infrequently to draw any firm conclusions about its habitat preferences. It was found in Themeda and Imperata, but never in Cymbopogon or bush (fig. 10 and table 2).

Mus triton was found in all grass communities but never by bushes. Imperata was preferred in all areas, and it also occurred in high numbers in Cymbopogon in the burnt areas (fig. 11 and table 2).

Myomys cuninghamei was found in the three major grass communities, but was never trapped by bushes. It was found in the

greatest numbers in Imperata, (fig. 11 and table 2).

Otomys irroratus was rarely caught, but seemed to prefer Cymbopogon, although it was also caught in Imperata and Themeda (fig. 11 and table 2).

Zelotomys hildegardeae was seldom caught. It was found in all grass communities, but never by bushes (table 2).

Tatera valida was found in all vegetation types, showing a preference for Imperata and Hyparrhenia, (fig. 11 and table 2).

(C) Discussion

The distribution of most species was discontinuous in this area of grassland. Most species were not found in equal abundance in the different types of vegetation, but showed quite marked preferences in their choice of habitat. If the different species have the same diets as reported by Delany (1964 b) and Hanney (1965), a general relationship appears to exist between the distribution and the diets of the different species. The insectivorous species, Lophuromys, Zelotomys and Tatera, and the omnivorous species which are mainly insectivorous Mus minutoides and M. triton, were rarely found in bushes, and were most abundant in Imperata and Cymbopogon. The omnivorous species which were mainly vegetarian, Lemniscomys and Mastomys, were found in all types of vegetation but were most abundant under bushes. Aethomys, another omnivorous species which was mainly vegetarian, preferred bushes almost to the exclusion of the other types of vegetation. The herbivorous species, Arvicanthis, Mylomys, and Otomys, like the insectivorous species avoided bushes but had different vegetation preferences. Arvicanthis preferred Themeda, Mylomys preferred Imperata, and Otomys preferred Cymbopogon. The distribution, and habitat preferences of some species was quite markedly affected by burning. Eight to ten months after burning, the habitat preferences in the burnt and unburnt areas were quite similar, but the numbers caught in the two areas were still very different.

V. THE EFFECT OF FIRE ON THE SMALL MAMMAL POPULATION

(A) Introduction

The burning of the grasslands of Africa is a regular feature of the habitat, without which it would never have developed, and without continued burning it would inevitably disappear. Although burning is such a regular feature of the habitat, the effects of fire on the small population in the grasslands of Africa is virtually unknown. Certain effects of fire on the population of small mammals have been noted by Delany (1964b) and Hanney (1965), but no systematic study appears to have been carried out in Africa. Cook (1959) and Lawrence (1966) have made studies of the effects of fire on populations of small mammals in America, but the habitats they studied were quite different to the area of grassland in which the present study was made.

Much of the Crater Track Area was burnt during the day and night of July 3, 1965. It is not known whether the fire was started by accident or intent. The extent of the burn in the trapping area is shown in fig. 7.

(B) Changes in the Vegetation

Only a charred stubble remained of the grasses in the burnt area, and bushes and Acacia sp. seedlings of less than three feet high were also completely burnt. The larger bushes and trees were scorched, but were otherwise little affected. There were very few patches of unburnt grass in the burnt area, and the boundaries of the burn were usually quite straight, there being an abrupt transition from the burn to the high dense cover of grass in the unburnt areas. The grasses were scorched and dried for a few feet around the edges of the burn (figs. 12 and 13).

Within about ten days of the area being burnt, Imperata and Cymbopogon began to grow again. The shoots of Imperata were well separated and soon reached a height of about six inches. However, there was little cover provided by the growth, and animals released from live-traps could easily be followed and seen. The Cymbopogon regenerated from the charred tussocks and grew to about the same height as the Imperata. However, more cover was provided in the areas dominated by this grass; animals in or around the bases of the grass tussocks were not easily seen, particularly from above. The other grasses in the area showed no signs of growth at this time.

By the beginning of August, one month after the burn, Imperata and Cymbopogon had grown to a height of six to nine inches at which level it was kept by grazing buffalo. The Imperata was

in flower, but small mammals could still be followed in the area. The other grasses, such as Themeda, were only just beginning to grow in a few isolated patches, so that there were still many bare patches in the burnt area. In various areas, usually in quite dense patches, a variety of annual herbs had grown up and were in flower (figs. 14 and 15).

Towards the end of September, nearly three months after the burn, Imperata and Cymbopogon were about one foot high and were still being heavily grazed by buffalo. The Cymbopogon was beginning to flower, and Imperata had seeded and the silver white flower heads had been washed off by rain. There was a fresh flush of Themeda, Hyparrhenia filipendula and H. dissoluta, Heteropogon contortus, Sporobolus stapfianus which was in flower, Michrochloa kunthii, and Brachiaria brizanthum. The general height of these grasses was about six inches. The cover provided by all the grass communities was fairly good, and there was almost no bare ground (fig. 16).

By the end of October, the grasses provided a lush, thick cover. The Imperata and Cymbopogon were at least three feet high, and the other grasses in the area, such as Themeda, were also about three feet high. The smaller grasses, such as Sporobolus stapfianus and Michrochloa had reached their usual height of about one foot. All the grasses in the area, except Imperata, were in flower or had seeded (fig. 17).

From then onwards the grass cover in the burnt area was much the same as in the unburnt areas, and the two areas became increasingly difficult to distinguish from one another. They differed in that the grasses in the burnt areas appeared to be more succulent, and there was very little litter in these areas.

(C) Immediate Effects of Fire on Small Mammals

The Crater Track Area was burnt in July after six days snap-trapping had been completed. The fire reached the trapping area at about 6.00 p.m., a little before dark on July 3, 1965 and extended about half-way along the trap lines. When the traps were visited the next day, all the animals caught in the burnt part of the trap line were burnt, showing that they were caught before the burn. No movement in the burnt area immediately after the burn was indicated. Trapping for a further five days established that there was a reduction both in the number of animals, and in the number of species occurring in the burnt areas (tables 3 and 4, and fig. 18). Certain species appeared to be little affected by the burn. These were Mastomys, Mus triton and Tatera valida, and probably Zelotomys, Mus minutoides, Aethomys, and Crocidura sp. were little affected either. Hanney (1965) found that Mastomys and Mus triton survived in burnt areas in Malawi. All these species are nocturnal, Hanney (1965), Delany and Neal (1966) and table 5, and most, if not all, are burrowers.

The immediate effect of the fire on Otomys, Arvicanthis, and Dendromus could not be established because so few of these species were caught. However, it would appear that Arvicanthis was reduced in numbers in the burnt areas. Delany (1964b) found that Arvicanthis survived in burnt areas after a fire, though they were reduced in numbers. He also found that Mastomys, Mus minutoides, Dendromus melanotis and Crocidura flavesiens also

survived in burnt areas.

Three species, Lophuromys, Mylomys and Lemniscomys were drastically affected by the fire. Lophuromys and Mylomys were not trapped in areas affected by the burn for five and seven months respectively after the fire. Hanney (1965) found that Lophuromys flavopunctatus was similarly affected by the burn. Lemniscomys, although still occurring in burnt areas, did so in very reduced numbers (tables 3 and 4). The 44 individuals trapped in the Live Trap Study Area in June were reduced to four in July after the fire. The three species were both nocturnal and diurnal (table 5), and live above ground. It should be noted that the few Lemniscomys that remained in the burnt Live Trap Study Area, tended to become more nocturnal after the fire (table 5), until thick cover had grown up again. The few animals that did remain in the burnt areas probably used the burrows of other small mammals or the ventilation shafts of termites that abounded in the area, until enough cover had grown up again for them to live above ground. When they were released from live traps, they always ran and disappeared down holes close by the traps. The fire probably did not directly kill the species drastically affected by the burn. In working in the burnt areas on the days immediately following the burn, no dead rats were seen. The fire only slightly burnt the animals caught in the traps in the burnt part of the trap-line, so that it seems likely that any animal seeking refuge in even a shallow burrow would not have been killed. It is probable that

most of the reduction in numbers of these species was due to emigration into the unburnt areas. Lophuromys and Myomys were caught in too few numbers to conclude that the numbers in the unburnt areas significantly increased after the fire. The overall figures in tables 3 and 4 show very little, because these two species showed marked preferences for particular grass types, and the proportion of the different grass communities trapped before and after the burn were not the same. However, Lemniscomys was caught in high numbers and did not show any marked preference for any one type of vegetation. Consequently, the figures in tables 3 and 4 probably reflect changes in the numbers of animals occurring before and after the burn in the two areas. It may be noted that the numbers caught did increase in the unburnt areas, whilst decreasing in the burnt areas, and that an average for the burnt and unburnt areas is nearly the same as that for the area before the burn. This does suggest that migration did take place, and that this factor was responsible for most of the reduction in numbers of Lemniscomys in the burnt areas. To support this conclusion, two marked animals from the Live Trap Study Area were trapped about half a mile away in unburnt areas in July and August. Two other marked animals absent from the burnt Live Trap Study Area after the burn, reappeared in September and October. Hanney (1965) similarly found evidence for the migration of Lophuromys flavopunctatus from the burnt areas into unburnt areas. However, Cook (1959) found no evidence for migration out of the

burnt areas, but could not account for the reduction in numbers of the rodents.

(D) Long Term Effects of Fire

Many of the long term effects of the fire must remain a matter of conjecture. Burning of the grassland undoubtedly causes modifications in such phenomena as behaviour and diet of the different species. In the section on the habitat preferences of the various species, it was noted that certain species had different habitat preferences in the burnt and unburnt areas. Such long term effects of burning, covering the period July 1965 to May 1966, are considered here.

The burn probably had little effect on the habitat preferences of Aethomys nyikae. It lives mainly in bushes which were seen to be effected very little by the fire. From fig. 9 and table 2, there is no reason to suppose that the fire markedly changed the habitat preferences of this species.

Arvicanthis niloticus was probably reduced in numbers by the fire because very few were trapped in burnt areas until January, seven months after the fire. Fig. 9 and table 2 suggest that bushes and Imperata were more preferred in the burnt than in the unburnt areas.

It was seen in the previous section that Lemniscomys striatus was drastically reduced in numbers in the burnt areas by migration from there into the unburnt areas. For a long time after the burn this species had different habitat preferences in the burnt and unburnt areas (fig. 9). One month after the fire, the most preferred community in the burnt areas was

Cymbopogon. This marked preference for Cymbopogon lasted for seven months, after which the numbers in these areas became drastically reduced. Eventually, it was the least preferred of the three major grass communities, as it was in the unburnt areas. The initial preference for Cymbopogon probably reflected the greater amount of cover offered by those areas, but why the preference was maintained is not known. The sudden reduction in numbers in these areas after seven months also occurred in Mastomys. Presumably, there was a change in the Cymbopogon habitat at about this time, such as a decrease in the palatability of the grass, which caused this sudden decrease in numbers in the area. One month after the burn, this species was trapped twice as frequently in the unburnt Imperata than in the burnt Imperata, and it was not trapped in any of the bare burnt patches or where Themeda was beginning to grow. Presumably this species was beginning to reinvade the burnt areas again because more individuals were trapped in the Live Trap Study Area (table 5). Individuals were first trapped in Themeda in low numbers in September, two months after the burn. At this time the numbers in the unburnt areas fell sharply to a relatively low level, at which level they remained for the rest of the study. The numbers in the burnt Imperata and Themeda areas showed a slow general increase until April 1966, after which the numbers fell. Four months after the burn these two communities were slightly more favoured in the burnt than unburnt areas, and by January this

preference for the burnt areas was very marked. This preference for the burnt areas was probably because the grasses were more succulent and palatable in these areas than in the unburnt areas.

Lophuromys sikapusi either migrated out of the burnt areas or was killed by the fire. It was first recorded in November in the burnt areas. However, the unburnt areas still seemed to be favoured even ten months after the fire (fig. 10), although the habitat preferences appeared to be little affected.

It was seen that Mastomys natalensis was little affected by the burn at first, but one month after the burn the numbers were drastically lowered in the unburnt areas and increased in the burnt areas (fig. 10). This indicates that there was a migration into the burnt areas by this species. The burnt areas were preferred for at least seven months after the burn, after which the numbers declined in these areas until there were similar numbers in the burnt and unburnt areas. The habitat preferences appeared to be the same in the burnt and unburnt areas, except that Cymbopogon was preferred much more in the burnt areas, so that the species occurred in much the same numbers in all the grass communities. After seven months the numbers trapped in Cymbopogon fell, which paralleled the reduction in numbers of Lemniscomys.

The fire seemed to have very little effect on Mus triton, both in its immediate and long term effects (fig. 11). There appeared to be no difference in the habitat preferences of this

species in the burnt and unburnt areas.

Myomys cuninghamei, like Lophuromys sikapusi was not found in the burnt areas after the fire. It was first caught in the burnt areas in January, and although no major changes in its choice of habitat were indicated by the results, too few were caught to draw any firm conclusions about this matter (fig. 11).

Tatera valida did not appear to be adversely affected by the fire and after December it was only caught in the burnt areas. The habitat preferences appeared to be very similar in the burnt and unburnt areas (fig. 11).

No conclusions could be drawn about the long term effects of the fire on the other species trapped because so few were caught.

(E) Discussion

The grasslands of Africa have largely been developed and maintained by the occurrence of frequent, usually annual, burns. Because burning is such a regular feature of the habitat it seems likely that the species of small rodents occurring in this habitat are adapted to withstand the effects that the fires have. The numbers and distribution of certain species, such as Mylomys and Lophuromys, are probably greatly influenced by burning. All the species that are present in burnt areas immediately after burning, appear to be burrowing and nocturnal, whilst those species that live above ground either migrate into the unburnt areas, or are killed by the fire. There is no evidence for direct mortality. Delany (1964b) suggested that aridity and lack of food in the burnt areas might cause an increase in the death rate, which would account for the drop in numbers he observed in the burnt areas. When live-trapping in July, a few days after the burn, many dead animals of some species were found in the traps. This suggests that they were weakened by the burn. The reinvasion of the burnt areas by those species adversely affected by the fire was probably controlled at first by the regeneration of the grasses, and later was probably affected by the range of activity of the different species. If this is so, then it would appear that Lemniscomys is more active than Lophuromys which is in turn more active than Mylomys.

The re-establishment of small mammals in burnt areas appears to take place faster in tropical regions than in temperate regions. In the present study, every species was present in the burnt areas seven months after burning, and ten months after burning, the differences between the two areas was small. However, Cook (1959) found that much of the reinvasion of burnt areas by small mammals in North America did not take place until the second year after burning, and two years after burning, considerable differences still existed between the burnt and unburnt areas. The difference in the rate of recovery of the two study areas is no doubt largely due to the higher productivity of the tropical environment, which allows food and cover to be quickly re-established.

This study indicates that it is desirable that the past burning history of any grassland trapped should be known. Otherwise a very misleading picture of the ecology of these small rodents may be built up. Furthermore, the comparison of different grassland areas is made more difficult.

VI. BIOLOGY OF REPRODUCTION

(A) Introduction

There is very little information about the breeding of African rodents, and what information there is comes from widely scattered localities.

Certain authors, such as Sanderson (1940) in West Africa and Rahm and Christiaensen (1963) in the Eastern Congo, have recorded pregnancies which they have observed during the course of more general studies. Unfortunately, they have not recorded from what sized samples the pregnancies have occurred, neither have they indicated whether the absence of pregnancies in certain months was due to small sized samples or to a probable break in breeding. Consequently, such records are only of limited value, but may be useful in giving added weight to the findings of other workers.

General studies on the breeding of African rodents have been made by Pirlot (1954, 1957a) in Katanga and near Lake Kivu; Southern and Hook (1963b) in Kenya and Uganda; Delany (1964a, b) in Uganda; Hanney (1965) in Malawi; and Happold (1966b) in the Sudan. These studies all indicate that for many species the period of maximum reproductive activity occurs during the wet season and early part of the dry season, although all the species of rodents from one habitat do not necessarily breed simultaneously. Such conclusions, however, are by no means final because of the nature of these studies. The

conclusions drawn by Southern and Hook (1963b), Delany (1964a, b), and Happold (1966b) are severely limited by the shortness of their studies and the scarcity of material for most species. Pirlot (1954, 1957a) examined large samples of animals and both his studies were made over long periods in their respective areas. However, as the animals were only identified to the generic level (the species being determined by reference to their distributions established by Schouteden 1947), and were classed as adults or juveniles without reference to the actual states of the reproductive organs, the conclusions he drew must be regarded with extreme caution. In contrast, in his magnificent study in Malawi, Hanney (1965) considered about thirty species of rodents, and it is hardly surprising that he gives little information for a number of species. The collections were made bimonthly over the year in three different habitats, and as a result, the seasonal changes in breeding could not be traced very accurately. He established that different species occurring in the same habitat did vary in their breeding patterns.

All the detailed studies on the breeding of African rodents have found seasonal variation in the breeding rates.

Mastomys natalensis has been studied by Brambell and David (1941) in Sierra Leone, Chapman et al (1959) in Tanzania, Coetzee (1965) in the Transvaal, and by Oliff (1953) and Johnston and Oliff (1954) in the laboratory. Petter et al (1964) studied the breeding of Lemniscomys striatus near Bangui in the Central African Republic, and in the laboratory. The biology, including breeding, has been

studied of Lophuromys flavopunctatus by Hanney (1964), and Beamys major by Hanney and Morris (1962). Finally the breeding of Tatera brantsi and T. afra has been studied by Measroch (1954) and Allanson (1958). In all these studies a general relationship was found to exist between the breeding and the periods of rainfall, rather than with changes in day length (when they occurred) as in temperate regions.

The present study was carried out between five and fourteen miles south of the equator, and as a result changes in light can be ignored. Fluctuations in temperature over the year were so slight that this factor can also be discounted. The rains provide the only form of seasonal variation in the climate and any temporal variations in the breeding of small mammals are probably best related to them. The Crater Track Area and Mweya Peninsula were the two main areas of study, and were trapped every month of the year. Seasonal changes in the breeding of several species of small rodents were accurately followed.

(B) Accounts of Species

(1) Reproduction in Arvicanthis niloticus

(a) Introduction

This is one of the commonest African rodents, and is widely distributed, ranging from Zambia in the South, to Senegal in the West and Egypt and Arabia in the East. It is typically a grassland species, but is also found in bush and cultivated land. It is strictly herbivorous. It often lives in close association with man and is known to play an important role in the transmission of bubonic plague in the Eastern Congo and in Kenya.

There is remarkably little information about the breeding of this species. Watson (1950) suggested a possible breeding season in Eastern Uganda towards the end of the rains as they were very numerous during the early months of the dry season. Delany (1964b) found that there were two distinct peaks in the population at Mweya Peninsula, in the body weight, occipitonasal length, and testes length, which suggested that breeding covered limited periods, possibly during the rains. However, Happold (1966b) found pregnant females in July, September and February and young were seen at all times of the year. He concluded that the rainy season did not appear to regulate or initiate the breeding season in the Nile valley in the Sudan where his studies were made.

In the present study animals were trapped on Mweya Peninsula and in the Crater Track area (table 1). Those trapped

at Mweya were mostly living in close proximity to man, whilst those in the Crater Track area were truly wild rodents. The two populations were found to be different in many respects and for this reason their breeding will be considered separately. The Mweya Peninsula population was heavier and larger in all body measurements except the ear, much lighter in colour, and the reproductive organs of the male were much heavier.

(b) Mweya Peninsula Population

(i) Reproductive Cycle of the Female

(a) Growth and Breeding Season

The heaviest foetus weighed 2.72 gm. when preserved, and the mean weight of the litter of four of which it was a member was 2.56 gm. They were probably almost full term because the vibrissae and body hairs were growing. Two other pregnancies in a similar condition, of four and three embryos, had mean weights of 2.28 gm. and 2.21 gm. respectively. The estimated weight at birth is, therefore, approximately 2.5 gm. to 3.0 gm.

It can be seen (fig. 19) that the lightest animal had a clean body-weight of 11 gm., but only eight had clean weights of less than 20 gm. It would appear that the females become weaned when 15 - 20 gm. in weight. Only three females had clean body-weights of over 90 gm., the heaviest being 104 gm., and most mature females had clean weights of 50 - 90 gm. There appeared to be no seasonal loss in weight.

The weight distribution of immature, mature but not parous, pregnant, and parous animals is shown in table 6. It can be seen

from this table and fig. 19 that most females become sexually mature at a body-weight of approximately 50 gm, although one animal with a clean weight of 29 gm was found to be sexually active. From the weight distributions of pregnant and parous females (table 6), there would not appear to be any loss in weight after pregnancy.

The total number of females examined each month, and their reproductive condition are given in table 7. The percentage of visibly pregnant and immature females, together with the total rainfall for each month are represented graphically in fig. 20.

It can be seen that visibly pregnant females were trapped in every month except June 1965, although a female with all the embryos resorbing was trapped in this month. Females in a similar condition were trapped in July and August 1965, and March 1966. There was a tendency for breeding to be at a low level during these months, which were generally the driest of the year. A remarkably close relationship appears to exist between breeding and the rainfall, (fig. 20). Breeding was at a maximum during the rains and at a minimum in the driest months, July 1965 and March 1966. As the immature females trapped were all between weaning and puberty, the curve of immature females shows a time-lag in comparison with the fluctuation in the number of pregnant animals (fig. 20). The periods of breeding are such that an inverse relationship seems to hold between the numbers of pregnant and immature females. Most immature animals are about

during the drier months, which corresponds to the observations of Watson (1950) in Eastern Uganda.

(B) Fertility

Since females may become pregnant in every month of the year, it is possible that some become pregnant again at the post partum oestrus. The occurrence of some females with embryos at an early stage, which were also lactating, would appear to confirm this. Some females appeared to be in anoestrus whilst lactating, but without microscopical examination it was impossible to confirm the occurrence of a lactation anoestrus. Approximately half the parous females appeared to be in anoestrus (table 7), which suggests that females may be in anoestrus for long periods.

Most parous females had only one or two sets of placental scars, but as many as 26 placental scars in one female have been counted. As will be shown subsequently, the average number of implanted embryos is 4.6, and it would therefore appear that some females are able to have as many as five litters.

The number of implanted embryos (i.e. including resorbing) and the number of healthy embryos are represented as frequency polygons in fig. 21. Two pregnancies were excluded from this data, one of which the number of embryos was not known, and the other which had one embryo growing in the body cavity.

The mean number of healthy embryos of 41 pregnancies was 4.39, with a range 2 to 10 and standard deviation 1.50.

The mean number of implanted embryos of 44 pregnancies was 4.64 with a range of 3 to 10. Nearly 12 per cent of the total number of implanted embryos of this sample were resorbing. Happold (1966b) recorded 2 to 10 young, but Misonne and Verschuren (1966) only recorded 3 to 5 embryos.

The number of implanted embryos, which may reflect the number of ova ovulated, appears to vary with the body-weight, as is shown in table 8. The number of implanted embryos increases with increase in the clean body-weight.

The total prenatal mortality could not be estimated as the number of corpora lutea was not counted. However, the proportion of resorbing embryos of 12 per cent, indicates that the post implantation mortality was quite considerable. The regression coefficient of the number of embryos on the weight of embryos was calculated to be -0.32, but was not found to be significantly different from zero. The level of probability was approximately 70 per cent. This suggests that either much of the resorption of embryos takes place early in development, or so few are resorbed that a larger sample, particularly of embryos late in development, would be needed to find the regression coefficient to be statistically significant.

The variation in the mean number of healthy embryos over the year is represented graphically in fig. 22. Although the variations cannot be regarded as statistically significant because of the small samples, a rise is indicated towards the end of the rains, in April, May and December.

(ii) Reproductive Cycle of the Male

(♂) Growth and Breeding Season

It can be seen (fig. 23) that the main influx of immature males, like the females, occurs at the end of the rains and beginning of the dry season. The lightest had a clean body-weight of 12 gm., with only two others weighing less than 20 gm. The male may, therefore, be heavier at weaning than the females. The heaviest male had a clean body-weight of 115 gm., and although only three females weighed over 90 gm., it can be seen that a considerable proportion of males weighed more than 90 gm. A comparison of figs. 19 and 23 confirms that on average the males weigh more than the females.

Fecund males were found at all times of the year.

Animals with spermatozoa ratings of (0) were immature, and those with spermatozoa ratings of ($\frac{1}{2}$) were regarded as infertile, being composed of immature animals and mature males in a state of anoestrus. Animals with spermatozoa ratings of ($\frac{3}{4}$) and (1) were regarded as fully mature.

The clean body-weight at which fecundity is attained is not sharply defined (fig. 23 and table 9). The lightest animal with spermatozoa had a clean body-weight of 46 gm., and the heaviest animal without spermatozoa weighed 67 gm. The males weighing 34-73 gm. with spermatozoa ratings of ($\frac{1}{4}$) and ($\frac{1}{2}$) were all just maturing, and the two males weighing 92 gm. and 101 gm. with the same fecundity rating were mature males, which appeared to be in anoestrus. From table 8 it would seem that the males

mature at approximately 60 gm., which is about 10 gm. heavier than the weight at which the females mature.

The monthly variation of animals with spermatozoa in the testes, given in table 10, merely reflects the number of immature and adult animals, since it is very rare that males once fecund become sexually inactive. Most of the male population appear to be mature during the periods of maximum reproductive activity in the females.

(B) Changes in the Testes

The combined weights of the two testes of 226 animals are given in the form of a scatter diagram in fig. 24. Where only one testis was available, twice its weight was taken.

It can be seen that most mature males have a testes weight between 1.1 gm. and 2.0 gm. There was a marked seasonal variation in the weight of the mature testes. They reached a maximum weight towards the end of the wet season and beginning of the dry season, in April and May, and October until December 1965. During the dry season there was a steady decline in the weights of the testes, and it was only after the rains had started, in August, that they began to increase in weight. The testes of the immature males remained at a low weight during the drier months, and it was only after the rains had begun that there was a rapid increase in weight, as can be seen in September 1965.

(Y) Changes in the Epididymides

The changes in weight of these accessory sexual organs (fig. 24) appear to closely follow those of the testes, so that

it is probable that a close correlation between the weights of these two organs exists. The seasonal variation in the weight, and the growth of the immature animals closely resemble those described for the testes.

(g) Changes in Seminal Vesicles

The changes in the weights of these organs (fig. 24) generally follow the changes in weight of the testes, except that there is a considerable range in their weights. The correlation between the weights of these organs and the testes, would, therefore, not be expected to be as close as that which exists between the testes and epididymides. The weights of the seminal vesicles of the immature animals are always very low, and a marked increase in their weights was only seen at the beginning of the rains in September 1965.

(c) Crater Track Population

(i) Reproductive Cycle of the Female

(o) Growth and Breeding Season

Only one full term litter (as judged by the growth of body hair) was found. The two foetuses of the litter weighed 3.13 gm. and 2.52 gm. when preserved. Therefore, the estimated weight at birth is about 2.5 gm. to just over 3.0 gm., which is very similar to that estimated for the Mweya Peninsula population.

The small sample of 49 females makes any estimates of the weight at weaning and the size range of adults subject to review. The lightest female had a clean body-weight of 16 gm.

(fig. 25) and the estimate of the clean body-weight at weaning is 15-20 gm., which is the same as was estimated for the Mweya Peninsula population. Almost all the mature females had clean body-weights of 45-75 gm. It thus appears that this adult population is lighter in weight than the Mweya Peninsula population, which normally weighed 50-90 gm.

The weight distribution of immature, mature but not visibly pregnant or parous, pregnant, and parous females is shown in table 11. From this table and fig. 25 it can be seen that females mature at about 45 gm., which is approximately 5 gm. less than that estimated for the Mweya Peninsula population. It can be seen that the Mweya Peninsula population appear to be able to grow to a much greater weight than the Crater Track population.

The total number of females examined each month and their reproductive conditions are given in table 12. The percentages of visibly pregnant and immature females, together with the total rainfall each month is represented graphically in fig. 26.

Visibly pregnant females were collected in March-July, and September-December 1965, and March 1966. In view of the extremely low numbers caught, the absence of pregnancies at other times may not be significant, and it seems likely that breeding occurs at all times of the year, as on Mweya Peninsula. As a result of small monthly samples, there is not such a close relationship between the breeding and the rainfall as exists for the Mweya Peninsula population. The results do indicate, however,

that there is maximum reproductive activity during the wettest months of the year.

(B) Fertility

Only one visibly pregnant female with an embryo at an early stage was found to be lactating, which suggests that normally they do not become pregnant again at the post partum oestrus. As about 50 per cent of the parous females appeared to be in anoestrus, it appears that females are in anoestrus for long periods.

The number of implanted (i.e. including resorbing) embryos, and the number of healthy embryos are represented as frequency polygons in fig. 27.

The mean number of healthy embryos of 15 pregnancies was 3.60 with a range of 1 to 5 and standard deviation 1.05. The mean number of implanted embryos was 3.67, with a range of 2 to 5. Approximately 2 per cent of the embryos were found to be resorbing.

The mean number of healthy embryos which this population carries appears to be very different from the Mweya Peninsula population. It was noted that Happold (1966b) reported 2 to 10 young, as in the population at Mweya Peninsula, whilst Misonne and Verschuren (1966) only recorded 3 to 5 embryos, which resembles that found for the Crater Track population. The population that Happold studied in the Nile valley was likely to be in close contact with man, whilst Misonne and Verschuren studied wild

rodents in the Serengeti National Park. There is a possibility that Arvicanthis, in close contact with man, is able to carry more embryos and is, therefore, more fertile than the wild populations.

To test if the mean number of embryos of the two populations was different, Student's t-test, as explained in Simpson et al (1960), was used to test the significance of difference between the two means.

<u>Population</u>	<u>Number</u>	<u>Mean</u>	<u>Variance</u>
Mweya Peninsula	41	4.39	2.25
Crater Track	15	3.60	1.11

t was found to be 1.89 with 54 degrees of freedom. This is 90 - 95 per cent significant. Although it is not significant at the 5 per cent level, it suggests very strongly that the two samples are different. Comparing figs. 21 and 27 it would seem that the Crater Track population rarely have more than five embryos, whilst this number is common in the Crater Track population. Perhaps the overall larger size of the Mweya Peninsula population, or even a more constant food supply, contribute to cause this observed difference between the two populations.

No parous female had more than two sets of placental scars. It would appear that females do not have so many litters as the Mweya Peninsula population, therefore, if they live to the same age, there would probably be longer periods of anoestrus.

Any relationship between the number of implanted embryos

and the clean body-weight could not be established, because too few pregnancies were recorded. For the same reason, seasonal changes in the number of embryos could not be investigated.

(ii) Reproductive Cycle of the Male

(a) Growth and Breeding Season

A scatter diagram of the clean body-weights of 37 males is shown in fig. 28.

Such a small sample means that only the most obvious factors can be noted here. Most of the mature males weighed between 50 gm. and 70 gm. and the heaviest had a clean body-weight of 85 gm. It can be seen by comparison with fig. 23 that the males of this population were considerably lighter than the males of the Mweya Peninsula population.

The weight distribution of immature, maturing, and mature males is given in table 13. From this table and fig. 28, it seems likely that most males mature at a clean body-weight of approximately 50 gm., which is a little heavier than the weight at which the females mature, and which is 10 gm. less than the weight estimated for the population at Mweya Peninsula.

The seasonal variation in fecundity has not been estimated because of the lack of material.

(b) Changes in the Testes, Epididymides and Seminal Vesicles

The variation in the size of these organs (fig. 29) in the mature males and the growth of the immature animals cannot be followed accurately because of the scarcity of material. The

general trends are probably the same as seen in the Mweya Peninsula population. However, it should be noted that the weights of the organs are all very different from those of the population at Mweya Peninsula.

The testes weights of most mature males were between 0.3 gm. and 0.5 gm., with an observed range of 0.26 gm. to 0.51 gm. Therefore, the heaviest mature male did not reach the weight at which spermatozoa were first recorded in the Mweya Peninsula population. The testes weights at maturity were about one quarter that generally observed for the males at Mweya Peninsula.

Similarly, the weights of the epididymides and seminal vesicles were heavier in the Mweya Peninsula population. The epididymides generally weighed three to four times as much, and the seminal vesicles about three times as much as those of the Crater Track population.

It may be seen that the difference between the two populations is emphasised in the weights of the male reproductive organs. It would be interesting to know whether they represent two distinct species or subspecies.

(2) Reproduction in Lemniscomys striatus

(a) Introduction

This species is widely distributed and has been recorded from Northern Angola in the South, throughout the Congo and East Africa to the Sudan and Ethiopia in the East, and as far West as Sierra Leone. It is omnivorous, and lives in a wide variety of habitats, ranging from open grassland, through savanna and dense scrub, to thick forest, usually occurring at the edges of the latter. Hopkins (manuscript) suggests that this species is of some agricultural importance because it is known to eat sweet potatoes, cassava, and other crops.

There is very little known about the breeding of this species in Uganda. A few breeding records are contained in Delany and Neal (1966).

Petter, Chippaux and Monmignaut (1964) studied the breeding of this species near Bangui in the Central African Republic, and in the laboratory. Nearly 200 animals were captured but little was found out about their breeding in the wild. They suggested a correlation between the birth of the young and the rainy season. Most of the study consisted of determining growth curves in weight and length of those born in the laboratory, and the duration of the oestrus cycle and gestation.

During the present study this species was trapped in the Crater Track, Royal Circuit and Katwe Count areas (table 1). The first two areas were so similar that the results have been grouped together. There was reason to suspect that the Katwe

Count area population was behaving differently to the Crater Track population. The only female trapped from the area in July was pregnant. No pregnancies were recorded at this time in the Crater Track area, and as will be shown subsequently, there was no evidence for any breeding at this time. For this reason, this pregnancy has only been included in assessing the average number of embryos in a litter, and has been ignored when calculating the variation in the breeding rates throughout the year.

(b) Reproductive Cycle of the Female

(i) Growth and Breeding Season

The heaviest foetus weighed 1.46 gm. when preserved and the average weight of the litter of seven of which it was a member was 1.30 gm. The mean embryo weight of another pregnancy with five embryos was 1.32 gm., the heaviest of the litter weighing 1.37 gm. when preserved. Both these litters appeared to be nearly full term as the body hairs were just beginning to grow. Two new-born animals found in one of the live traps weighed 1.32 gm. and 1.43 gm. when preserved. The weight at birth is estimated to be 1.3 - 1.5 gm. However, Petter et al (1964) state that the young weigh approximately 3.00 gm. at birth. The difference is so great that it seems likely that the two populations are quite different.

It can be seen (fig. 30) that the lightest animals had a clean body-weight of 5.00 gm., and only eight weighed less than

10.00 gm. It is inferred that the weight at weaning is approximately 10.00 gm. A small proportion of mature females had very high weights compared with the remainder of the adult population, which generally had clean body-weights of 20 - 35 gm. The appearance of young in the population can be seen to take place towards the end of each wet season and beginning of the dry season. Allowing for the time lag when animals are being weaned, this suggests that breeding only occurs during the rains. There was a seasonal variation in the weights of the adult females. The weights were at a maximum during the rains and at a minimum during the dry season, suggesting that animals lost weight in the drier months of the year.

The distribution of immature, mature but not parous, visibly pregnant, and parous females, according to the clean body-weight is shown in table 14.

From this table and fig. 30 it can be seen that females mature at a clean body-weight of approximately 20.00 gm. The lightest mature female weighed 12.00 gm., and the heaviest immature female weighed 30.00 gm. There appeared to be a seasonal variation of the weights at which the females mature, females maturing at a lower weight during the wetter months of the year than in the dry season.

The total number of females examined each month and their reproductive conditions are given in table 15. The percentages of visibly pregnant and immature females, together with

the total rainfall each month are represented graphically in fig. 31.

Visibly pregnant animals were only trapped in the periods April - June and September - December 1965, and in April 1966, although one gravid female was trapped in the Katwe Count area in July 1965. There was a marked difference in the April - June breeding season in 1965 and 1966. In 1965 pregnant animals were trapped in all three months, whilst in 1966 breeding had clearly stopped by the latter half of May. It can be seen that breeding only takes place during the rains and at the beginning of the dry season.

The incidence of breeding found in the present study is in full agreement with other information about the breeding of this species. Petter et al (1964) recorded pregnancies and new-born animals in March, May, July and September - November in the Central African Republic. They suggested a correlation between births and the rainy season, which had two maxima in May and September. Sanderson (1940) only recorded pregnancies in the period October - December, which corresponds to the end of the rains and beginning of the dry season in the Cameroons. Rahm and Christiaensen (1963) recorded pregnancies from December - February, which corresponds to the rainy season in Kivu. Finally Delany (1964b) recorded no pregnancies when trapping in the Crater Track area in July - August 1963, which gives added weight to the findings of the present study.

It is not known why the breeding in April and May of 1965 and 1966 should have been so different. As will be shown subsequently, the breeding of other species was similarly affected, which suggests that some environmental factor was responsible for the difference.

(ii) Fertility

During the April - June breeding season, most females only had one litter, but in May and more commonly in June, some females with small implanted embryos were lactating. This suggests that a proportion of females had two litters. The same was true for the September - December breeding season. Several lactating females with small embryos were collected in November, and a few in December. Theoretically, as the gestation period was found to be 28 days by Petter et al (1964), it would be possible for some females to have three litters in the first breeding season, and four in the second breeding season. No direct evidence was found to confirm this, as it was not possible to distinguish animals with more than one set of placental scars when pregnant. Non-pregnant parous females, with up to 19 placental scars have been counted, which suggests that some animals have at least three litters, since the mean number of implanted embryos was 5.02. Whether all these litters were born in the same breeding season is not known.

Although Petter et al found that females would not reproduce in the same year as their birth in the laboratory, it is clear from fig. 30 that in the wild, animals born in one

breeding season will all breed in the next, about five months later. As will be shown subsequently in the section on age-structure of the population, a few females born towards the beginning of both breeding seasons in 1965 were found to be pregnant at the end of the same breeding season. Thus a few females are able to mature in about two months during the rains, but normally take four or five months to mature during the dry season. During the driest months, all the adult females were in anoestrus (table 15).

The number of implanted (i.e. including resorbing) embryos, and the number of healthy embryos are represented as frequency polygons in fig. 32.

The mean number of healthy embryos of 58 pregnancies was 4.78, with a range of 2 to 8, and a standard deviation of 1.30. The mean number of implanted embryos was 5.02 with a range of 3 to 8. About 5 per cent of the total number of implanted embryos were found to be resorbing.

Petter et al (1964) reported 36 embryos in 7 pregnancies, with a range of 3 to 6 embryos. This would give a mean of 5.14 embryos, which is similar to that found in the present study. In captivity, the mean number of embryos born was 3.91 with a range of 2 to 7. This seems to indicate a high post implantation mortality.

The number of implanted embryos, which may reflect the number of ova ovulated, shows a slight increase with increase in

the clean body-weight (table 16). However, in view of the small samples for each weight class, such an increase is probably not statistically significant.

The variation in the number of healthy embryos throughout the periods of breeding is shown in table 17. The mean number of embryos appears to increase as the breeding period progresses. This may reflect an increase in the food supply, because the grasses begin to seed from the middle of the rains onwards.

(c) Reproductive Cycle of the Male

(i) Growth and Breeding Season

The appearance of immature males in the population (fig. 33) occurs towards the end of the rains and beginning of the dry season, at the same time as the immature females. The lightest male had a clean body-weight of 4.00 gm., and like the females, an estimate of the weight at weaning would be about 10 gm. Like the females, a few males had exceptionally high body-weights compared with the rest of the population. Most of the adult males had clean body-weights between 20 and 35 gm., therefore, the males and females had similar body-weights at maturity.

Three classes of males were recognised, as in Arvicanthis. Animals with a spermatozoa rating of (0) were immature; animals with spermatozoa ratings of ($\frac{1}{4}$) and ($\frac{1}{2}$) were either just maturing, or the testes were regressing after the breeding season; and

animals with spermatozoa ratings of ($\frac{3}{4}$) and (1) were regarded as fecund. The distribution of these classes with respect to the clean body-weight is shown in table 18.

It can be seen that the males first begin to mature at a clean body-weight of 20.00 gm., so that the weight at puberty appears to be slightly higher than that estimated for the females. Like the females, the males mature at a lower body-weight during the rains than in the dry season.

The monthly variation in the fecundity ratings is shown in table 19. From this table and fig. 33, it appears that, like the females, the young males do not mature until after the rains have begun. From the distribution of the body-weights, it seems evident that a few males born towards the beginning of the breeding season mature before the end of the same breeding season. This was confirmed when the age structure of the population was studied (section VII). During the rains most of the mature males are fecund, but the spermatozoa ratings of these mature males goes down during the dry season, so that there are then few fecund males. Once the rains begin, those mature males with regressed testes become fecund once more.

It would appear that the males show a cycle in their fertility, similar to that of the females, although it may not be so pronounced. Seasonal anoestrus has been found in the males of other tropical rodents during the dry season, by Hanney (1965) in Steatomys pratensis Peters, Tatera leucogaster (Peters), and Lophuromys flavopunctatus in Malawi, and by Prasad

(1956) in Tatera indica cuvierii (Waterhouse) in India.

(ii) Changes in the Testes

The combined weights of the two testes of about 350 animals are given in the form of a scatter diagram in fig. 34. Where only one testis was available, twice its weight was taken.

The striking feature of this diagram is the marked seasonal variation in the testes weights of the mature males. The testes reach their maximum weight towards the end of the rains, and then quickly regress to approximately one-half to one-third of this weight during the dry season. Most of the males with testes weights over 0.15 gm. appear to be fecund. Most of the growth in weight of the testes of immature animals takes place during the rains. During both breeding seasons in 1965, a few males born towards the beginning were mature by the end of the same breeding season. Thus, like the females, a few males can mature in about two months during the rains.

A comparison of the samples collected in May of both years reveals that in May 1966 the testes were already beginning to regress, whilst in May 1965 they were at their maximum weight. Thus the difference seen between the two years, in the reproductive cycle of the females is also seen in the males.

(iii) Changes in the Epididymides

It can be seen from fig. 34 that these organs show a similar seasonal variation in weight as the testes, and therefore, it would appear that the two are linearly correlated.

(iv) Changes in the Seminal Vesicles

The seasonal variation (fig. 34) in the weights of this organ are more pronounced than, and in phase with, the changes in weights of the testes and epididymides. During the dry season in July and August 1965, they became reduced to about one-tenth of their maximum size during the previous rains. After the rains had begun in August, they quickly regained their large size and the immature males grew for the first time. The reduction in weight in the less severe January - February dry season was not so pronounced. This was also true for the testes and epididymides.

(3) Reproduction in Mastomys natalensis

(a) Introduction

This is a common and widely distributed African rodent, occurring throughout Africa south of Morocco and the Sudan. It is omnivorous, and lives typically in grassland savanna, although it is frequently found in human habitation. Its importance as a vector of bubonic plague has been well established, and it is probably the chief agent in Africa in spreading this disease to man. It is also an important pest in agriculture. Serious damage to cotton crops in Kenya has been reported by Harris (1937), and Hanney (1965) reports frequent plagues of this rat in cotton growing areas in Malawi. These periodic increases to plague proportions are very sudden, and are probably mainly due to the tremendous powers of increase that this animal has, the litters being the largest recorded for placental mammals.

As a result of the considerable economic importance of this rat, the breeding and other aspects of its biology have been studied in detail in many areas of Africa. However, all of these studies have been made on populations occurring around human habitation or cultivated land, or in the laboratory.

During the course of the present study this species was trapped in all the areas studied (table 1). Only the truly wild populations have been considered, and in consequence those trapped on Mweya Peninsula have not been included in the evaluation of the reproductive data.

(b) Reproductive Cycle of the Female

(i) Growth and Breeding Season

The heaviest foetus weighed 1.39 gm. when preserved, and the mean weight of the litter of twelve of which it was a member was 1.28 gm. Another litter of twelve had a mean weight of 1.36 gm. and two other litters of thirteen and ten, had mean weights of 1.06 gm. and 1.07 gm. respectively. The embryos of all these litters had body-hair growing and so would appear to be near term, although the litter with the heaviest mean weight of 1.36 gm. was the most developed. An estimate of the weight at birth is, therefore, approximately 1.5 gm. Meester (1960) found that the mean weight at birth in the laboratory was 2.2 gm. with a range of 1.9 gm. to 3.00 gm. The population considered in the present study would, therefore, appear to be appreciably lighter than that studied by Meester.

From fig. 35 it can be seen that the lightest animal had a clean weight of $5\frac{1}{2}$ gm., but only five other individuals of less than 10 gm. were trapped. Mastomys is, therefore, estimated to be weaned at a clean weight of about 10.00 gm. The weight at weaning was found to be 11.7 gm. by Meester (1960) and 13.00 gm. by Johnston and Oliff (1954), and estimated to be 20 - 25 gm. by Brambell and Davis (1941). Allowing for the weight of the alimentary canal, the first two values are comparable to that estimated in the present study, but that estimated by Brambell and Davis appears to be very high. Perhaps the traps

used in the latter study were not sensitive enough to catch many juveniles weighing less than 20.00 gm.

Immature animals only appeared in the population in June and November, which demonstrated that the breeding periods are very short. There are two points of interest that should be noted about the weight growth of the young. Those trapped in the Royal Circuit area between the 15th and 23rd of June 1965, generally had much higher body-weights than one would expect (fig. 35). It would seem either that breeding took place earlier in the Royal Circuit area, or if the young were born at the same time as the Crater Track population, the rate of growth was faster. The rate of weight increase of animals weaned in June 1965 also appeared to be different from those weaned in November 1965. Those weaned in June took a further four months to mature, whilst those weaned in November took a further five months to mature, and appeared to mature at a slightly reduced weight.

Once the females matured there appeared to be a sudden increase in the clean body-weight associated with pregnancy. This sudden increase in the clean body-weight at pregnancy was also noted for the parous females breeding for a second time. After breeding the body-weight was reduced, especially over the period December 1965 to March 1966.

Two parous females had exceptionally high weights of 62 gm. and 78 gm., whilst most mature females weighed 27 - 55 gm. The weight distribution of immature, sexually active but not parous, visibly pregnant, and parous females is shown in

table 20.

From this table and fig. 35, it can be seen that females mature at a clean body-weight of approximately 27.00 gm. The total body-weight would be about 35.00 gm. This is less than has been estimated in other studies. Brambell and Davis (1941), Johnston and Oliff (1954) and Chapman et al (1959) have all estimated the body-weight at maturity to be 39.00 gm. or 40.00 gm. Pirlot (1957c) reported that the females matured at a weight of less than 40.00 gm., but did not give a precise figure.

The number of females examined each month and their reproductive conditions are given in table 21. The percentage of visibly pregnant and immature females, together with the total monthly rainfall are represented graphically in fig. 36.

Visibly pregnant females were only trapped in May and the first half of June, and in the latter half of October until the beginning of December 1965. Although no pregnancies were recorded in 1966, breeding must have taken place between the second half of April and the first half of May, when no trapping took place, because a lactating female was collected in the second half of May, and two very small juvenile males were collected at this time. The breeding periods in Mastomys in this area are, therefore, very restricted. Allowing for the time it would take for embryos to become implanted, it seems likely that females first became pregnant in the latter half of April and the beginning of October in 1965. All the mature females would appear to become pregnant during the breeding periods, since no

female with an adult body-weight was found without placental scars after the breeding periods.

Further evidence for the timing of the onset of breeding is supplied by the appearance of young at the beginning of June and end of November 1965, and at the end of May 1966. If the gestation period is 23 days, as reported by Johnston and Oliff (1954), and weaning takes three weeks as reported by Johnston and Oliff (1954) and Meester (1960), then the immature animals must have been conceived about six weeks before. This would be just after the middle of April and at the beginning of October 1965, and at the middle of April 1966. Further evidence for the onset of breeding at these times was supplied by the occurrence of vaginal plugs, denoting recent copulation, on the 29th September and 12th October 1965, and on the 14th and 15th April 1966.

The breeding periods are, therefore, sharply defined, no evidence being found for breeding outside of the periods calculated above. Brambell and Davis (1941) in Sierra Leone, Pirlot (1954) in Katanga, Chapman et al in Tanzania, and Coetzee (1965) in the Transvaal, have all found that breeding was at a maximum at the end of the rains and beginning of the dry season, as in the present study, but breeding continued at a reduced level for most or all of the other times of the year. However, Hanney (1965) only found pregnant females during a four month period, with no breeding taking place at other times of the year.

From the results of the present study, it is suggested that a relationship may exist between the breeding of this rodent in the wild, and the occurrence of seeds in abundance. As will be shown subsequently, the litter size for this species is extremely high, therefore, the energy that the female must supply for their development will also be very high. The females show an increase in the clean body-weight at the time of pregnancy, consequently, the energy supplied for the growth of the embryos is not accompanied by a net loss in energy of the female. Presumably, the females must increase their intake of energy by way of food, and it seems likely that the high energy supplied by seeds would be a possible way in which this could be achieved.

(ii) Fertility

In 1965 breeding occurred over two months and two and a half months towards the end of both of the rainy periods. As the gestation period is 23 days (Johnston and Oliff 1954), it seems likely that some females would become pregnant again at the post partum oestrus, and so have two litters in one breeding season. Confirmation of this was provided by pregnant females with early implanted stages which were also lactating, being trapped at the end of May and throughout November 1965. Counts of the numbers of placental scars after each breeding period suggested, however, that very few females did have two litters. Females born in one breeding season, unlike Lemniscomys, did not mature and start breeding before the end of the same breeding

period. A large proportion of the females breeding in the breeding season after their birth, survived to breed in the next period. Outside of these breeding periods the females appeared to be in a permanent anoestrus condition.

The number of implanted and healthy embryos are represented as frequency polygons in fig. 37.

The mean number of healthy embryos of 41 pregnancies was 12.10 with a range of 6 to 19 and standard deviation of 3.24. The mean number of implanted embryos was 12.61, therefore, about 4 per cent of all embryos were resorbing.

The sample estimate of the mean number of healthy embryos is very similar to those reported by other workers. Brambell and Davis (1941) recorded a mean of 11.8 for 17 litters (range 7 to 17) in Sierra Leone, Chapman et al a mean of 11.2 for 10 litters (range 3 to 16) in Tanzania, Coetzee (1965) a mean of 9.46 for 114 litters (range 2 to 19) in the Transvaal, and extracting from the data presented in Hanney (1965) a mean litter size of 11.0 (range 7 to 17) for 27 litters in Malawi. The mean size of litters born in the laboratory are rather lower, being 7.3 (Oliff 1953) and 8.53 (range 1 to 17) for 19 litters (Meester 1960).

The mean number of implanted embryos which may reflect the number of ova ovulated, appear to increase slightly with increase in the clean body-weight (table 22). Brambell and Davis (1941) found such a correlation between the number of ova

ovulated and the body-weight, and Hanney (1965) found that the litter size increased with the size of the parent.

The seasonal variation in the litter size was not investigated because breeding took place over such a short period of time. Coetzee (1965) found a marked reduction in the number of embryos during the drier months in the Transvaal.

(c) Reproductive Cycle of the Male

(i) Growth and Breeding Season

The first appearance of immature males in the population (fig. 38) occurs at the same time as the immature females. The weights at which the two sexes first appear are also very similar, thus the weight at weaning of the males is estimated to be 10 gm., the same weight as that of the females. A comparison of figs. 35 and 38 clearly shows that the males grow in weight much faster than the females, and they mature about a month earlier than the females. Like the females, the immature male Royal Circuit population weighed heavier than one would expect, and the growth rate of those weaned in June 1965 was faster than for those weaned in November 1965. The majority of fecund males had clean body-weights of 28 - 60 gm. The lightest fecund male weighed 23 gm. and the heaviest 67 gm. The full sized adult male had a clean body-weight between 40 gm. and 60 gm., which is heavier than the female.

The males were divided into three classes as in the previous species considered. The distribution of the fecundity ratings with respect to the clean body-weight is given in table 23.

It can be seen from this table and fig. 38 that the males mature at a clean weight of approximately 27.00 gm., a similar weight to that of the females. This is lighter than estimates in other areas of Africa (p. 88), where the males have usually been found to mature at a heavier weight than the females. The distribution of males with fecundity ratings of (0) to ($\frac{1}{2}$) was discontinuous. This discontinuity is due to a few mature animals having an absence or reduced number of spermatozoa in the epididymides, i.e. they are not active sexually. Only a small proportion of the population appeared to be affected, and mature males were found throughout the year. This reduction in fertility occurred during the dry season (table 24). Hanney (1965) similarly found mature males with no spermatozoa in the testes during the dry season in Malawi, and Coetzee (1965) suggested that the testes of a few males may become atrophied. Although none of the other breeding studies of Mastomys found evidence for reduced fertility of some males during the dry season, they were of such a nature that such evidence could not be obtained.

(ii) Changes in the Testes

The lightest testes (fig. 39) with the full fecundity rating weighed 0.28 gm. and the heaviest 1.62 gm. Nearly all the males with testes weighing more than 0.6 gm. were fully mature. The testes showed a very slight seasonal variation in weight, being at a maximum towards the end of the rains. The testes of the immature animals grew faster during the rains than

in the drier months of the year.

(iii) Changes in the Epididymides

The seasonal changes in the weights of this organ (fig. 39) of the mature males appears to be more pronounced than for the testes. The changes in the weights of the adult epididymides, and the growth of the epididymides in the immature animals appear to be in phase with the testes.

(iv) Changes in the Seminal Vesicles

It can be seen (fig. 39) that the seasonal changes in weight are very pronounced. The organs regress during the dry season to about one tenth of their maximum weight, and the changes in the weight of this organ follow the breeding cycle of the female remarkably closely. Although males with mature sperm are present throughout the dry season, they may be effectively infertile because the secretions from the seminal vesicles must be very reduced at this time. The same may be true for Lemniscomys which has a similar cycle in the weights of the seminal vesicles.

(4) Reproduction in Lophuromys sikapusi

(a) Introduction

This species is distributed over much of tropical Africa, being recorded as far south as Angola, and Kenya in the North-east and Ghana in the North-west. It is insectivorous and lives typically in heavily grassed bush country.

Very little is known about the biology of this species, although Hanney (1964) has studied the biology of a closely related species, Lophuromys flavopunctatus, in Malawi. Pirlot (1957a) considered the breeding of Lophuromys in Kivu, but did not identify the species.

In the present study this species was trapped in the Crater Track and Royal Circuit areas (table 1). The results from the two areas have been grouped together.

(b) Reproductive Cycle of the Female

(i) Growth and Breeding Season

The heaviest foetus weighed 6.35 gm. when preserved, and the mean embryo weight of the litter of three of which it was a member was 6.11 gm. The embryos appeared to be full term as the body-hairs were growing. A litter of two in a similar condition had a mean weight of 5.94 gm. The estimated weight at birth is, therefore, 6.0 - 6.5 gm. This is very much heavier than the estimates for the other species considered in this study. Arvicanthis, which is a comparable size when adult, had an estimated birth weight of up to 3.0 gm. From the data supplied by Delany (1964a) it would appear that L. flavopunctatus has embryos

of at least 4.5 gm. in weight. The embryos of this genus seem to grow to a very large size compared with other species.

The lightest animal had a clean body-weight of 27 gm. (fig. 40) and although so few animals were caught as to make an estimate of weight at weaning unreliable, it would appear that animals are weaned at about 30.00 gm. in weight. This estimate is supported by Delany (1964a, b) who caught approximately 40 individuals of this species, none of which weighed less than 30.00 gm. Most adult females had clean body-weights between 55.00 gm. and 95.00 gm., and there appeared to be no seasonal fluctuation in weight.

The distribution of immature, sexually active but not parous, visibly pregnant, and parous females according to the clean body-weight is shown in table 25. It would appear that the clean body-weight at maturity is approximately 50.00 gm.

The total number of females examined each month, and their reproductive conditions are given in table 26. The percentage of visibly pregnant females and the total rainfall each month is represented graphically in fig. 41.

Visibly pregnant females were trapped in every month except August 1965 and February 1966. In view of the low numbers caught, it seems likely that animals were breeding throughout the year, although a marked reduction in the breeding rate in July and August is clearly indicated. Delany (1964b) trapping in the same general area in 1963, noted a total absence of breeding in July and August. Breeding would appear to be at a

maximum during the rains, and to be reduced during the drier months of the year. This contrasts with L. flavopunctatus which was found to have a marked breeding season with no breeding at other times of the year, by Hanney (1964).

(ii) Fertility

The proportion of visibly pregnant females is very striking. Of the total number of adults, 74 per cent were visibly pregnant and a further 11 per cent were lactating. Only 8 per cent of all adults appeared to be in anoestrus, and nearly all of the females that were neither visibly pregnant nor lactating, were trapped in July and August 1965. It would appear that the females are very fertile, and normally become pregnant again at the post partum oestrus. The occurrence of several lactating females with early implanting stages, would appear to confirm this. Some females are known to have at least three litters, but the average number of litters per female is not known.

The number of implanted and healthy embryos is represented as frequency polygons in fig. 42.

The mean number of healthy embryos for 46 pregnancies was 3.17 with a range of 1 to 5 and a standard deviation of 0.85. The mean number of implanted embryos was 3.24 with a range of 2 to 5, therefore, approximately 2 per cent of the embryos were resorbing. Watson (1950) reported that there were usually 2 to a litter in Eastern Uganda, whereas in the present study 3 embryos was the mode.

The number of implanted embryos appeared to increase with increase in body-weight (table 27), and there seemed to be a seasonal variation in the number of healthy embryos (fig. 43). Although the monthly samples were small (table 26), the results suggest that the number of embryos in a litter are at a maximum in the wettest months and at a minimum in the dry months. This may explain why Watson (1950) found smaller litters in Eastern Uganda, because the area is much drier than Western Uganda, where the present study was made.

(c) Reproductive Cycle of the Male

(i) Growth and Breeding Season

The lightest male (fig. 44) had a clean body-weight of 28 gm. and the heaviest 99 gm. The weight at weaning is probably very similar to that of the females. The weights of the fully adult males seemed to be 75 - 100 gm., which implies that they are heavier than the females on average. The lightest fecund male weighed 51 gm.

The distribution of the various spermatozoa ratings, corresponding to those of the previous species, with the clean body-weight is given in table 28. From this table and fig. 44, it can be seen that the males mature at a clean body-weight of approximately 60 gm., which is 10 gm. heavier than that estimated for the females.

The monthly proportions of the three classes of males are given in table 29. This table illustrates that, like the females, immature males appear in the population at the end of

the wet season and beginning of the dry season, and mature during the dry months. This periodic entry of both immature males and females into the population, would suggest periodic breeding, but this is clearly not the case from an analysis of the females. This suggests a mortality of young born towards the end of the dry season, but too few were collected to confirm this.

(ii) Changes in the Testes, Epididymides and Seminal Vesicles

Any variation in the sizes of these organs could not be followed accurately because of the scarcity of material. There do not appear to be any marked seasonal changes in the weights of these organs, unlike the other species in the present study (fig. 45).

(5) Reproduction in *Mus triton*

(a) Introduction

This species is distributed throughout East Africa and the Congo, and ranges as far south as Malawi, Zambia and Angola. It is omnivorous, but primarily insectivorous and is usually confined to the wetter areas of grassland, heath and scrub.

Surprisingly little is known about the biology of this species, and there are no breeding records available in Uganda. Hanney (1965) has made some useful observations on the biology of this species in Malawi.

During the present study, this species was only trapped in the Crater Track area. However, Delany (1964b) trapping in the same area two years earlier, did not catch any specimens of this species. There were large seasonal variations in the numbers caught, also noted by Hanney (1965), which may account for the apparent absence of this species in July 1963.

(b) Reproductive Cycle of the Female

(i) Growth and Breeding Season

No full term foetuses were found. The heaviest foetus weighed 0.37 gm. when preserved, and the litter of four of which it was a member had an average weight of 0.36 gm. The embryos were well developed, therefore, the weight at birth is probably little more than 0.5 gm.

The lightest female (fig. 46) had a clean body-weight of just under 4.00 gm., but the main appearance of young in the population was at a weight of 6 - 7 gm. This may not represent

the weight at weaning, however, because the traps may not be sensitive enough to catch many animals weighing less than 6.00 gm. The heaviest female had a clean weight of 16 gm., and most adult females were found to have clean weights between 10 gm. and 15 gm.

The weight distribution of immature, sexually active but not parous, visibly pregnant, and parous females is shown in table 30. From this table and fig. 46, it can be seen that females mature at a clean body-weight of 9 gm. to 10 gm.

The total number of females examined each month and their reproductive conditions are given in table 31. The percentages of visibly pregnant and immature females, together with the total rainfall each month, are represented graphically in fig. 47.

Visibly pregnant females were trapped in May and June, and September - December 1965, and in April 1966. Pregnancies probably occurred in April 1965, when no females were trapped. The breeding periods of this rodent would, therefore, appear to be very similar to Lemniscomys striatus. Like the other species studied, there was a marked difference in the duration of the April - June breeding period in 1965 and 1966. In 1965, breeding continued until June, whilst in 1966 it had clearly finished by the latter half of May.

The breeding of this species appears to be confined to the wetter months of the year and early part of the dry season when the habitat is still moist. Hanney (1965) similarly found breeding to be at a maximum at the end of the rains and beginning

of the dry season, with no breeding in evidence at other times of the year.

(ii) Fertility

During the April - June 1965 breeding period, it seems likely that a proportion of females had two litters, as seen in Lemniscomys. It would be theoretically possible for some females to have three litters during this time, if the gestation period is 18 to 20 days as it is in Mus musculus (Asdell 1946).

One female was found to be lactating, with an early implanted stage in May 1965, which suggests that some females do become pregnant at the post partum oestrus and so have two litters in the one breeding season. In the September to December breeding season, no pregnant females which were also lactating were found.

The only evidence for females having more than one litter during this period was one parous female which had a vaginal plug, indicating recent copulation, which was trapped in October 1965.

Counts of the placental scars revealed that a few females had as many as 15. As will be shown subsequently, the average number of implanted embryos was 4.5, therefore, it seems likely that a few females have at least 3 litters. Whether these were from one breeding period or the result of breeding in two periods is not known. Probably only 2 litters are normal in any one breeding period, as females with more than 10 placental scars were rarely found.

A few females (see section VII) born towards the beginning of both breeding periods, matured and became pregnant

before the end of the same breeding period. Such females were trapped in June and December 1965. Precocious breeding was also found in Lemniscomys. During the dry season all the mature females appeared to be in a state of permanent anoestrus (table 31).

The number of implanted and healthy embryos are represented as frequency polygons in fig. 48. Three pregnancies were excluded because the animals concerned were so badly damaged that the number of embryos could not be counted.

The mean number of healthy embryos of 14 pregnancies was 4.36 with a range of 1 to 6 and a standard deviation of 1.63. The mean number of implanted embryos was 4.5 with a range of 2 to 6. Approximately 6 per cent of all embryos were resorbing. Hanney (1965) found the mean litter size of 5 pregnancies to be 6 with a range of 5 to 7.

Too few pregnancies were recorded for any relationship between the number of embryos and the clean body-weight, and the seasonal variation to be investigated.

(c) Reproductive Cycle of the Male

(i) Growth and Breeding Season

The lightest male (fig. 49) had a clean body-weight of 5.5 gm. and the heaviest 17 gm. Very few light weight males were caught, which probably reflects the weight selection of the traps used. No marked seasonal changes in the weights of the mature males were obvious.

From table 32, it can be seen that the clean body-weight at which the males attain the full fecundity rating is not sharply defined. However, most males mature at a clean weight of approximately 10 gm. The class of males with fecundity ratings of $(\frac{1}{4})$ and $(\frac{1}{2})$ consists of males which are just maturing, and males which have been mature but which have reduced fecundity ratings, and which are probably not active sexually. Table 33 shows that this class of males is at a maximum in the drier months of the year, and are not present at all during the peak of the rains. It can be seen that a large proportion of males are in an anoestrus state in the dry season. Thus the seasonal cycle of both the males and females is very similar to Lemniscomys. Hanney (1965) did not find any evidence for seasonal anoestrus in Mus triton, although he recorded this condition in other species of rodents.

(ii) Changes in the Testes, Epididymides and Seminal Vesicles

The combined weights of the right and left testes, epididymides and seminal vesicles of 73 animals are shown in fig. 50.

Although the seasonal cycle in fecundity appeared to be similar to Lemniscomys, no obvious seasonal variation in the weights of the testes and epididymides was evident.

There was, however, a marked seasonal variation in the weights of the seminal vesicles reminiscent of Lemniscomys. The weights of these organs were at a maximum during the rains, which corresponded to the periods of reproduction, and regressed

to approximately one-tenth of their maximum size in the dry months of June and July 1965, and January and February 1966.

The variations in the weights of the three reproductive organs considered here, were more similar to those found in Mastomys than Lemniscomys, although the breeding periods of M. triton more closely resembled the latter species.

(6) Reproduction in Mylomys cuninghamei

(a) Introduction

This species is distributed in the Northern Tropics, from Kenya in the East, through Uganda, the Sudan and the Congo, to Ghana in the West. It is strictly herivorous, and lives in thick grassland, heath and scrub.

It appears to have been caught very little, and as a consequence little is known about its biology. Delany (1964a, b) apparently records the only breeding noted in this species.

In the present study this species was collected in the Crater Track and Royal Circuit areas (table 1). The data from the two areas ^{1/2} has been grouped together.

(b) Reproductive Cycle of the Female

(i) Growth and Breeding Season

The heaviest foetus weighed 2.83 gm. when preserved, but as it was the only one of a litter it may have been heavier than usual. A litter of five in a similar condition, with body-hairs just beginning to grow, had an average weight of 2.18 gm. The weight at birth is estimated to be approximately 2.5 - 3.0 gm. The weights of Arvicantis at birth, which is a similar sized animal, were estimated to be of the same order of magnitude.

The clean body-weights of 59 females are represented in fig. 51. With such a small sample the weight at weaning cannot be estimated with any degree of certainty. However, the two females with clean weights of 16 gm. and 18 gm. only had two molars erupted, therefore, the weight at weaning is probably in

excess of 20 gm. Most adult females had clean body-weights between 60 gm. and 110 gm., with an observed range of 52 - 118 gm.

From the distribution of immature and mature females in table 34, it appears that females have a clean body-weight of about 55 gm. at maturity. A loss in weight after pregnancy is also indicated by the table, although it may be seasonal.

The total number of females examined each month and their reproductive conditions is given in table 35, and the percentage of visibly pregnant females together with the total monthly rainfall in fig. 52.

Visibly pregnant animals were trapped in April - June, and September - December 1965, and March and May 1966. As the monthly samples were so small, the variation in the breeding rate over the year could not be determined with certainty. A marked reduction in July and August is clearly indicated, but any reduction in the breeding rate in January and February could not be determined as no adult females were collected in those months. Delany (1964b) trapping in the same area in July 1963, only recorded two pregnancies from 31 females, which supports the conclusion of reduced breeding during this month made in the present study. However, Delany (1964a) trapping in nearby areas in August 1961, found that four out of six females were visibly pregnant. It would be interesting to know if the rainfall pattern in 1961 was the same as 1963 and 1965, which had very similar amounts of rain in July and August. It seems likely

that Myomys breeds at a maximum during the rains, and that breeding is reduced to a very low level in the driest months of the year.

(ii) Fertility

As Myomys breeds for long periods it is likely that some females become pregnant again at the post partum oestrus. A large proportion (4 out of 11) of females with freshly implanted embryos were also lactating, which suggests that normally females did become pregnant again at the post partum oestrus, thus breeding continuously at least throughout the rains.

Although anoestrus females were found at various times of the year (table 35), most were found in July and August, which suggests that there was a seasonal anoestrus during the dry months.

The maximum number of placental scars recorded was 14. The mean number of implanted embryos is 4.3, therefore, some females have at least 3 litters. In view of the large size and probable longevity of this species, it seems likely that some females have more than three litters.

The number of implanted and healthy embryos is represented as frequency polygons in fig. 53.

The mean number of healthy embryos of 21 litters was 4.29 with a range of 1 to 6 and a standard deviation of 1.27. The mean number of implanted embryos was 4.33 with a range of 2 to 6. Only one embryo was found to be resorbing, which is about 1 per cent of the total number of implanted embryos. Delany

(1964a, b) recorded 6 pregnancies with a mean litter size of 4.0, with a range of 3 to 5. From the limited data available, there appeared to be no relationship between the clean body-weight and number of embryos.

(c) Reproductive Cycle of the Male

(i) Growth and Breeding Season

As only 26 males were collected, little can be said with certainty about the reproductive cycle of the male.

The lightest fecund male (fig. 54) had a clean weight of 40 gm. and the heaviest 144 gm. Most adult males weighed 80 - 140 gm. and therefore appear to be heavier than the females.

The weight distribution of the three fecundity ratings of these males is given in table 36.

The males mature at a clean body-weight of approximately 70 gm., which is 15 gm. heavier than that estimated for the females.

Males with the full fecundity rating were found in every month they were trapped, except January, and it seems likely that they were present in the population throughout the year.

(ii) Changes in the Testes, Epididymides and Seminal Vesicles

The weights of the paired testes, epididymides and seminal vesicles of 24 males are shown in fig. 55. Any seasonal variation in the weights of these organs cannot be revealed by so few specimens, but a reduction in the weights of these organs during the dry season, as seen in other species, could take place as no males with full sized reproductive organs were trapped in those months.

(7) Reproduction in Tatera valida

(a) Introduction

This species appears to be confined to the tropics, having been recorded in Angola, Zambia, Rhodesia and Mozambique in the South, and ranging through the Congo into Uganda and Kenya in the North. It is insectivorous, and lives typically in grassland, heath and scrub.

Very little appears to be known about the biology of this species, and information about its reproduction in Uganda is limited to two recorded pregnancies. The breeding of two other species of this genus, Tatera afra and T. brantsi have been studied in detail in South Africa and the Transvaal by Measroch (1954) and Allanson (1958). Pirlot (1954) studied the breeding of a species of Tatera in Katanga, and Hanney (1965) made notes on the biology, including the breeding of T. bohmi (Noack) and T. leucogaster (Peters) in Malawi.

In the present study this species was trapped in the Crater Track and Royal Circuit areas, and the material from both areas has been grouped together in the analysis of the results.

(b) Reproductive Cycle of the Female

(i) Growth and Breeding Season

The heaviest foetus of a litter of four weighed 3.02 gm. when preserved, but although it was well developed, there were no body-hairs developing and, therefore, it was probably not full term. The weight at birth of other species of the genus has been estimated by Measroch (1954) to be 5.5 gm. for T. bratsi

and 4.5 gm. for T. afra.

The lightest female had a clean weight of 21 gm. (fig. 56) and the clean weight at weaning was estimated to be about 25 gm. Most adult females had clean weights between 80 gm. and 110 gm., with an observed range of 74 gm. to 108 gm.

Females weaned in June appeared to grow faster in weight and mature earlier than those weaned about October 1965. A similar difference in growth rates of animals born in different breeding periods was noticed in Mastomys.

It can be seen from fig. 56 and table 36 that the clean body-weight at which females mature is approximately 75 gm.

The number of females examined each month and their reproductive conditions are given in table 38, and the percentage of visibly pregnant and immature females, together with the total rainfall each month are represented graphically in fig. 57.

Visibly pregnant females were only trapped in June, October and November 1965. It seems likely that gravid females were also present in the population in May and September 1965, as lactating females were trapped in June and October. The appearance of young in June and October suggests that the onset of breeding may have been even earlier. However, the gestation and weaning periods are not known, therefore, the onset of breeding cannot be estimated from the appearance of immature animals. Delany (1964a) recorded one pregnancy in July 1961, and one specimen in the collections at the British Museum (Natural History) was also recorded as being pregnant in July.

The evidence suggests that this species breeds for a limited period towards the end of the rains and well into the dry season in the short March - May rains, but apparently starts to breed again at the beginning of the 'long' rains which are at a maximum in September and October. However, the present estimates of the breeding periods may be more limited than they really are. Of the other species of Tatera studied, this species appears to resemble T. afra in its breeding. The latter species only breeds for a limited period at the end of the rains and into the dry season in South Africa, but the rains only occur once a year in that area.

(ii) Fertility

Only five gravid females were trapped, two of which, with freshly implanted embryos, were found to be lactating in June and November. This suggests that a large proportion of females became pregnant again at the post partum oestrus, and so had two litters in each of the two breeding seasons. However, counts of the placental scars of parous females suggested that only one litter was normal in each of the two breeding periods.

Of the five visibly pregnant females, four had 4 embryos and one had 3 embryos. The mean number of embryos per litter was, therefore, 3.8. Measroch (1954) recorded a mean litter size for T. brantsi of 2.94 (range 1 to 4) for 42 litters, and for T. afra of 3.98 (range 2 to 6) for 62 litters. Hanney (1965) recorded a mean litter size of 4.6 (range 3 to 7) for 7 litters of T. leucogaster. Prasad (1961) recorded the average number

of embryos per pregnant female as 6.3 in Tatera indica cuvierii in India. It thus appears that there is a wide range of litter size within the genus.

(c) Reproductive Cycle of the Male

(i) Growth and Breeding Season

It can be seen that most adult males had clean weights of 90 - 130 gm. (fig. 58) and, therefore, tend to weigh more than the females. The lightest adult male weighed 77 gm. and the heaviest 146 gm. The growth in weight of young born at different times of the year did not appear to be different, unlike the females. There appeared to be no seasonal variation in the weights of the adult animals.

The clean weight at puberty is estimated to be approximately 75 gm. from fig. 58 and table 39. Thus, the males and females seem to mature at about the same weight, although the males appear to grow to a heavier weight than the females.

Fecund males were present in every month they were trapped, and there was no evidence for any seasonal anoestrus. This contrasts with T. afra (Allanson 1958) and T. indica cuvierii (Prasad 1956) which both undergo complete seasonal anoestrus at the end of the dry season and beginning of the rains.

The monthly variation in the proportion of fecund males, shown in table 40, merely reflects the presence of juveniles in the population as there is no seasonal anoestrus. The proportion of fecund males is generally at a maximum during the breeding periods of the female.

(ii) Changes in the Testes, Epididymides and Seminal Vesicles

The weights of the testes in the fecund males were 2.5 gm. to just over 4 gm. (fig. 59) so they are much lighter than the mean weights recorded for other species of gerbils.

Allanson (1958) noted that the size of the reproductive organs in gerbils was exceptionally high compared with other species of small rodents, and this is true even for T. valida.

There appeared to be no seasonal variation in the weights of the testes and epididymides (fig. 59), but the seminal vesicles appeared to regress in July and August 1965, to about half their maximum size during the rains. Thus, the seasonal variations in the weights of the male reproductive organs most closely resemble those of Mastomys in the present study, and the breeding periods in the females were fairly similar too.

(8) Remaining Species

The remaining species present in the Crater Track area were only caught in very low numbers. As a result, only a few notes on the breeding of some of these species are available.

(a) Aethomys nyikae

Only 19 females were collected and visibly pregnant animals were trapped in October and November 1965, and January and April 1966. Lactating females were collected in May, June and November 1965, and in April 1966. No adult females were collected in the other months of the year, and it is therefore not known whether breeding continues throughout the drier months of the year. Hanney (1965) included this species with Aethomys chrysophilus (De Winton), which apparently breeds throughout the year in Malawi.

The four gravid females each carried three healthy embryos; and one of them had a fourth embryo which was resorbing. Hanney (1965) recorded a mean litter size of 3.2 (range 2 to 5) for 15 pregnancies of A. chrysophilus.

The heaviest litter examined had an average preserved weight of 4.18 gm. per embryo (maximum 4.39 gm.). The embryos appeared to be near full term, as the body-hairs were growing. The mean weight at birth is, therefore, estimated to be approximately 4.5 gm.

(b) Mus minutoides

Pregnant females were trapped in May, June, November and December 1965. Adult females were not trapped at any other

time of the year except August 1965, and February and May 1966. It is, therefore, not possible to ascertain breeding rates throughout most of the year. A lactating female with an early implanting embryo was trapped in June 1965, which suggests it had become pregnant again at the post partum oestrus.

The five gravid females collected had a mean litter size of 3.8 with a range of 2 to 5 embryos.

The heaviest embryo weighed 0.45 gm., and the mean weight for the litter of two was 0.43 gm. when preserved. It was well developed but hairless, and so was probably not full term.

(c) Otomys irroratus

One pregnant female was collected in each of the months of July 1965 and April 1966. The first had one embryo, and the latter contained two.

(d) Zelotomys hildegardae

One pregnant female with 3 embryos, was collected in May 1966. A lactating female which had just given birth was collected in December 1965, and two parous animals with active uteri were trapped in July 1965 and April 1966.

(C) Discussion

The rodentia display a wide variety of reproductive patterns; some species breed throughout the year, while others may have a short annual breeding season. As in most small mammals, the periods of reproductive activity in the males and females are usually very similar.

Similar sexual activity in the males and females has been recorded in the bank vole by Brambell (1936) and Rowlands (1936), in the gerbille, Tatera afra, by Measroch (1954) and Allanson (1958), and in the Indian gerbil, Tatera indica, by Prasad (1956, 1961). This is not always the case, however, e.g. in the grey squirrel the males are functional throughout the year (Allanson 1953), while the females are in complete anoestrus for about six months of the year (Deansley and Parkes 1933). In the present study, male Mastomys with mature spermatozoa were present throughout the year, although breeding in the female was limited to two short periods. However, there was a marked seasonal cycle in the weights of the seminal vesicles which leads one to suppose that the accessory reproductive organs were in anoestrus, while the testes were still active. Stoch (1954) observed a similar difference in the activity of the different reproductive organs of the male Elephantulus. Therefore, the presence of mature sperm in the testes or epididymides does not necessarily mean that the male is fertile, although it has generally been accepted to be a criterion of male fertility. Because of the differences that may exist between the male and

female reproductive cycles, and the difficulty of determining the fecundity of the males, in the following discussion on breeding seasons, only the reproductive cycle of the female will be considered.

Continuous reproductive activity throughout the year, with no marked seasonal variation has been recorded for Mus musculus in England, by Laurie (1946). Harrison (1952, 1955) concluded that for species of Rattus in Malasia, breeding was continuous throughout the year, although there were irregular variations in the breeding rate broadly related to the irregular pattern of rainfall. Perry (1945) and Leslie et al (1952) found that Rattus norvegicus breeds throughout the year in England, although there is a seasonal fluctuation in the breeding rate. Although Mastomys natalensis breeds throughout the year, a very pronounced seasonal variation in breeding has been recorded in Sierra Leone, by Brambell and Davis (1941) and in the Transvaal by Coetzee (1965).

Typically, however, rodents have a limited breeding season, as has already been noted in the bank vole in England (Brambell 1936 and Rowlands 1936); in Tatera afra in South Africa (Measroch 1954 and Allanson 1958); and in Tatera indica in India (Prasad 1956, 1961).

In the present study, all the varieties of the reproductive pattern, illustrated above, were found. The breeding periods of the various species studied are summarized in fig. 60. The Mweya Peninsula population of Arvicantis breeds throughout

the year, though there is an apparent seasonal variation broadly related to the rainfall, such that breeding is at a maximum during the wettest months of the year. The same is probably true for the Crater Track population of Arvicanthis, although the seasonal fluctuation in breeding may be more pronounced.

Mylomys appears to have a similar pattern of breeding to Arvicanthis (although inadequate evidence was collected to be certain), there being a marked seasonal fluctuation most closely resembling the Crater Track population of Arvicanthis. It is interesting that these two species should have similar breeding patterns, since their biology, superficially at least, is very similar. In particular, the diets of the two species are very similar, both being strictly herbivorous, eating grass leaves and stems (Delany and Neal 1966). The only other species breeding for most of the year was Lophuromys, which breeds at a maximum during the wetter months of the year, and shows a marked reduction in the breeding rate in the dry months of July and August. Its pattern of breeding showed a marked contrast to the only other insectivorous species, Tatera, which had limited breeding periods during the rains and beginning of the dry season. Lemniscomys and Mus triton also had limited breeding periods which again were confined to the rains and beginning of the dry season. They are apparently omnivorous, Lemniscomys being primarily herbivorous, and Mus triton insectivorous. Finally, the other omnivorous species, Mastomys, had the shortest breeding periods of all the species studied, only breeding from

the middle of the rains onwards to the early part of the dry season.

In general it can be seen that all species are breeding at a maximum rate during the rains, and breeding is very reduced or ceases during the drier months of the year. This confirms the general pattern of breeding of African rodents established by earlier studies (pp. 59-61 this section).

The proximate causes of breeding seasons have been discussed by Baker (1938a, 1947) who has divided them into two quite different kinds. First, there are the external factors such as temperature, light, rainfall and food, and then there is an internal rhythm of reproduction. This factor may at times be so strong as to apparently overide the effects of the external factors, e.g. Baker and Ransom (1938) noted that some southern hemisphere birds, imported into the northern hemisphere, continue breeding at the same time as the fellow members of their species in the south.

However, during the present study at least three species (Mus triton, Lemniscomys and Mastomys) showed similar marked reductions in the April - June breeding season in 1966, compared with 1965. This suggests that some external factor is mainly responsible for the regulation of breeding activity in these three species.

It should be noted that in the following discussion on environmental factors affecting the breeding season in mammals, no single factor is itself solely responsible for inducing

sexual periodicity of breeding.

Light has been shown to profoundly influence the reproduction of mammals by Baker and Ranson (1932a). However, Baker (1947) concluded that there was a tendency to exaggerate the part it plays in the control of breeding seasons. Undoubtedly light is an important factor in temperate and subarctic regions, since the productivity and seasonal changes in these areas are very largely controlled by changes in day-length over the year. However, in the tropics the importance of light is debatable. The present study was carried out so close to the equator that the effects of light can be ignored, but at what distance from the equator does light begin to exert an effect? Marshall and Corbet (1959) studied the reproduction of the bat Chaerophon hindei Thomas at about the same distance from the equator as in the present study. They concluded that there was no breeding season and the reproduction varied irregularly throughout the year. This led them to reconsider the factors which might be responsible for the timing of the breeding cycles which had been observed in other tropical bats studied by Baker and Baker (1936) and Baker and Bird (1936) at $15^{\circ}15' S$ in the New Hebrides, and by Marshall (1947) at $7^{\circ} N$ in Ceylon. They concluded that light may have influenced the breeding in these areas, and suggested that further studies of bats living on or very near the equator, were required to discover whether they retain a breeding cycle governed by external stimuli other than change in day length. It should be noted, however, that the influence of light had

been ruled out in the studies by Baker and Bird (1936) and Marshall (1947), and although Baker and Bird suggested that decrease in day-length and amount of ultra-violet light may be important in controlling the breeding cycle of Pteropus geddiei, this idea was subsequently abandoned (Baker 1947).

Prasad (1956) in studies of the Indian gerbille, found that cyclical variation of night-length and correlated physical activity corresponded with the sexual activity of the male, and the females were only sexually active when the night-length was more than a certain critical amount. However, as will be seen subsequently, other environmental factors seemed to exert effects, so he finally concluded that an internal rhythm, conditioned slightly by changes of environment, was responsible for the regulation of sexual activity in this species.

The onset of breeding in temperate regions may be earlier if the climate is warmer than usual, and egg-laying may be arrested if there is a sudden cold spell (Baker 1938a). Baker and Ranson (1932b) found that the field mouse (Microtus agrestis) breeds at a reduced rate at lower temperatures in the laboratory. However, Laurie (1946) did not find a reduction in the breeding of Mus musculus living in cold stores, though of course there may have been other factors which accounted for this. In the tropics, however, it seems unlikely that the lowest temperature would reduce or cause a cessation of breeding, and in the present study, the seasonal variation in temperature was so slight that it may be ignored. However, it is possible that

very high temperatures might cause a reduction in breeding, because of the lethal effect of high temperatures on spermatozoa. It is interesting to note that Prasad (1956) found that the percentage of fecund males decreased with increase in temperature, and only increased when the temperature fell. This apparent correlation between the sexual cycle of the male gerbille and the temperature may be misleading, since they may both be altered by a third factor such as day-length.

Rain is an environmental factor of great importance in the control of breeding seasons, especially in tropical and subtropical regions where there are regular alternations between the wet and dry seasons. Baker (1938a) cites a number of examples for amphibia, reptiles, and birds in the tropics, which correlate their reproductive periods with the periods of rain. Moreau (1936, 1950) has shown that the breeding of birds in Africa is generally correlated with the rainfall. Not all birds lay their eggs during the rains, however, when there is an abundance of food, cover and nesting materials for most species: e.g. raptorial and scavengers lay in the middle of the dry season, when perhaps prey and carrion are more accessible when cover is reduced. Rain has long been thought to influence the breeding of small African mammals, and evidence is now accumulating to substantiate this idea. The breeding of Mastomys which has been studied in many areas in Africa, is always at a maximum towards the end of the rains and beginning of the dry season.

(Brambell and Davis 1941; Chapman et al 1959; Coetzee 1965; and Hanney 1965). The detailed studies on other small African mammals by Measroch (1954), Allanson (1958), van der Horst (1946) and Stock (1954), and the general studies of other workers, (pp. 59-61 this section), have all found a general correlation between the breeding cycle and the rainfall, rather than for any other climatic factor. The results of the present study, in which rainfall was the only marked seasonal factor, suggests that breeding is at a maximum during the rains. This may not always be so; e.g. Wade (1958) concluded that the onset of breeding in a variety of small mammals in the lowland rain-forest of north Borneo was correlated with the period of minimum precipitation. It seems likely, as Prasad (1956) suggests for the gerbille, Tatera indica, that rainfall usually effects breeding in an indirect way, through the effect it produces in the food supply. In the present study, the lag that is seen between the onset of the rains and the onset of breeding in most species, suggests that these species are taking advantage of the effects of the rain on the food supply. The fact that the breeding of the small mammals living in similar habitats, but with different feeding habits, in the same general area is not synchronised, leads to the same conclusion.

Food may be variable in both quantity and quality at different times of the year. Baker (1938a) and Prasad (1956) both cite experimental evidence that shows conclusively that

deficiencies in the diet reduce reproductive activity. Baker and Ranson (1932a) found that, although normally one could control the breeding of Microtus agrestis by means of light, if it was fed on optimum food for rapid reproduction one could not stop it breeding, even in complete darkness. Prasad (1956) concluded that seasonal variation in the food supply was the most important factor conditioning sexual activity in the Indian gerbille.

In the present study seasonal fluctuations in the food supply are not known, and although the general diet is known for most species, seasonal fluctuations in the diet are unknown. Although variation in the quality of food over the year is probably a very important factor in the control of the breeding patterns seen, the relationship between the food supply and the breeding is by no means clear, since animals which appear to have similar diets may breed at very different times, e.g.

Lophuromys and Tatera.

It can be seen that the environmental factors which influence breeding vary in importance from one region of the world to another. Light and to a lesser extent, temperature, are very important in temperate and subarctic regions, but are probably of little importance in the tropics. In the tropics and subtropical regions, the dominant environmental factor influencing breeding would appear to be the rainfall. Much of the effect of these factors on breeding is probably indirect, by their effect on the food. In the present study, the ultimate

causes of breeding remain unknown, although the rainfall clearly effects the breeding, either directly or indirectly. However, until more is known about the biology of these animals, the precise factors affecting their breeding must remain a mystery.

VII. AGE STRUCTURE OF POPULATION

(A) Introduction

Hardly any studies have been made on the population structure of small African rodents, and apparently only one study (Coetzee 1965) exists where the age structure of the population throughout the year has been related to the breeding.

One of the problems of studying the age structure of small mammals is finding a criterion for ageing which is sensitive enough to show changes in the population from month to month. A variety of techniques has been used which are discussed in Mosby (1962). In the present study, the criterion used was tooth eruption and wear. Full details of the assessment of age are given on pp. 23-32.

Not all species could be studied satisfactorily, as large monthly samples are needed to adequately illustrate changes over the year. However, for most species, sufficient information has been obtained to make practicable comparison with data on breeding activity.

(B) Accounts of Species

(1) Arvicanthis niloticus (Mweya Peninsula population)

The monthly changes in the age composition of the Mweya Peninsula population are shown graphically in fig. 61.

It can be seen that there are, at all times of the year, two fairly distinct peaks in the population, representing immature and mature animals, which suggests that breeding is mainly confined to limited periods. However, from an analysis

of the material collected, it has already been shown that breeding continues throughout the year, although it is at a maximum during the rains. Such a variation in the breeding rate over the year would be expected to give two peaks in the population, but not as marked as that observed. This situation could be explained in terms of seasonal mortality factors which help to give such a distinct bimodal age structure. It should be noted that there were very few young animals trapped throughout the rains, most immature animals being trapped towards the end of the rains and throughout the dry season. This suggests that a large proportion of nestlings are being killed throughout the rains. This could possibly be the result of flooding of the nests during heavy rainfalls.

Some males and the females appear to mature at an early age, whilst the oldest animals caught were sexually active. Most animals appear to live only six to nine months, and only a few longer than a year. Thus, there is a rapid turnover of the population.

(2) Arvicanthis niloticus (Crater Track population)

The monthly changes in the age composition of the Crater Track population are represented graphically in fig. 62. As so few animals were caught, the males and females have been grouped together, but even so a clear picture is not presented. It can be seen, however, that the youngest animals were only caught towards the end of the rains and during the dry season. This suggests either seasonal breeding or seasonal mortality.

The results of the study of the reproductive cycle were not conclusive, although a marked seasonal variation in the breeding rate was indicated. Consequently, it is not known if there were any seasonal mortality factors as were inferred for the Mweya Peninsula population.

(3) Lemniscomys striatus

The monthly changes in the age composition of the Crater Track population (fig. 63), clearly reflect the cycle of breeding which has already been established. (pp. 75-84).

The youngest animals were trapped six to eight weeks after the onset of breeding, which suggests that the animals were breeding in March 1965. Since the gestation period was found to be approximately 28 days by Peter et al (1964), it follows that the young take two to four weeks to wean. This estimate is comparable to that for other murids. A few animals mature almost immediately on weaning: young in full reproductive condition were trapped in May and June, and November and December 1965, only four to eight weeks after birth. It can be seen, however, that normally they first begin to breed in the rainy season following that of their birth. The main periods of mortality appear to be towards the end of each breeding period, at about the same time that the young first appear. Most animals survive to breed in one breeding period, a few for a second breeding period, and very few for a third breeding period. Thus, the average life expectancy would be about six to nine months, and there is an almost complete turnover of the population twice

a year. There appeared to be no reduction in fertility with increased age.

(4) Mastomys natalensis

Like Lemniscomys the monthly changes in the age composition of the Crater Track population (fig. 64) clearly reflect the cycle of breeding which has already been established. (pp. 85-94). It can be seen that there is no evidence for breeding outside those periods already described. However, unlike Lemniscomys, young do not mature in the same breeding season in which they are born, and it appears that few animals survive to breed for a second period. Most animals disappear from the population almost immediately after breeding. Thus, there is an almost complete turnover of the population every six months, which is the probable maximum life expectancy for most members of the species in this area.

(5) Lophuromys sikapusi

The monthly changes in the age composition of the population are shown graphically in fig. 65.

Since so few animals were caught, the changes cannot be followed accurately, but there are no marked peaks which could suggest the existence of limited breeding periods. However, it is interesting to note that in August and September (1965) following the two months with few or no pregnancies, no very young animals were caught. The same was true for February and March 1966, following the second dry season in the study. This information suggests reduced breeding during these times,

which is in agreement with information obtained on reproduction (pp. 95-99).

(6) Mus triton

The monthly changes in the age structure of the population, shown graphically in fig. 66, are very similar to Lemniscomys, which would confirm the picture of the breeding cycle that has already been established (pp. 100-105). Like Lemniscomys, it can be seen that a few animals become mature and start breeding in the same breeding period of their birth, (i.e. six to eight weeks after birth), but most animals only mature and start breeding in the breeding period following that of their birth. It would appear that a large proportion of the population survive for at least one year, and like most of the other species studied, the main period of mortality is immediately after breeding.

(7) Myomys cuninghamei

The age structure of the population, shown in fig. 67, tells very little because so few animals were caught. The animals apparently mature while still relatively young, and there does not appear to be any reduction in fertility with age.

(8) Tatera valida

The monthly changes in the age structure of the population (fig. 68), are not clearly defined because of the small numbers of animals caught. In general, however, the fragmentary picture presented confirms the cycle of breeding which has already been described (pp. 110-114). That is, animals born in May

and June 1965, appeared to mature towards the middle of the following breeding season in October, and not at the beginning as in the other seasonal breeders studied. This is perhaps due to the large size they must attain before maturing, and also to the fact that the two breeding seasons in 1965 were very close together. Those born in October - December probably mature by the beginning of the following breeding season, as they have a longer time in which to mature. There was no indication of reduction in fertility with increased age.

(C) Discussion

If a large sample can be obtained, a study of the age structure of the population throughout the year is shown to be very valuable, especially for those species which have limited periods of reproduction. The breeding cycle and the age structure of the population should be studied simultaneously, since the two are inter-related.

The use of toothwear as an ageing criterion appears to be fairly satisfactory, although the method is in part subjective. However, in Mastomys, the variation in toothwear is so great that five months after the appearance of young, it is difficult to separate the young and old population by this method. In future studies the lens-weight technique, described by Lord (1959), may be the best method of ageing as it is more objective. A comparison with laboratory reared animals of known ages is also possible, so that the actual ages of the population can be

established. Tiermeier and Plenet (1964), comparing three methods for ageing black-tailed jackrabbits in North America, found that the lens-weight technique was far superior to age determining techniques based on body size, total weight, or epiphyseal closure.

VIII. FINAL DISCUSSION

The abundance and wide variety of species of small African rodents, together with the difficulty of obtaining an unbiased sample of each species, present unusual problems for an ecologist with experience of temperate mammals.

The methods of trapping small African mammals could undoubtedly be improved. In live trapping, one of the larger Havahart traps would be both sensitive enough to catch the smallest mammal, and also big enough to allow the largest myomorphs to enter (with the exception of Cricetomys). The problem of weight selection by break-back traps is not so easy to solve, since the trap must be large and have a strong spring to catch the larger myomorphs, but if it is too large, the break-back mechanism may pass over the smaller rodents without touching them. In practice, it is probably best to use a combination of small and large traps to catch the whole size range of small mammals.

In the present study it was found that each species had slightly different distributions within the habitat, according to the mosaic of plant communities. The degree of preference for the microhabitats offered varied. In general, the omnivorous species showed no marked preference for any one microhabitat, while those species with more specialized feeding habits were found in fewer microhabitats. Thus, the species were not uniformly distributed throughout the grassland. The distribution of small mammals in the grassland was profoundly

affected by burning, so that any consideration of their micro-distribution had to take into account the recent burning history of the area. Since burning is such a regular feature of African grasslands, and both the number of animals and species are drastically reduced in burnt areas immediately after burning, the small mammals must be able to reproduce very quickly if they are to be present in large numbers. From a study of the breeding cycles and age structure of the various species, it can be seen that the number of offspring is far in excess of what the area can support, and that mortality of both young and adults is very high immediately after breeding. Thus, if there is any catastrophic reduction of the population by fire, severe flooding, or influx of predators, the original population density can be very quickly restored. In the grasslands the breeding is at a maximum during the rains when the risk of burning is at a minimum, and it was noticed that all species in the Crater Track area had their minimum period of breeding in July and August when the area is driest and is normally burnt. Thus, in the tropics, the breeding of small mammals generally appears to be related to the pattern of rainfall, rather than light, as in temperate regions.

A study of small African rodents offers wide scope for research since so little is known about them. Future ecological studies should, I think, study the animals of one fairly uniform habitat, e.g. grassland, forest etc. over the full seasonal cycle

of the year. Where possible, such climatic factors as rainfall and temperature, should be recorded by the investigator in the area of study, since they vary slightly from year to year, and may be very different from the nearest meteorological station records. The following lines of research would seem to be the most profitable to follow: the biology of reproduction together with the age structure of the population; the distribution of the various species within each major habitat, and with respect to one another; the behaviour, especially such aspects as activity and home ranges; and finally their feeding habits, especially changes in the diet throughout the year. It is essential that the general biology of each species should be known, since any explanation of such phenomena as the breeding patterns and distribution etc. must consider other aspects of the animals' biology.

IX. SUMMARY

(1) A total of 2,390 small mammals, representing 14 species of rodents and various species of Insectivora, were collected in approximately 15,706 trap nights, from April 1965 to May 1966, in grassland areas of the Queen Elizabeth National Park, Uganda.

(2) The animals were collected from four areas, two of which, the Mweya Peninsula and Crater Track areas, were trapped throughout a complete year. The main seasonal changes occurring in the grassland were recorded.

(3) The distribution of the different rodent species with respect to the major plant communities was studied in the Crater Track area, and each species was found to have a slightly different distribution. The insectivorous species, Lophuromys, Zelotomys and Tatera, and the omnivorous species which are mainly insectivorous, Mus minutoides and M. triton, were rarely found in bushes and were most abundant in Imperata and Cymbopogon. The omnivorous species which were mainly vegetarian, Lemniscomys and Mastomys, were found in all types of vegetation but were most abundant under bushes. Aethomys, a species with similar feeding habits, preferred bushes almost to the exclusion of the other types of vegetation. The herbivorous species, Arvicanthis, Mylomys and Otomys like the insectivorous species, avoided bushes, but had different vegetation preferences. Arvicanthis preferred Themeda, Mylomys preferred Imperata, and Otomys preferred Cymbopogon.

(4) The distribution and habitat preferences of the rodents were profoundly modified when the grassland was burnt.

(5) The immediate effect of the fire was to reduce the number of animals and species present in the burnt areas. Mastomys, Mus triton and Tatera and probably Zelotomys, Mus minutoides and Aethomys were little affected by the burn. Lemniscomys occurred only in very reduced numbers in burnt areas, and Lophuromys and Mylomys were completely absent for five and seven months respectively after the fire. The reduction in numbers was probably mainly due to emigration into the unburnt areas.

(6) Two months after burning, there was a general increase in the number of animals present in the burnt areas, and for the next six months, some species preferred the burnt to the unburnt areas. All species were present in the burnt areas seven months after burning, and ten months after the fire there was little difference between the two areas.

(7) A study of the breeding biology revealed that all rodent species were breeding at a maximum during or towards the end of the two rainy seasons each year. Arvicanthis and Lophuromys breed throughout the year, although at a low rate during the driest months of the year. Mylomys may also breed throughout the year. Lemniscomys and Mus triton breed only during the rains, and Mastomys and Tatera towards the end of the rains and beginning of the dry season. There was no evidence of breeding at any other time in these last four species.

(8) There was evidence in Arvicanthis, Lemniscomys, Mastomys and Mus triton, that the testes, epididymides and seminal vesicles showed a similar cycle of activity to the reproductive cycle of the female of the species. One or all of these organs showed a marked loss in weight during the dry season.

(9) Ageing of the population each month, using tooth eruption and wear as a criterion, supported the cycle of breeding activity described. It revealed that a few Lemniscomys and Mus triton born towards the beginning of each breeding period, matured and were breeding before the end of the same breeding period. Mortality appeared to be at a maximum towards the end of each period of maximum reproductive activity in each species.

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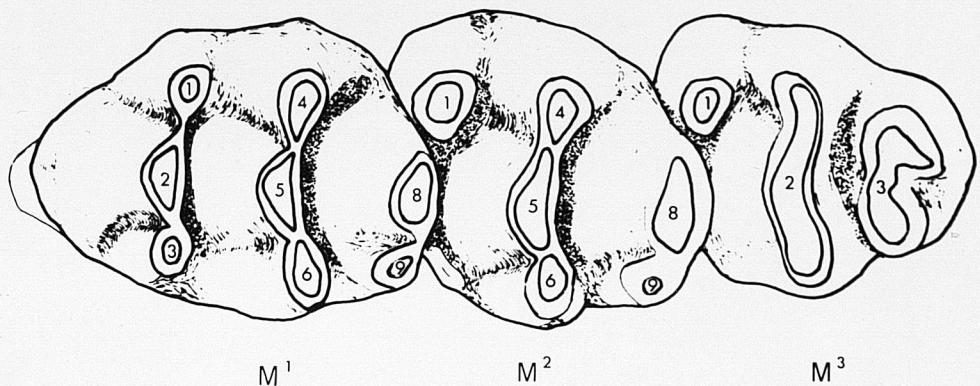
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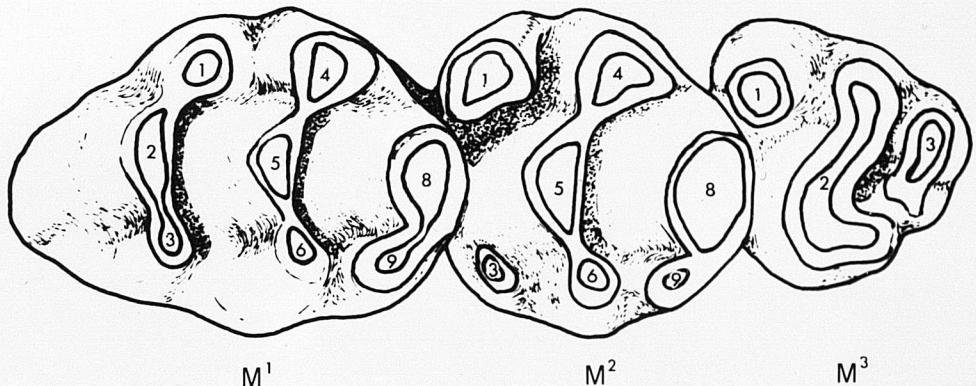
Fig. 1. Map of Africa showing place-names mentioned in text. The names of some of the territories have changed since the studies were carried out.

Fig. 2. Camera lucida drawings of right upper
molars showing cusp patterns of
Arvicanthis niloticus x 19
Lemniscomys striatus x 26
Lophuromys sikapusi x 24

Arvicanthis niloticus



Lemniscomys striatus



Lophuromys sikapusi

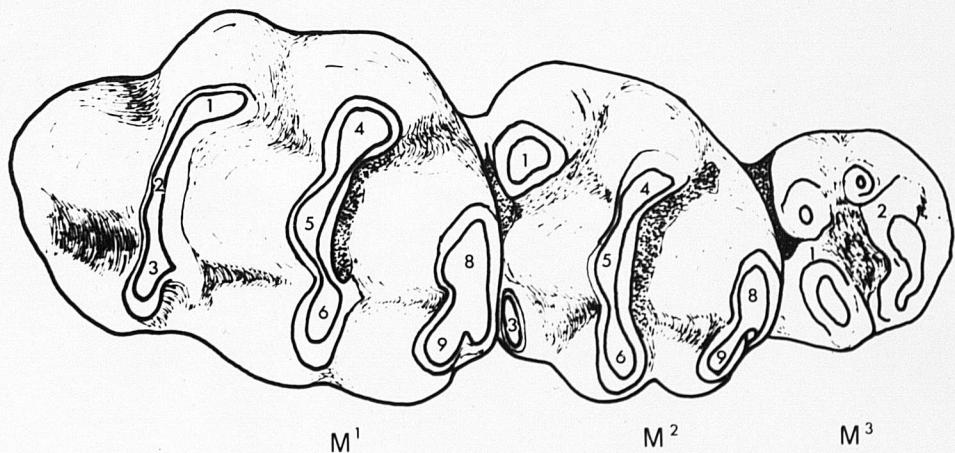
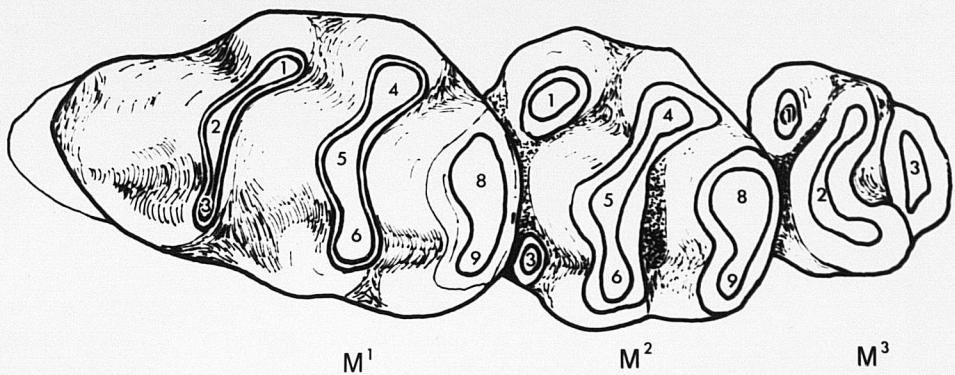
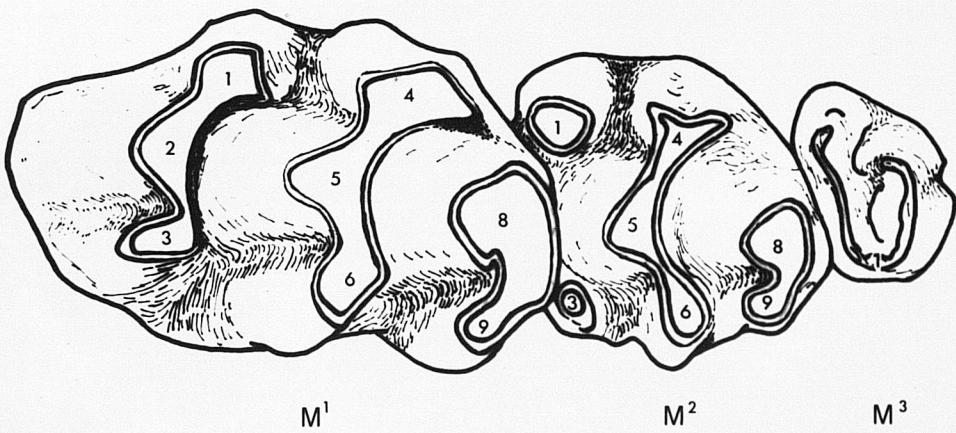


Fig. 3. Camera lucida drawings of right upper
molars showing cusp patterns of
Mastomys natalensis x 26
Mus triton x 33
Mylomys cuninghamei x 16

Mastomys natalensis



Mus triton



Myomys cuninghamei

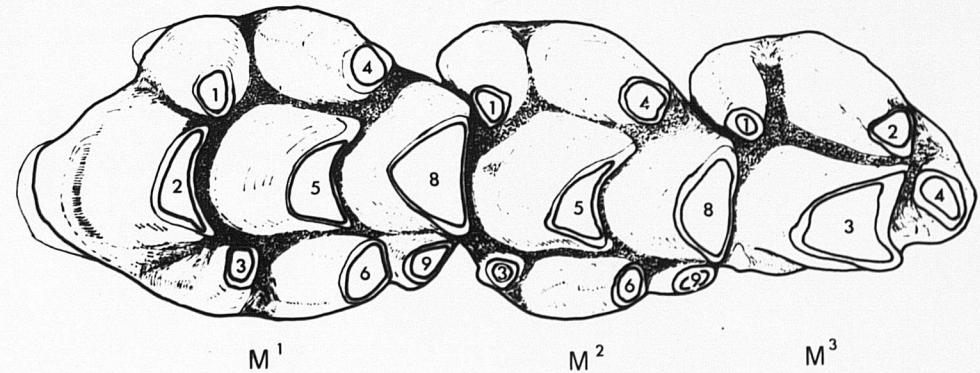


Fig. 4. Camera lucida drawing of the right upper
molars of Tatera valida x 25, showing
the pattern of cusps.

Tatera valida

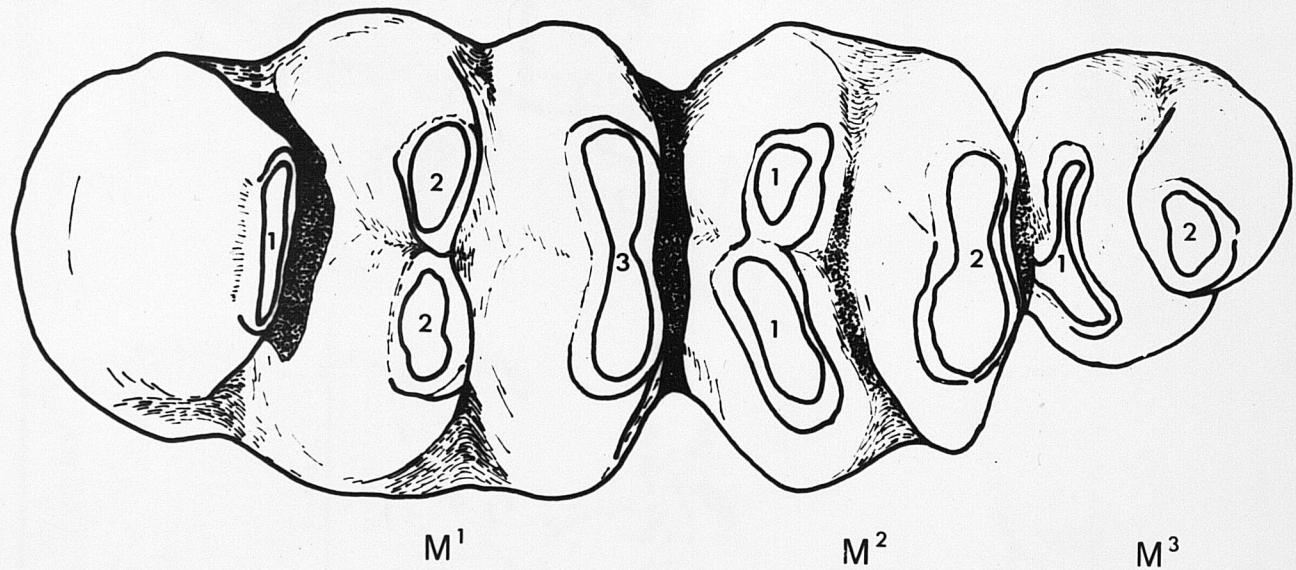
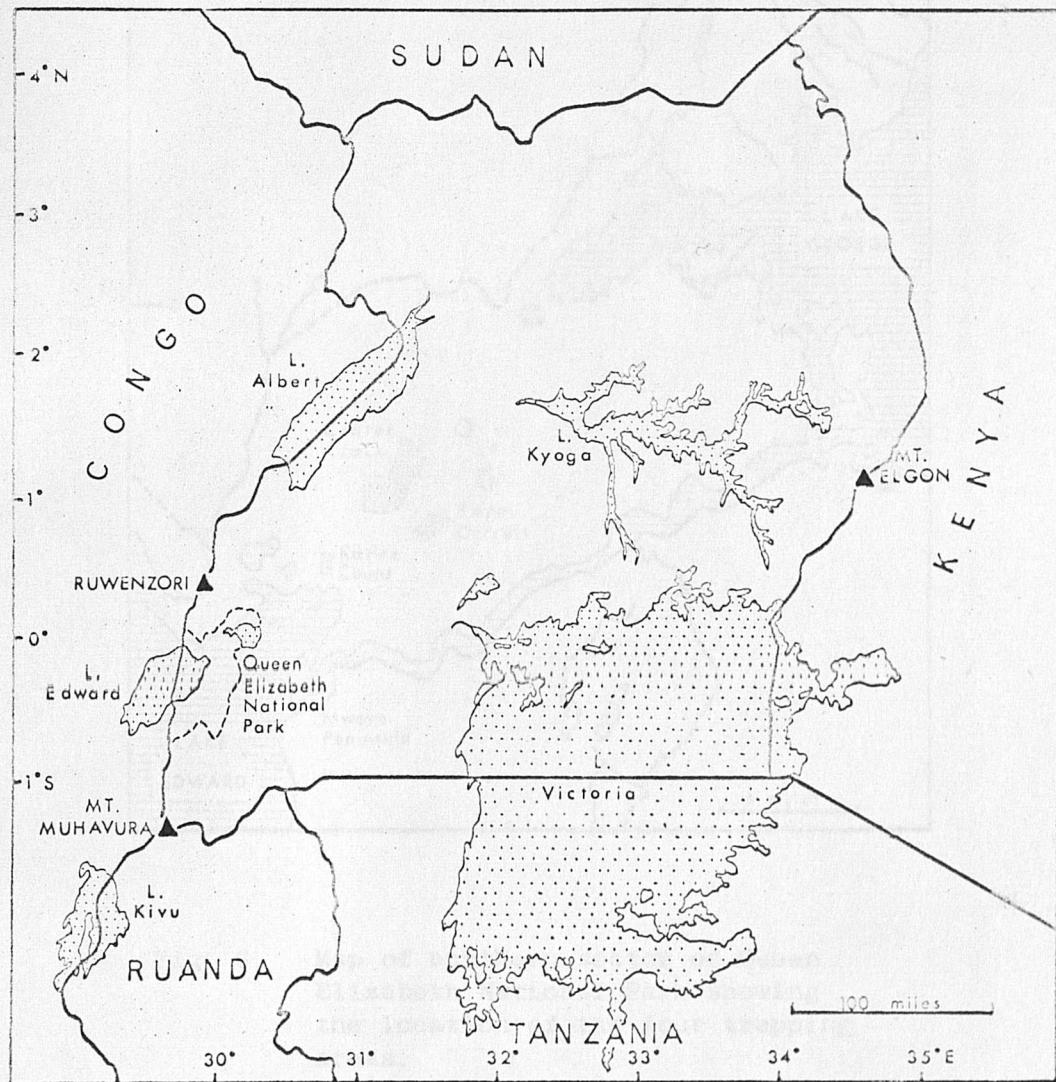


Fig. 5. Map of Uganda showing position of Queen Elizabeth National Park.



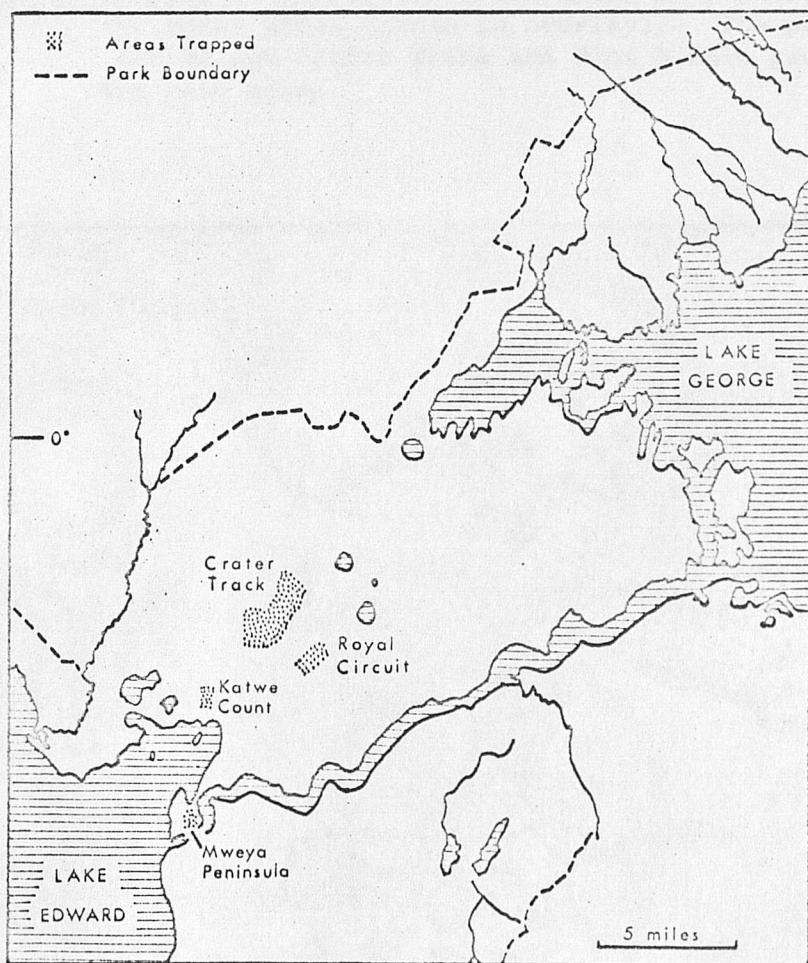


Fig. 6. Map of northern sector of Queen Elizabeth National Park showing the location of the four trapping areas.

Fig. 7. Map showing details of the topography and areas trapped in the Crater Track Area, in relation to the burnt areas (shown in overlay). The position of the Crater Track and Plot 5 rain gauges are also shown.

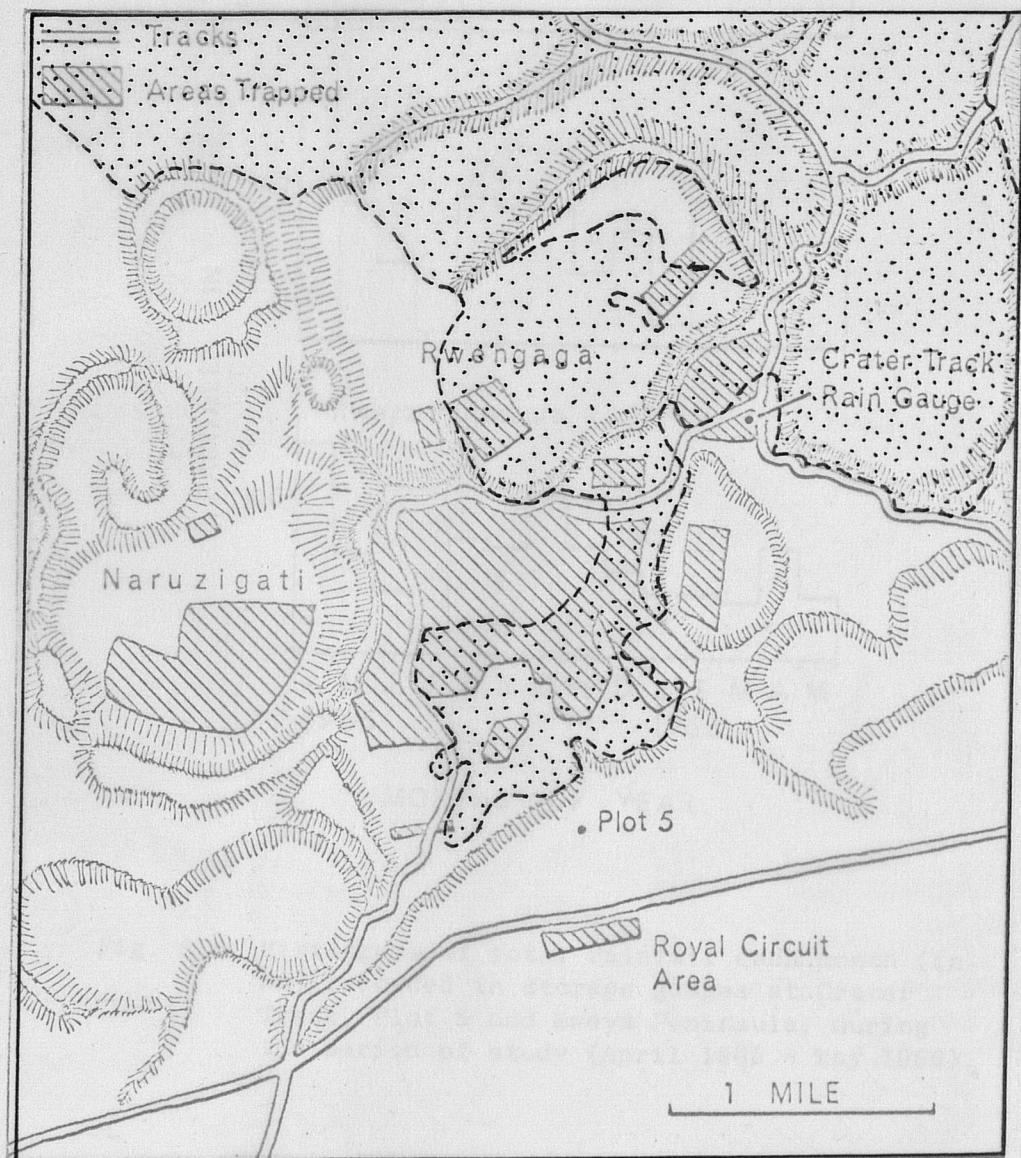
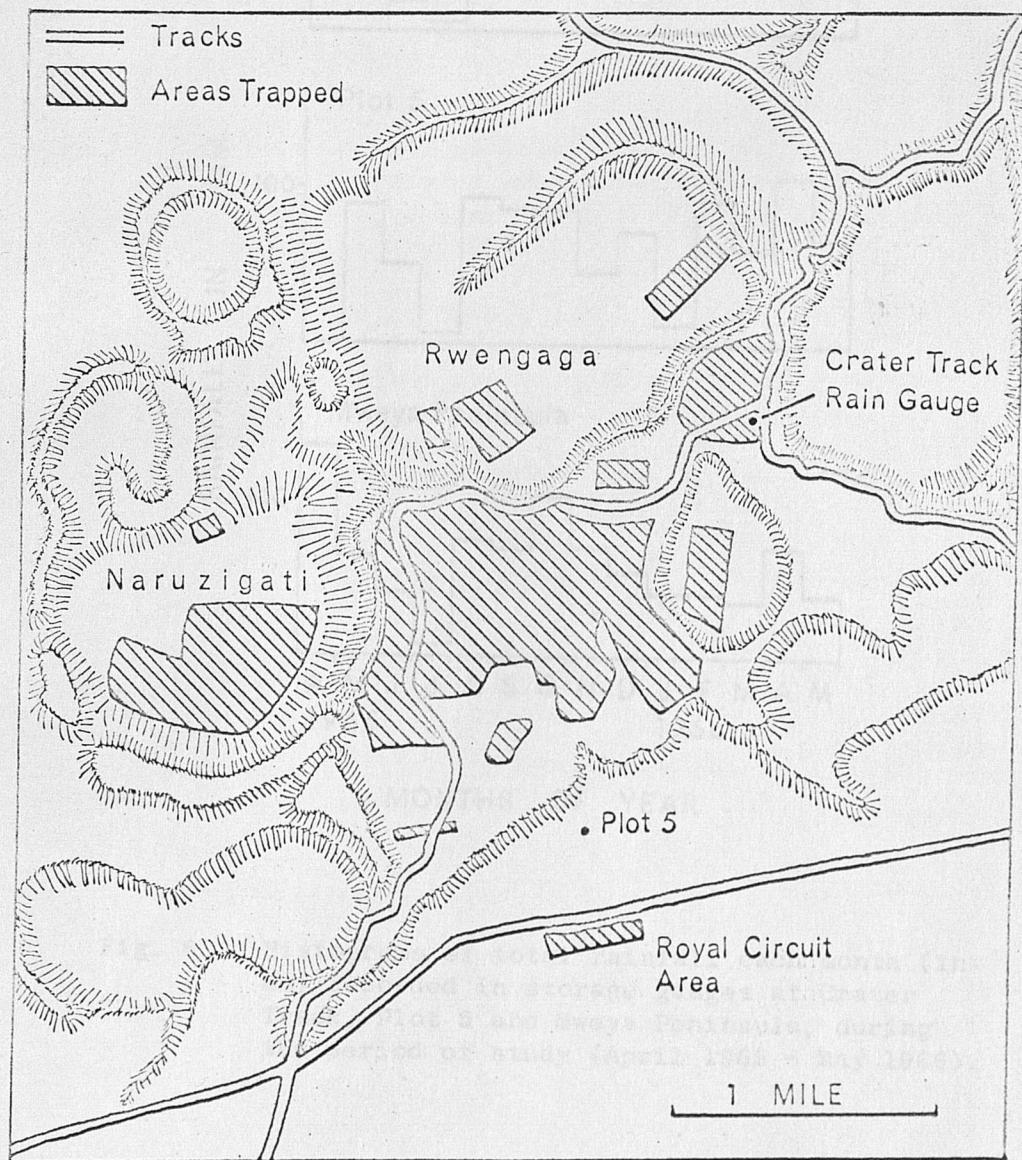


Fig. 7. Map showing details of the topography and areas trapped in the Crater Track Area, in relation to the burnt areas (shown in overlay). The position of the Crater Track and Plot 5 rain gauges are also shown.



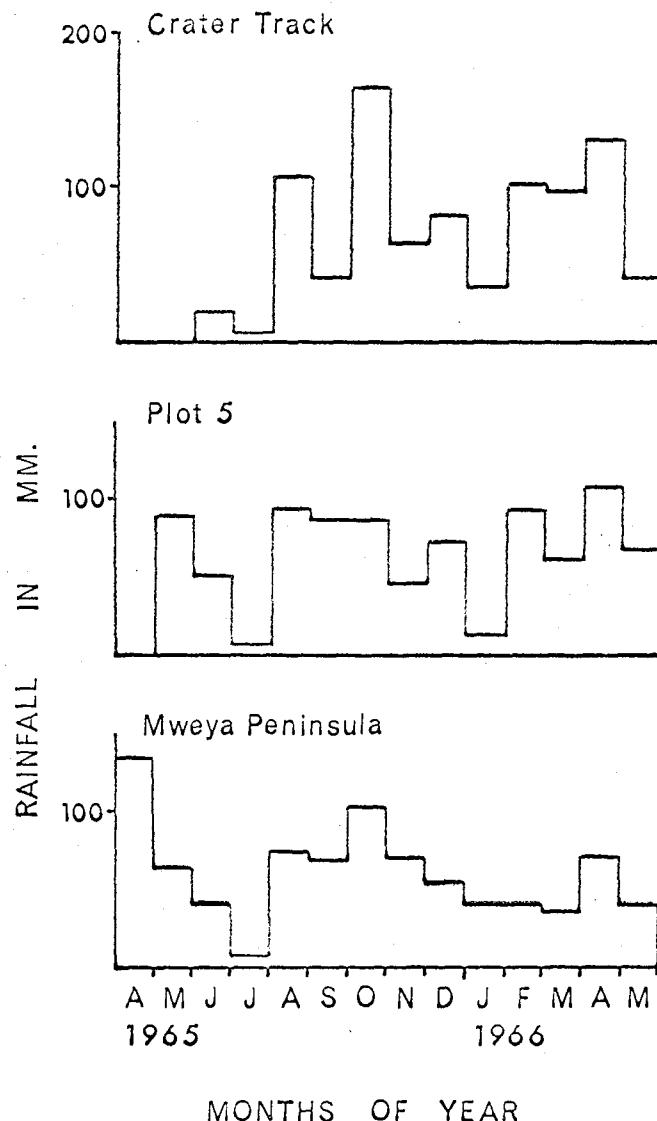


Fig. 8. - Histograms of total rainfall each month (in mm) recorded in storage gauges at Crater Track, Plot 5 and Mweya Peninsula, during the period of study (April 1965 - May 1966).

Figs. 9, 10, 11. Number of animals per 1000 traps in different grassland communities in the Crater Track Area from July 1965 to May 1966.

Solid symbols joined by dashed lines
●---● represent burnt areas, and
hollow symbols joined by solid lines
○---○ represent unburnt areas.

Imperata cylindrica unburnt △ burnt ▲

Themeda triandra unburnt □ burnt ■

Cymbopogon afronardus unburnt ○ burnt ◉

Bush (for Aethomys nyikae only) unburnt ◇

burnt ◆

Bare burnt ground +

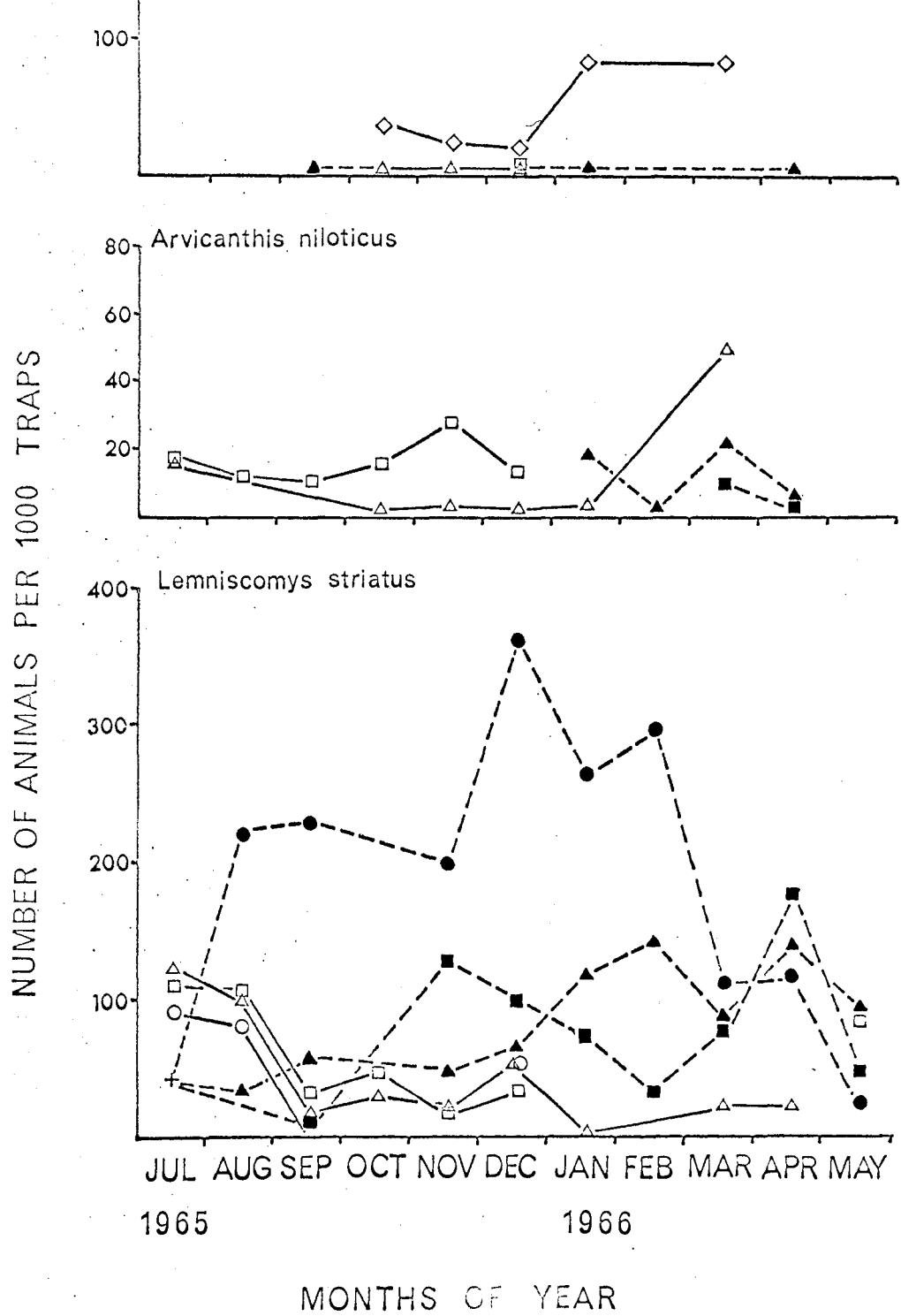


Fig. 9.

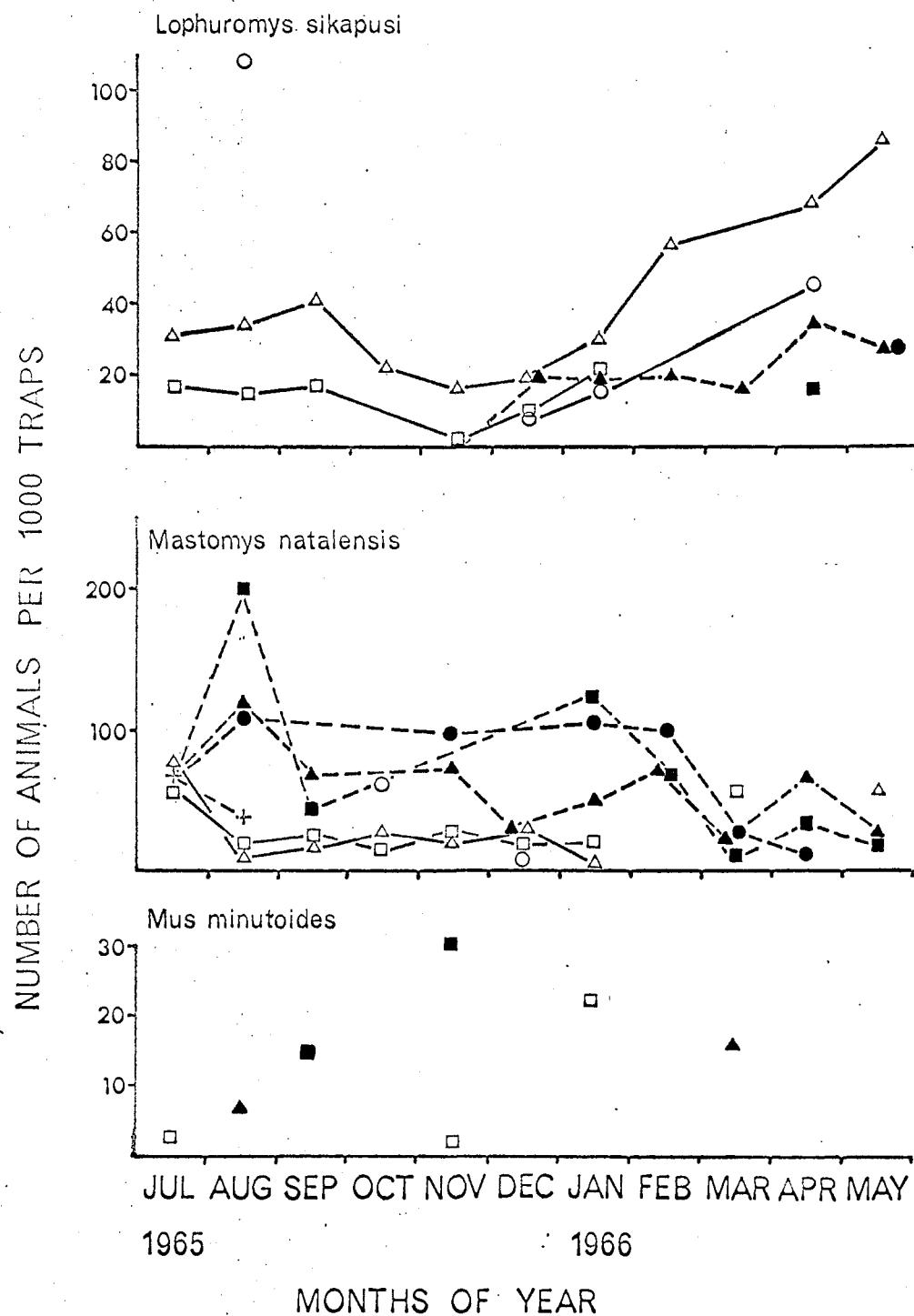


Fig. 10.

Fig. 11.

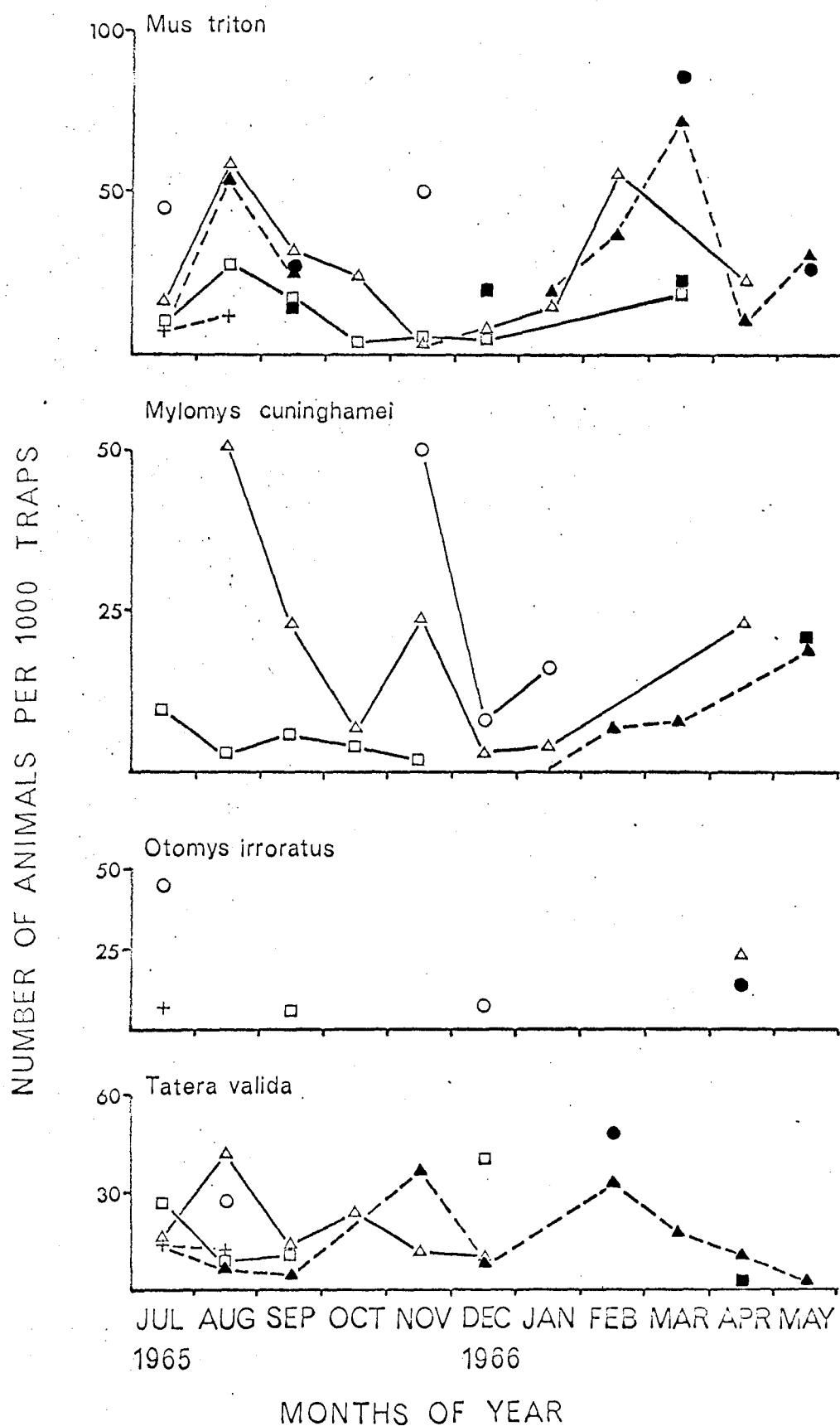


Fig. 12. Burnt and unburnt areas, 5th July 1965, two days after burning. In the foreground is charred stubble thick with ash, of the Imperata and Themeda communities. The line of thick stubble traversing the centre of the picture marks the Cymbopogon community. Note straight boundaries of unburnt areas, and trap line at upper right hand corner of burnt area.

Fig. 13. Boundary of burnt and unburnt areas, 5th July 1965, two days after burning. The abrupt transition between the two areas is clearly illustrated.



Fig. 12



Fig. 13

Fig. 14. Burnt live trap study area in August 1965.

Area in foreground, ultimately dominated by the Themeda community, showing no signs of regeneration of grasses. In the middle distance the silver-white flower heads of the Imperata community can be seen. Two trap placings of the live-trap grid are clearly marked by stakes and bundles of dried grass.

Fig. 15. Burnt Imperata community in August 1965

(picture taken same day as fig. 14).

Much of the ground is bare and the cover is still poor. Blue-green grass tussock at bottom centre is Cymbopogon afronardus.



Fig. 14



Fig. 15

Fig. 16. Burnt live trap study area (picture taken from almost same position as fig. 14), in late September 1965. The bare ground is now covered by grasses of the Themeda community, and the flower heads of Imperata have been washed away. Note the clear atmosphere, the smoke haze having been settled by the heavy rains.

Fig. 17. The burnt area in early December 1965.

Grass is very tall and thick, and is now little different from that in the unburnt areas. The Imperata community in the foreground gives way to the Themeda community in the middle distance. The bush is Capparis sp. Assistant is standing in trap line which stretches away into the distance.

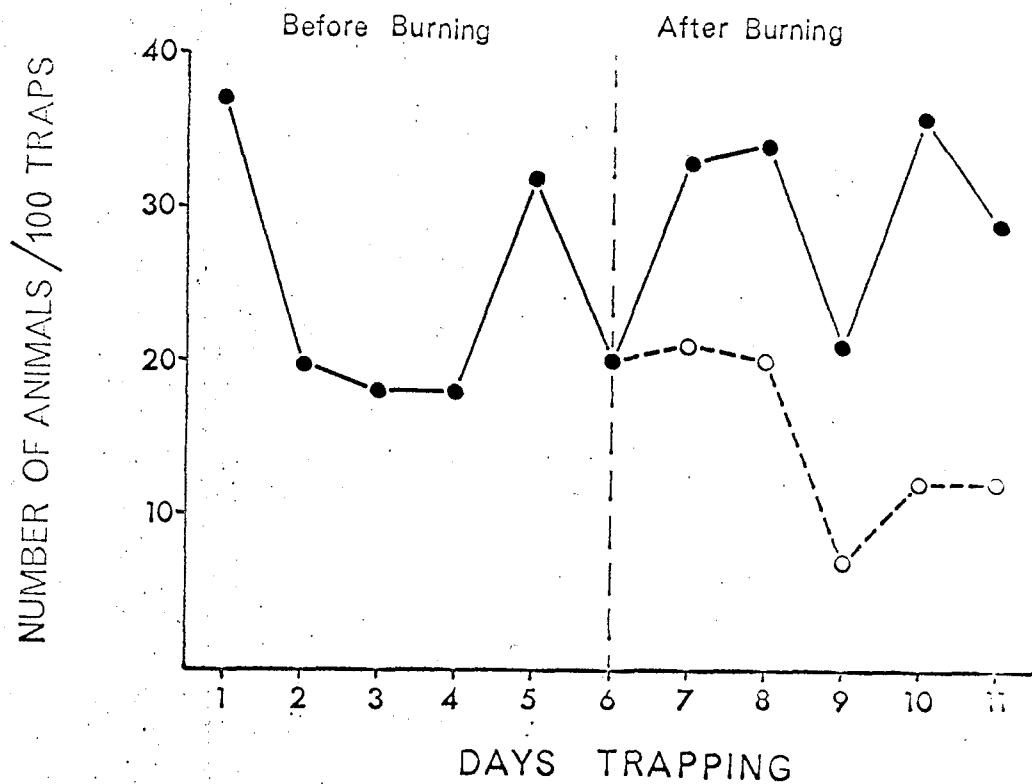


Fig. 16



Fig. 17

Fig. 18. Number of animals per 100 traps, collected each day before and after the burn on 3rd July, 1965, in the burnt areas o---o, and unburnt areas ●—●.



Arvicanthis niloticus

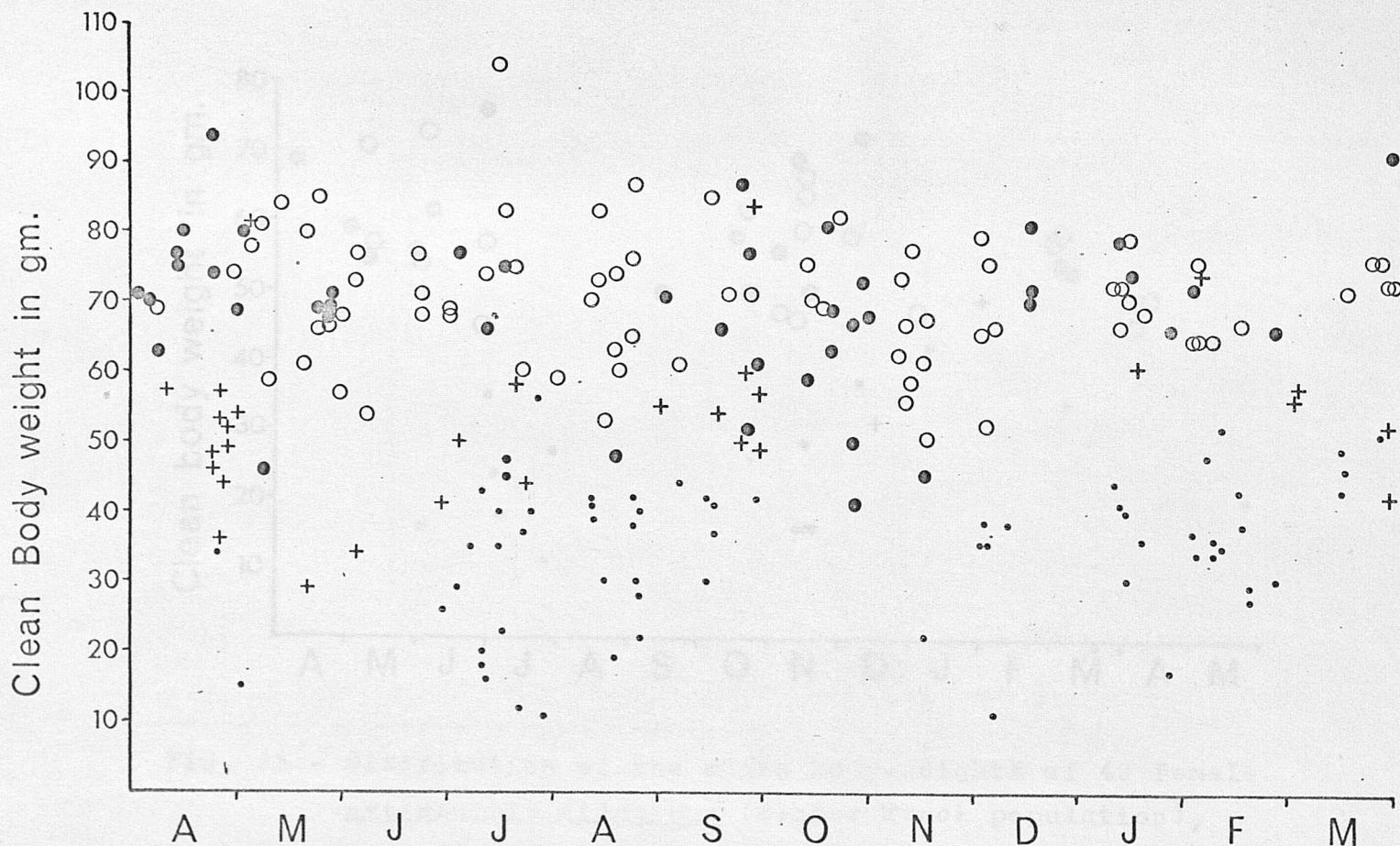


Fig. 19. - Scatter diagram of the clean body-weights of 212 females according to the days of the year. • immature animals; + mature non-parous non-pregnant animals; ○ parous non-pregnant animals; ● visibly pregnant animals.

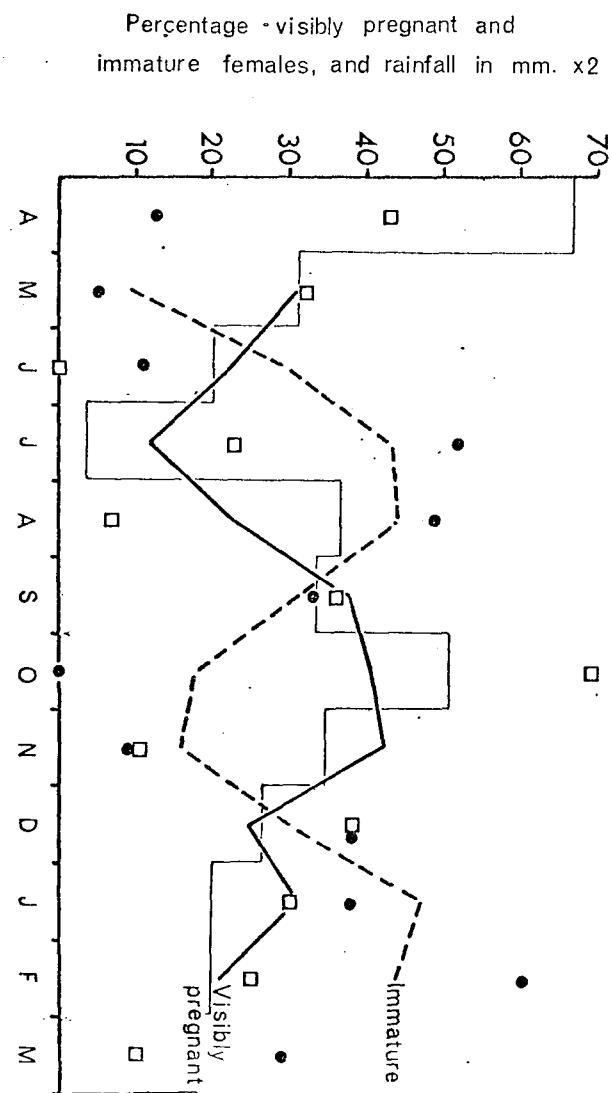


FIG. 20 - Pregnancy and number of juveniles in relation to rainfall during 1965-66. □ percentage females pregnant; ● percentage immature females; rainfall as histogram. Results have been smoothed by a 3-month sliding mean.

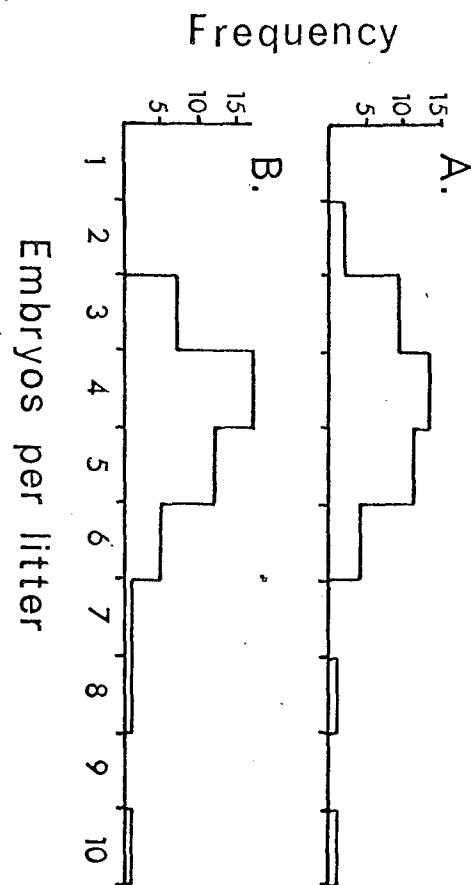


FIG. 21 - Frequency polygons illustrating size of litter as shown by the number of embryos in utero in a litter. A. - number of healthy embryos; B. - total number of implanted embryos.

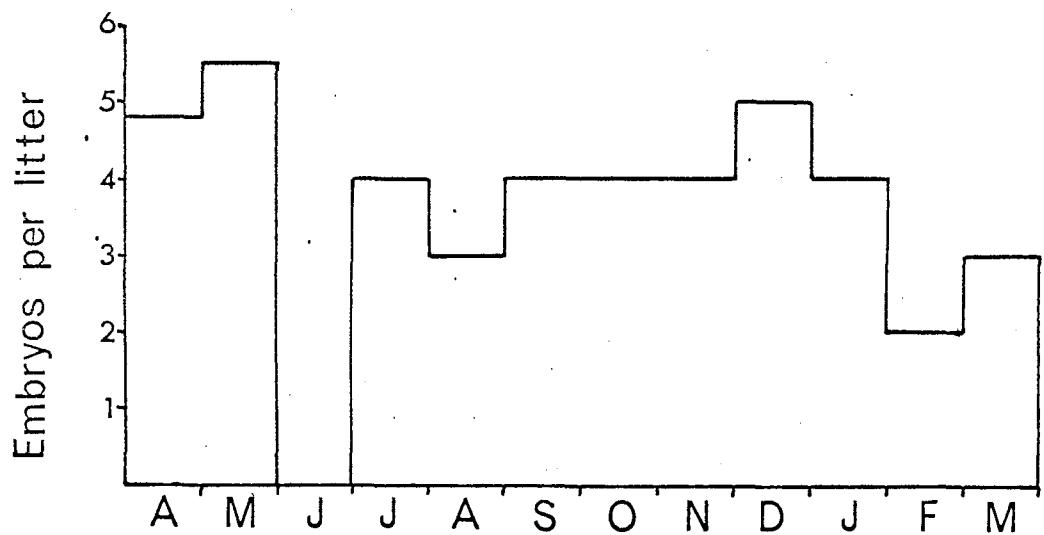


Fig. 22 - Histogram of the mean number of healthy embryos per litter according to the month.

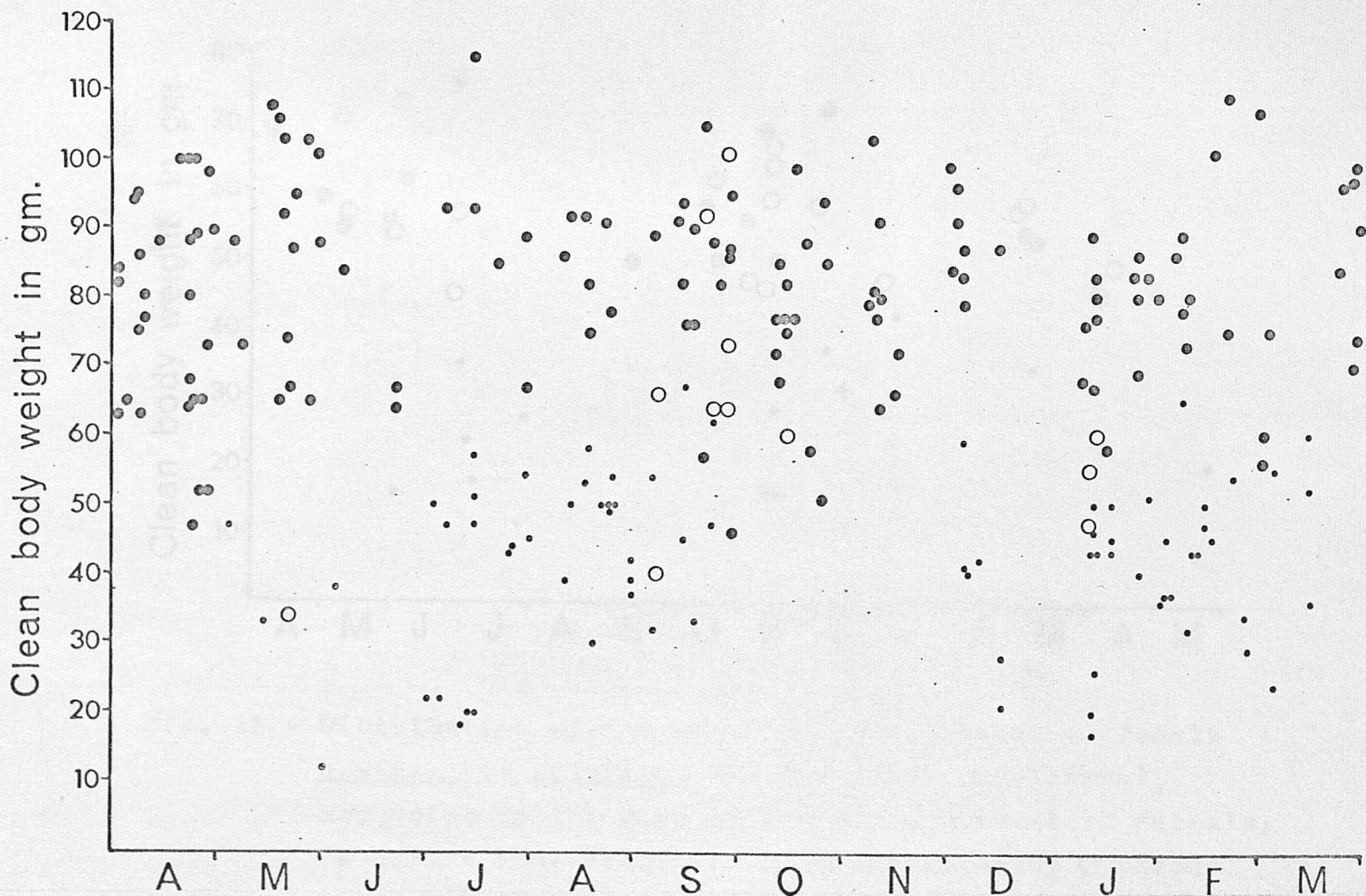


Fig. 23 - Scatter diagram of the clean body-weights of 226 male *Arvicanthis niloticus* according to the days of the year. • sperm rating (0); \circ sperm rating $(\frac{1}{4})$ and $(\frac{1}{2})$; • sperm ratings $(\frac{3}{4})$ and (1).

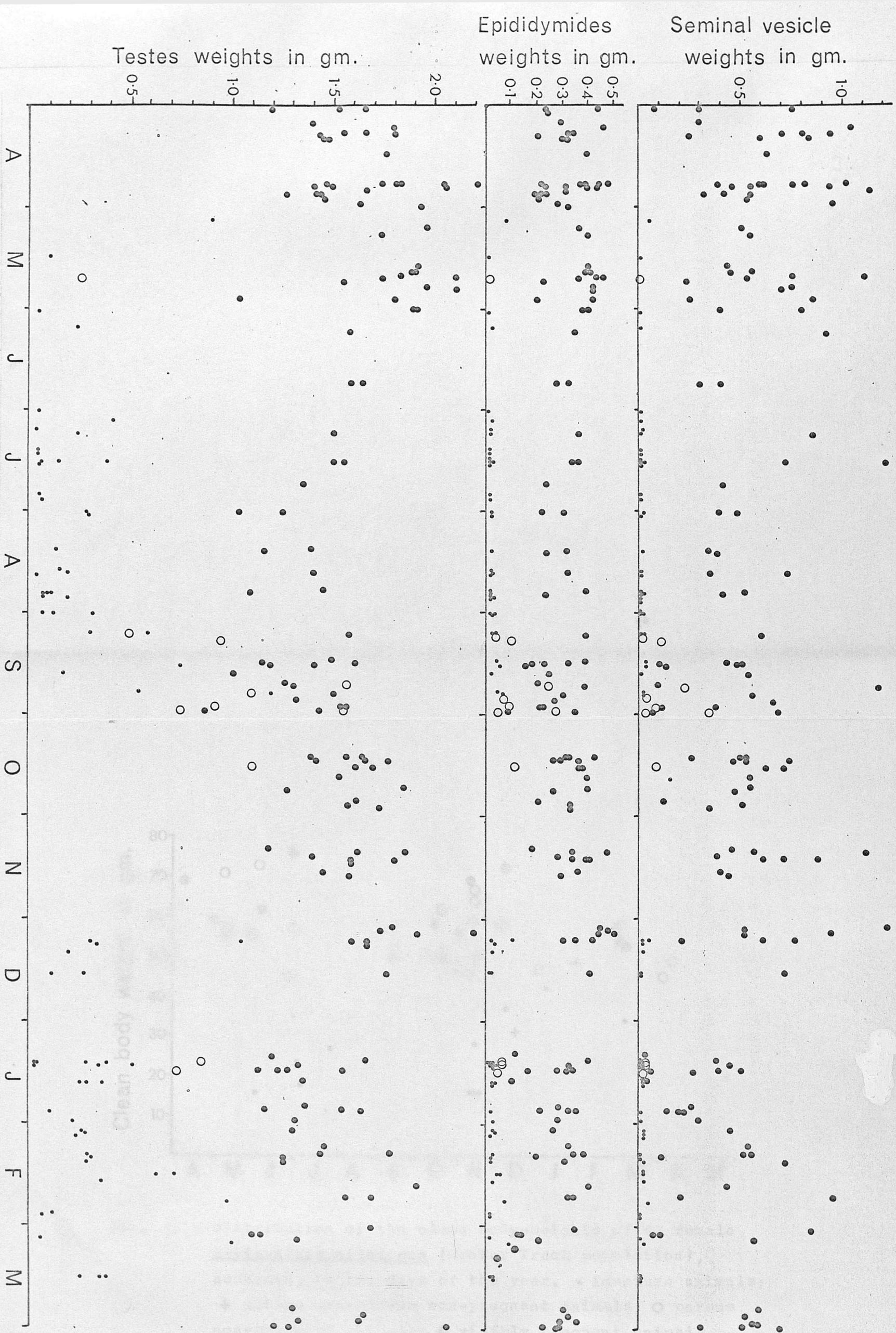


Fig. 24.—Distribution of the testes, epididymides, and seminal vesicle weights throughout the year.

• sperm rating (○); ○ sperm ratings ($\frac{1}{4}$) and ($\frac{1}{2}$); ● sperm ratings ($\frac{3}{4}$) and (1).

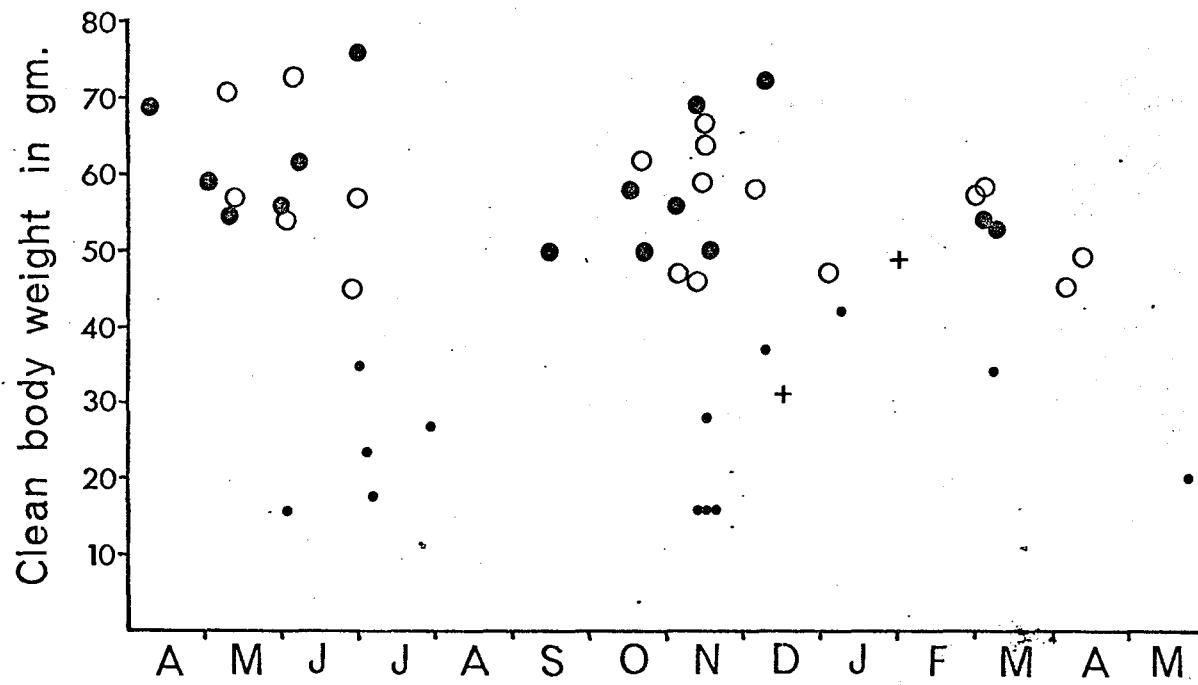


Fig. 25 - Distribution of the clean body-weights of 43 female *Aryicanthis niloticus* (Crater Track population), according to the days of the year. • immature animals; + nature non-parous non-pregnant animals; O parous non-pregnant animals; • visibly pregnant animals.

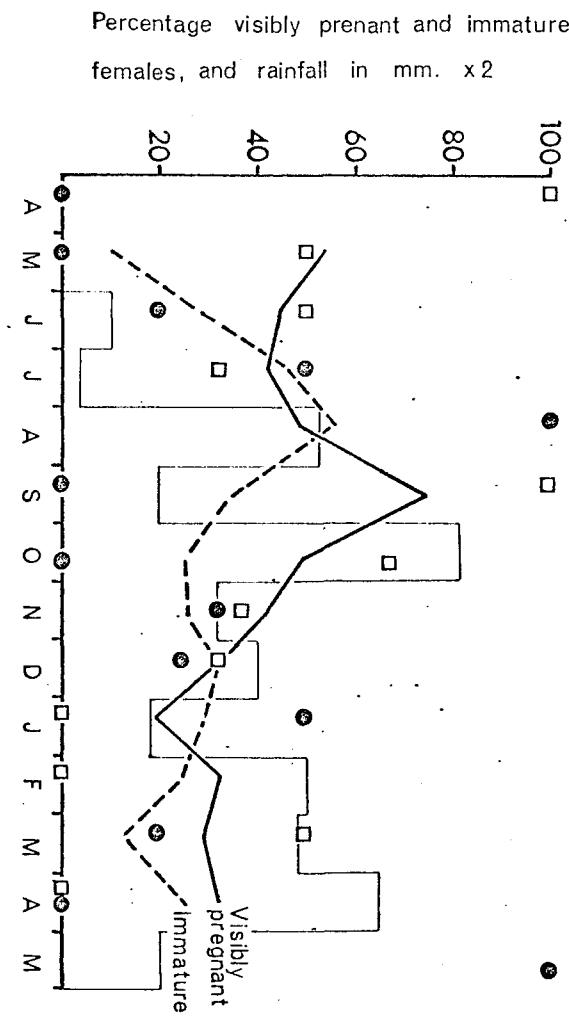


Fig. 26 - Pregnancy and number of juveniles in relation to rainfall during 1965-66. □ percentage visibly pregnant; ● percentage immature females; rainfall as histogram. Results have been smoothed by a 3-month sliding mean.

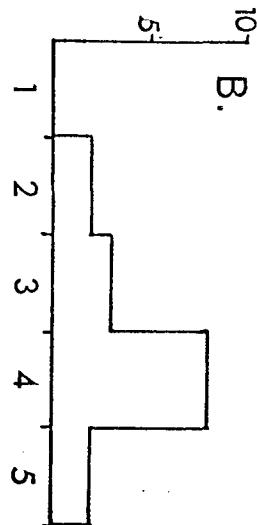
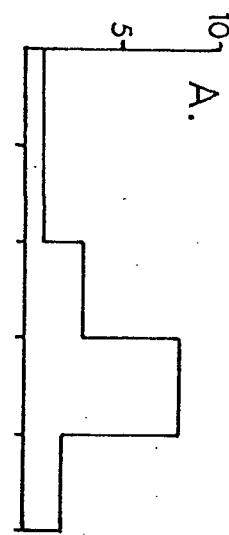


Fig. 27 - Frequency polygons illustrating size of litter as shown by A - number of healthy embryos, and B - total number of embryos in utero in a litter.

Fig. 27 - Frequency polygons illustrating size of litter as shown by A - number of healthy embryos, and B - total number of embryos in utero in a litter.

Clean body weight in gm.

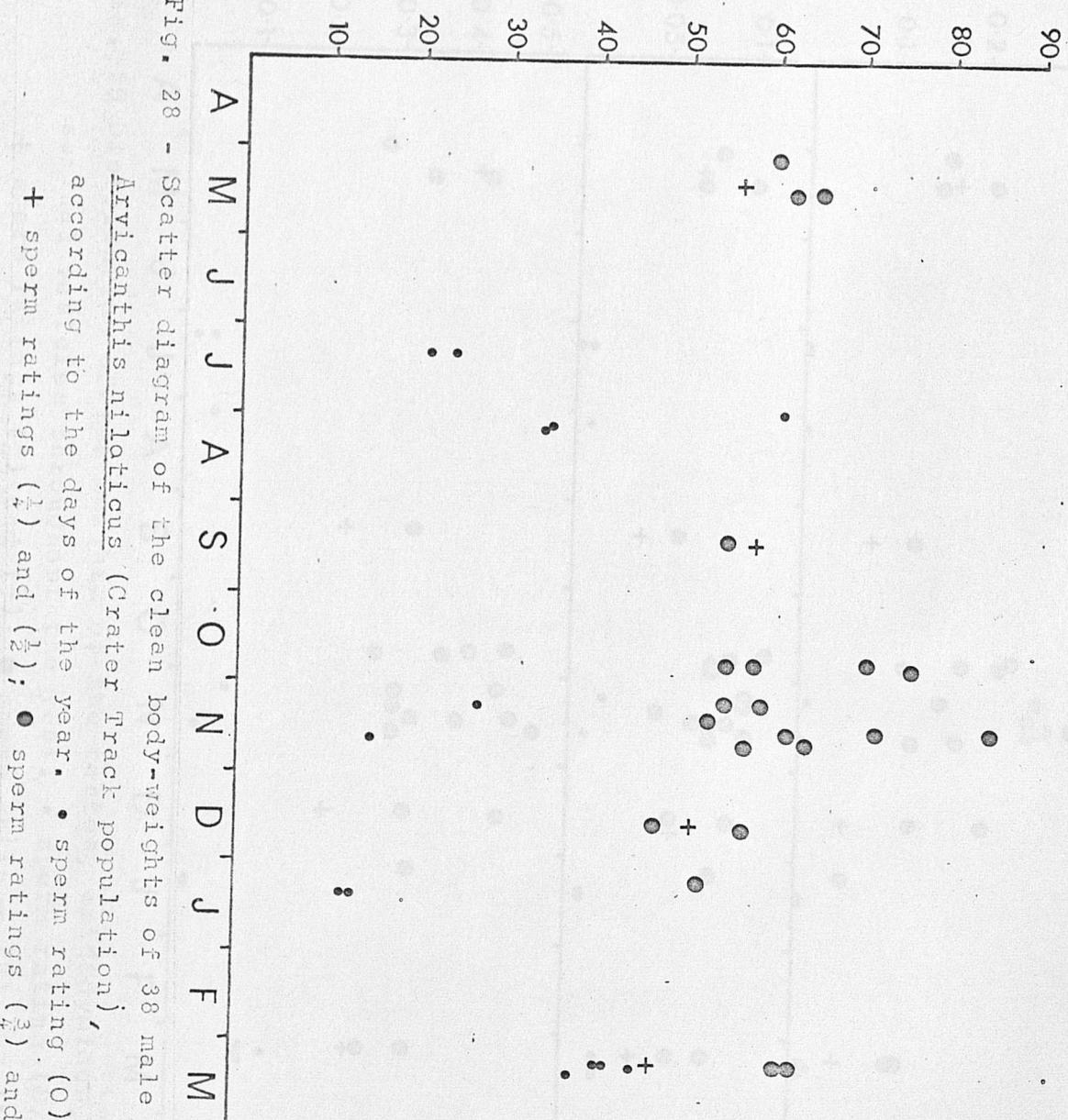


Fig. 28 - Scatter diagram of the clean body-weights of 38 male Arvicanthis niloticus (Crater Track population), according to the days of the year. • sperm rating (0); + sperm ratings ($\frac{1}{2}$) and ($\frac{1}{2}$); ● sperm ratings ($\frac{3}{4}$) and (1).

Weights in gm.

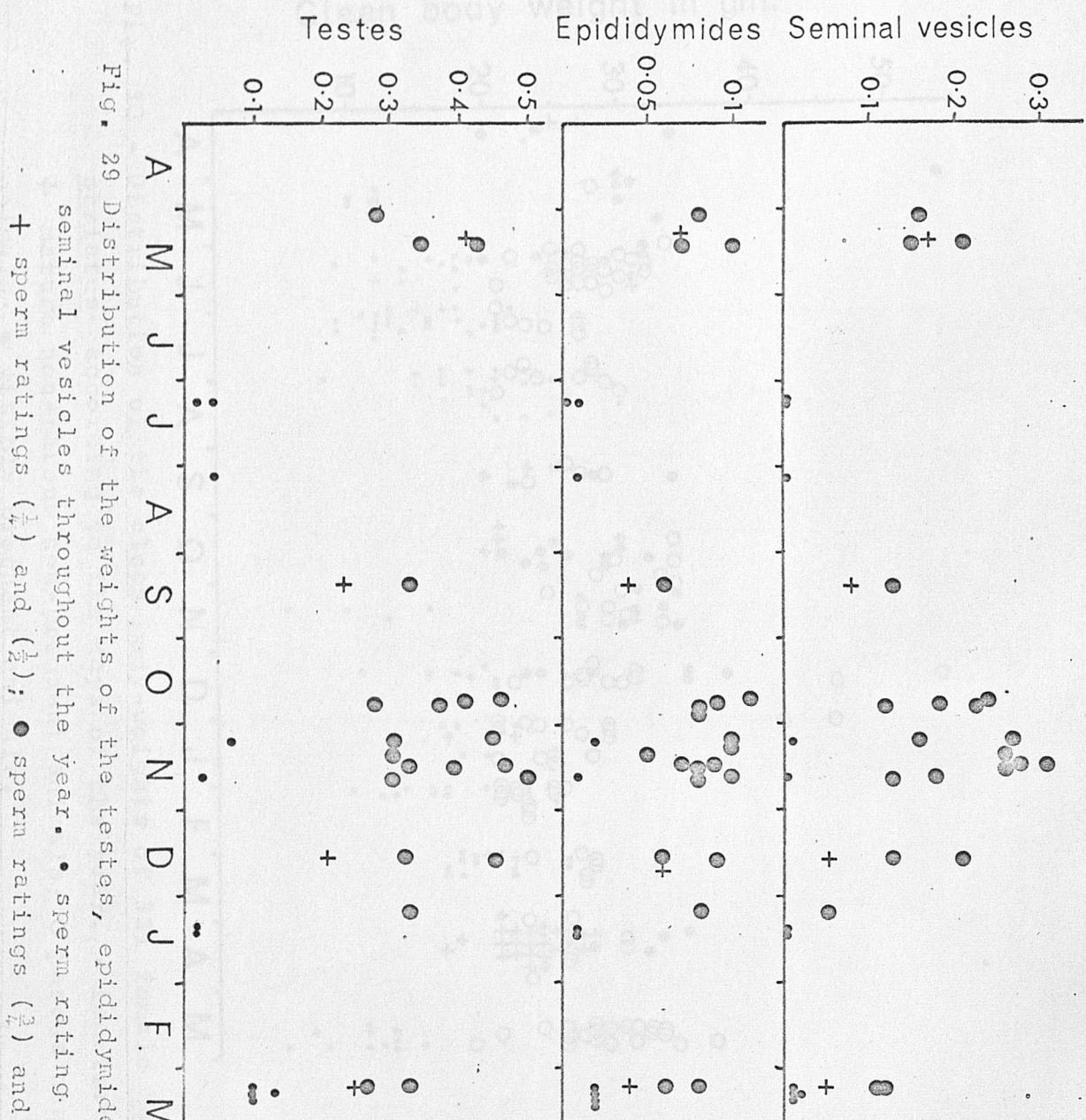


FIG. 29 Distribution of the weights of the testes, epididymides, and seminal vesicles throughout the year. ● sperm ratings (0); + sperm ratings ($\frac{1}{4}$) and ($\frac{1}{2}$); ○ sperm ratings ($\frac{3}{4}$) and (1).

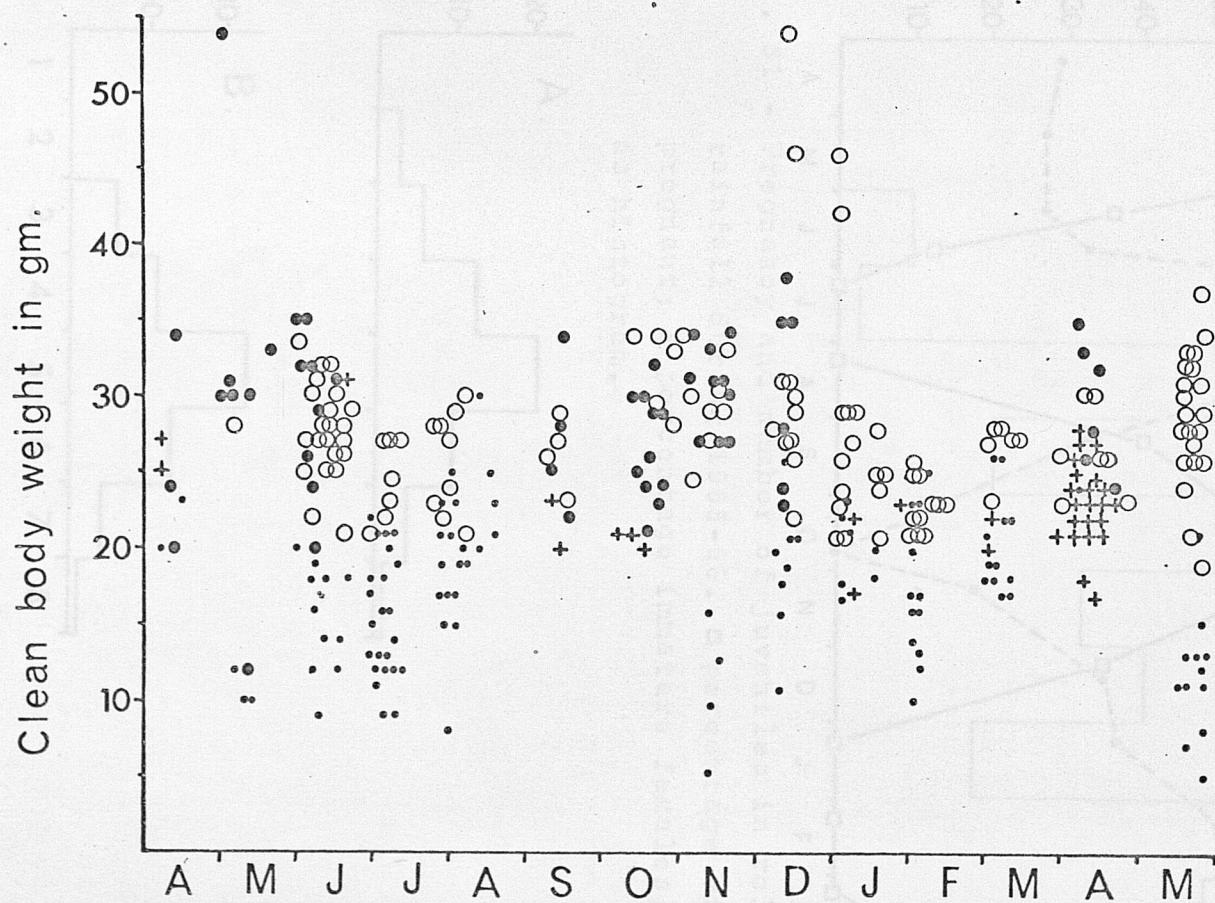


Fig. 30 - Distribution of the clean body-weights of 331 female Lemniscomys striatus according to the days of the year. • immature animals; + mature non-parous non-pregnant animals; ○ parous non-pregnant animals; ● visibly pregnant animals.

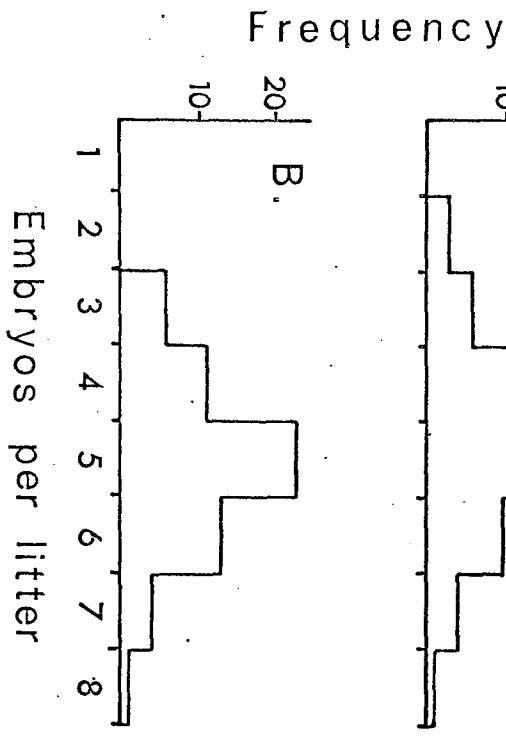
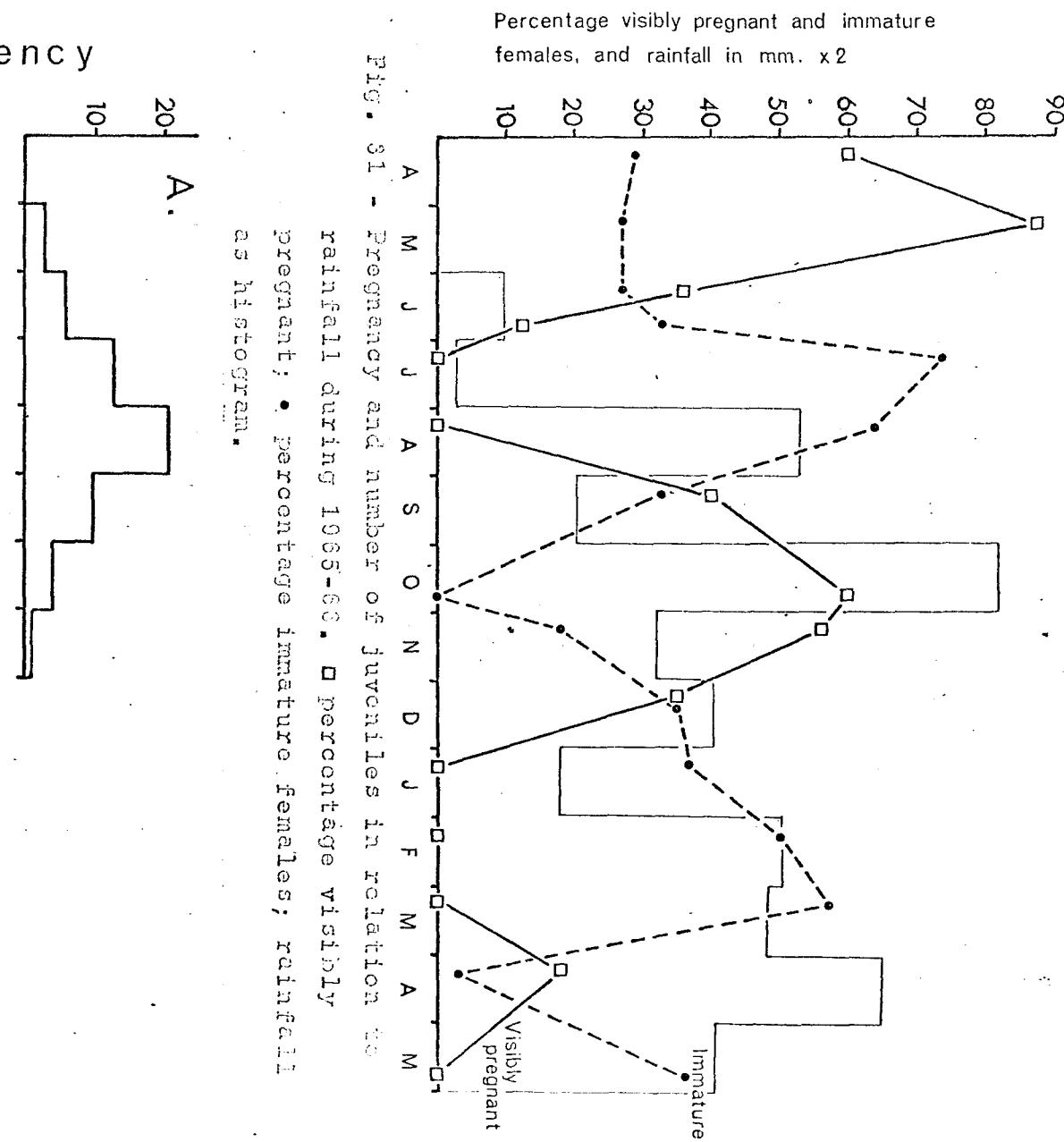


FIG. 32 - Frequency polygons illustrating size of litter as shown by A. - number of live embryos, and B. - total number of embryos in utero in a litter.

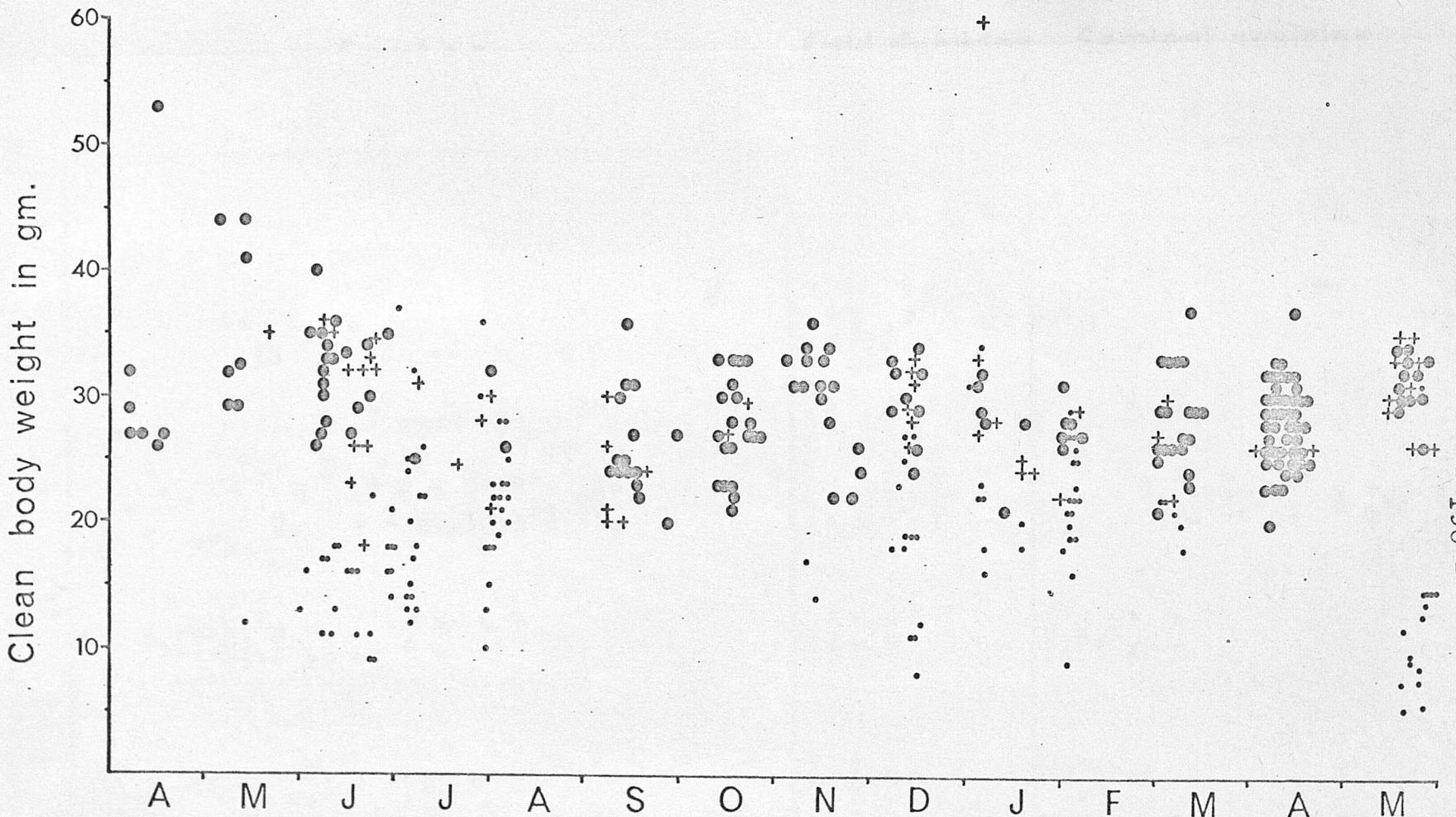


Fig. 33 - Distribution of clean body-weights of 383 male *Lemniscomys striatus* throughout the year. • sperm rating (0); + sperm rating ($\frac{1}{4}$) and ($\frac{1}{2}$); ● sperm ratings ($\frac{3}{4}$) and (1).

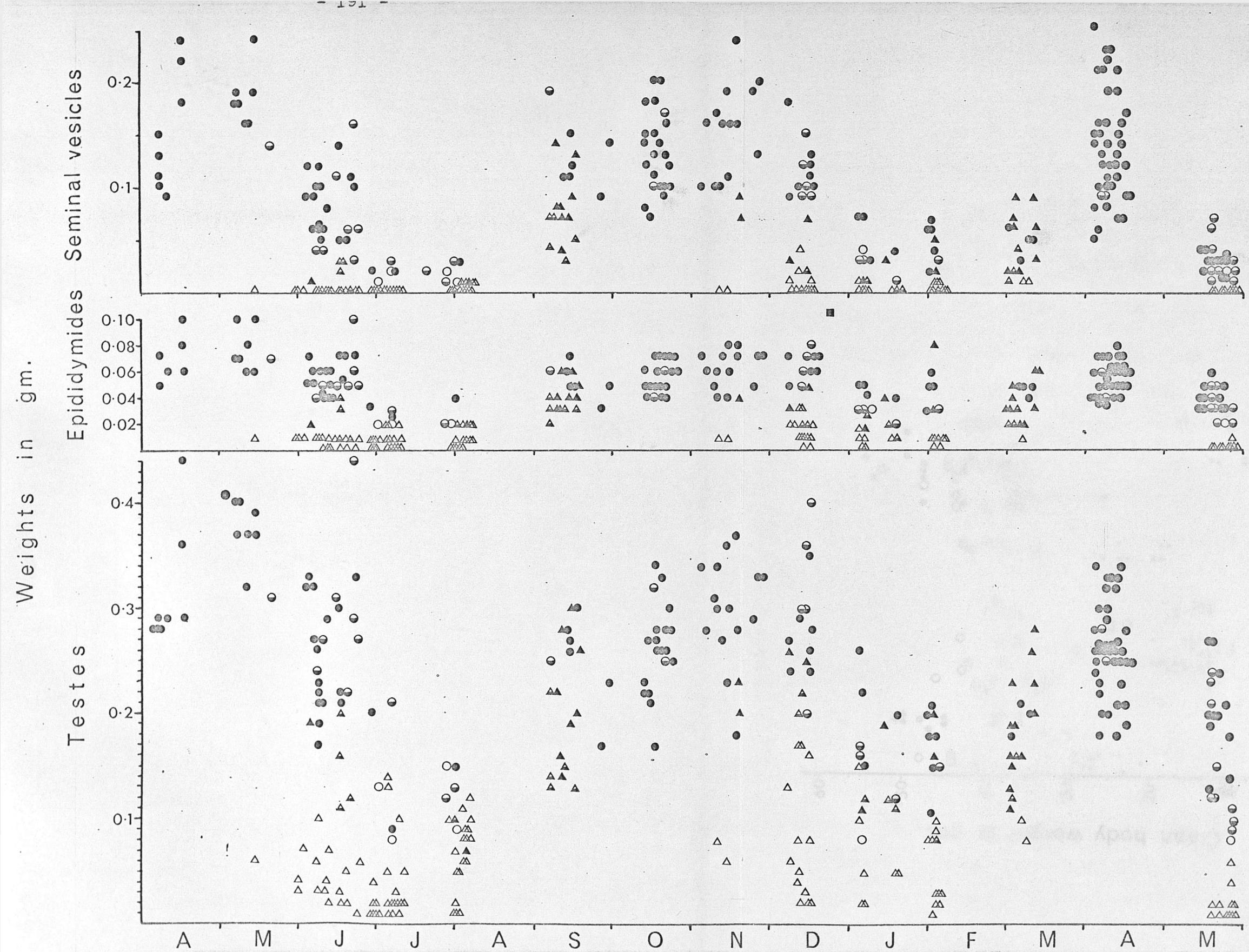


Fig. 34 - Distribution of the weights of the testes, epididymides, and seminal vesicles throughout the year. Circles represent the adult population which has passed through at least one breeding season, triangles represent the 'juvenile' population which is less than 6 months old. \circ A sperm rating (0), \triangle A sperm ratings ($\frac{1}{2}$) and ($\frac{1}{2}$), \bullet A sperm ratings ($\frac{3}{4}$) and (1).

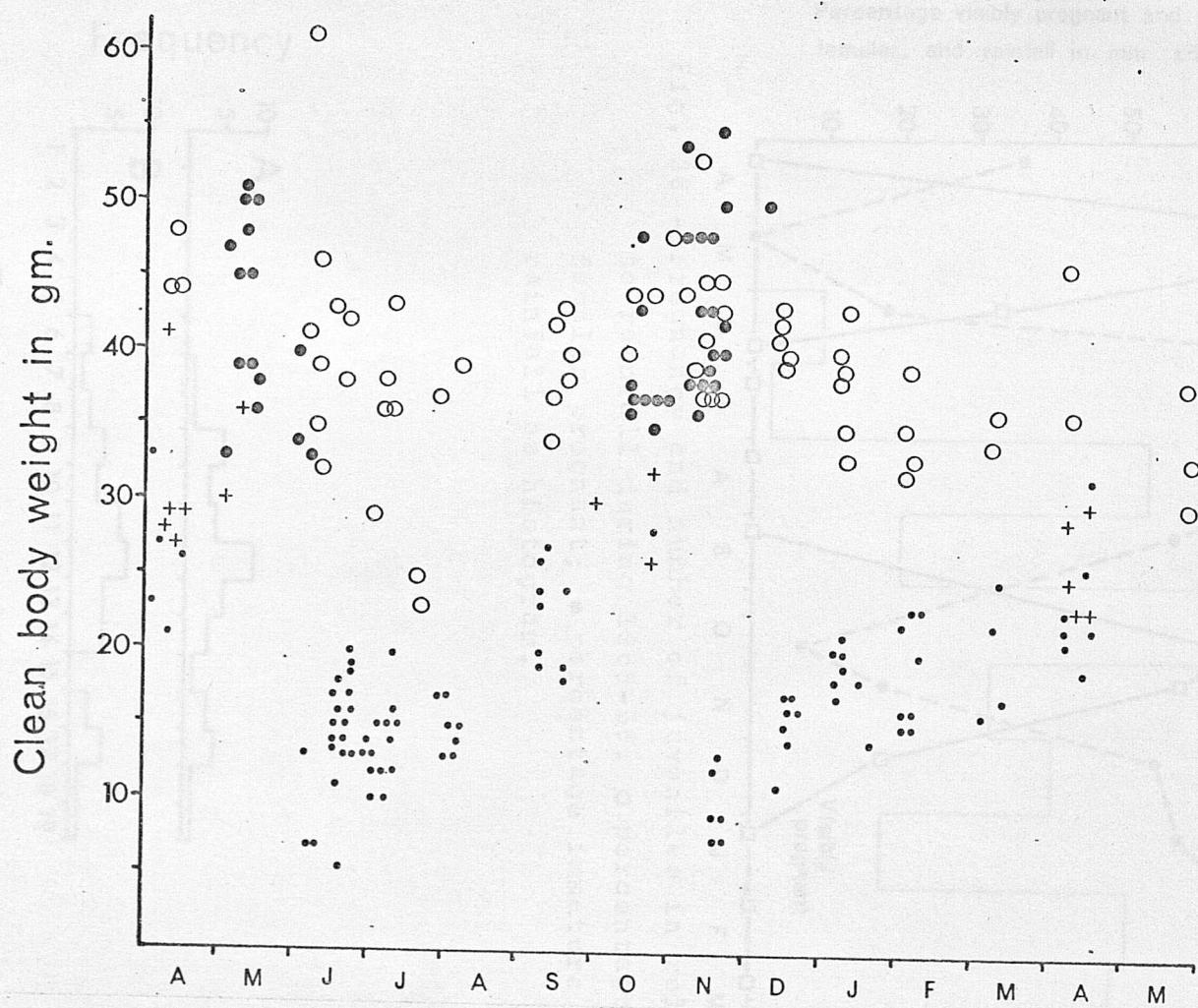


Fig. 35 - Distribution of the clean body-weights of 211 female Mastomys natalensis according to the day of the year. • immature animals; + mature non-parous non-pregnant animals; ○ parous non-pregnant animals; * visibly pregnant animals.

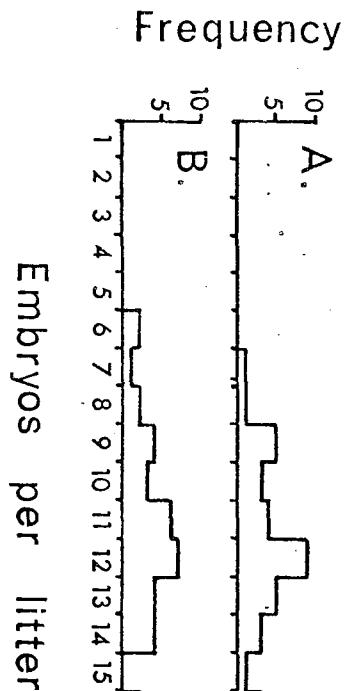
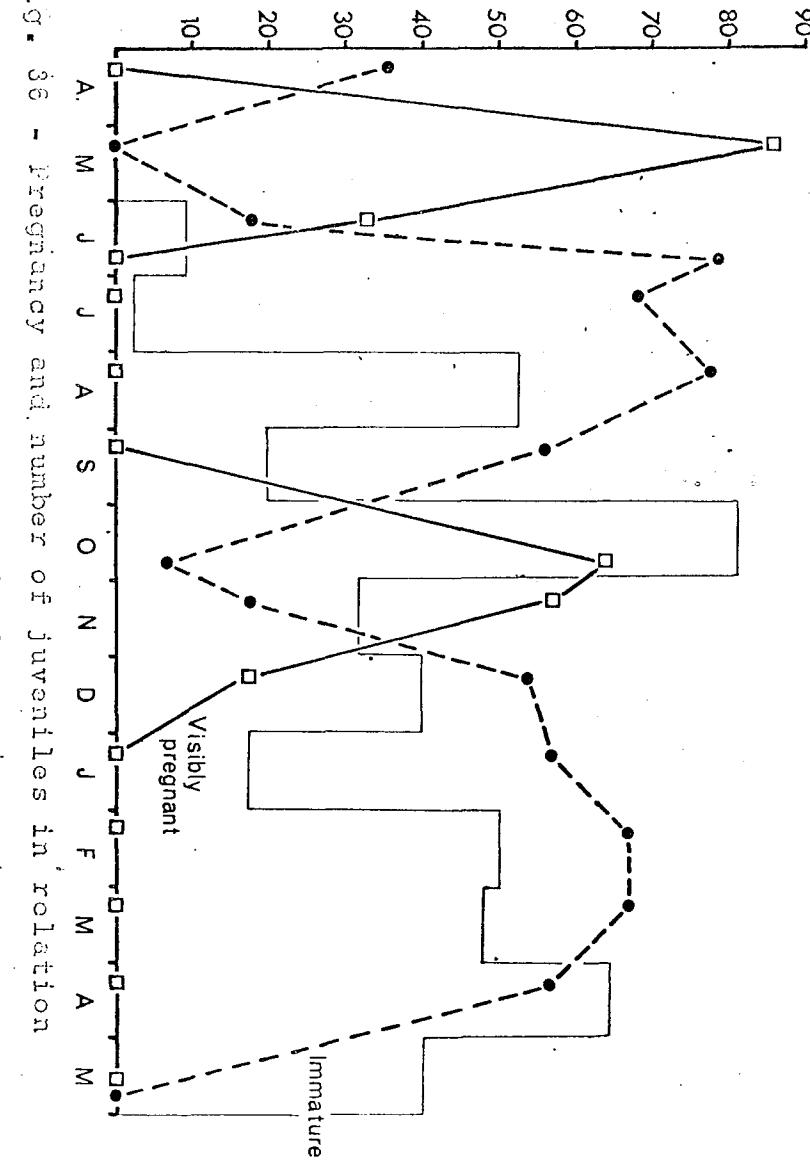


FIG. 37 - Frequency polygons illustrating size of litter as shown by A. - total number of implanted embryos,

B. - number of live embryos in utero in a litter.

Percentage visibly pregnant and immature females, and rainfall in mm. $\times 2$



Clean body weight in gm.

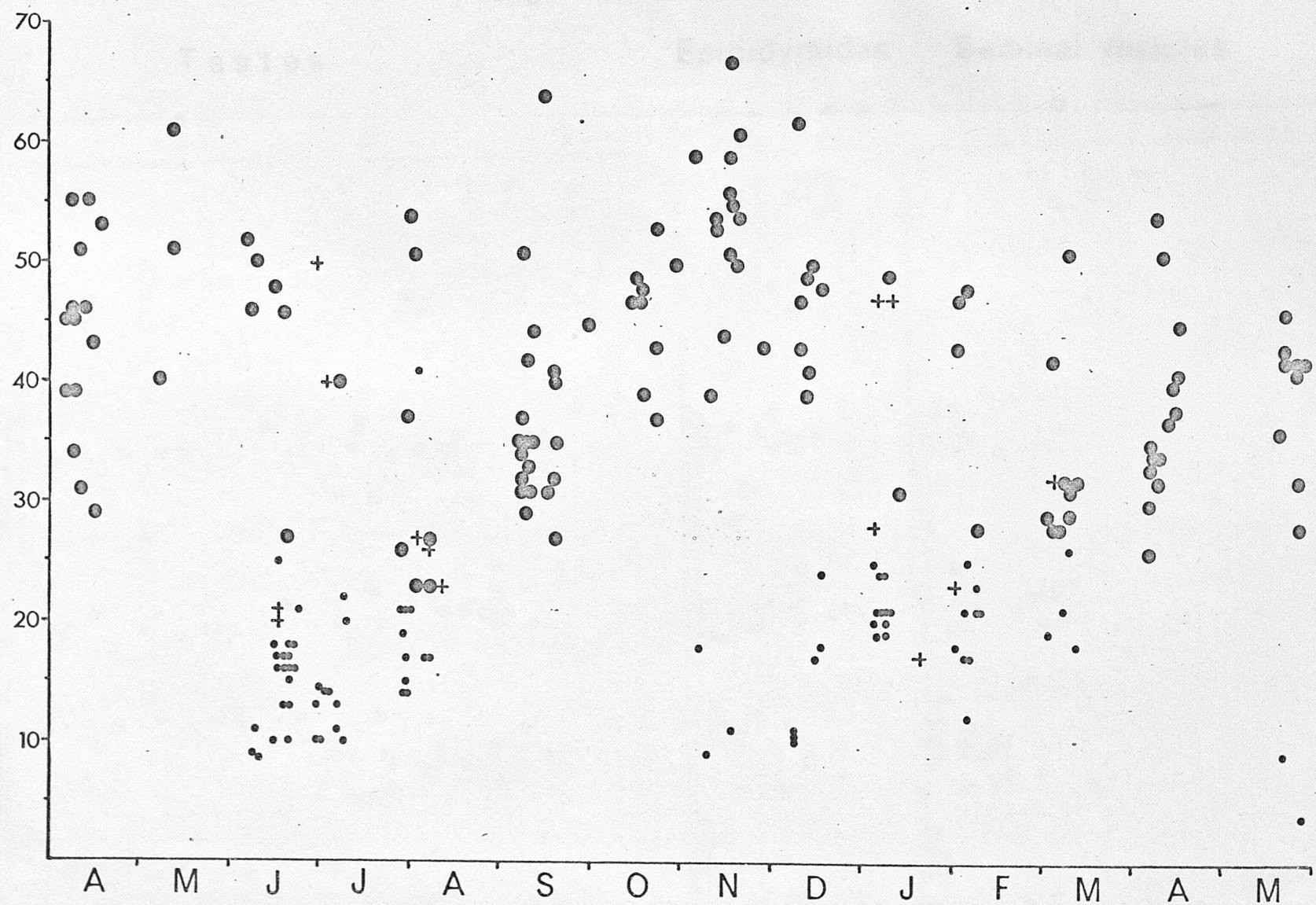


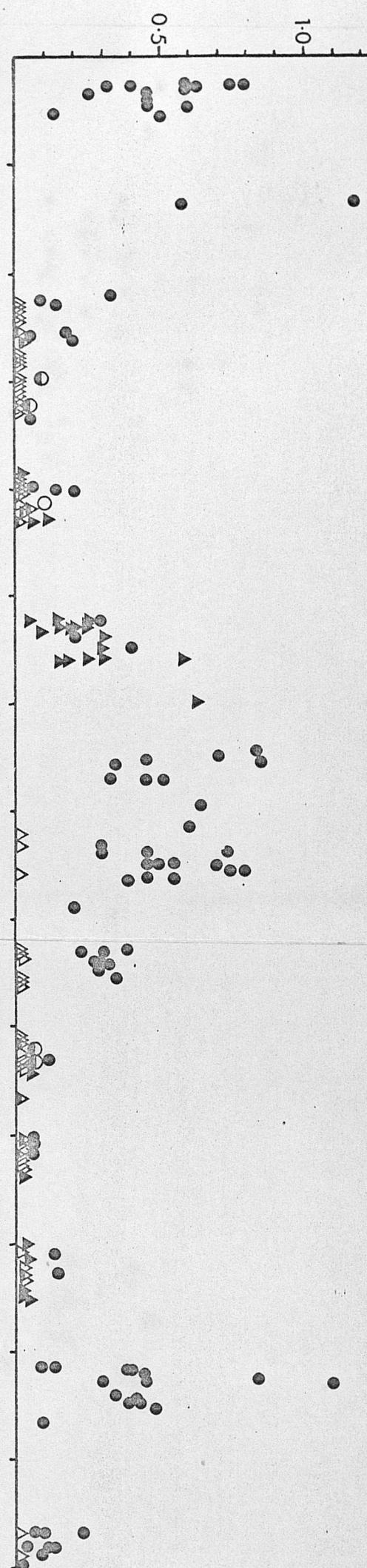
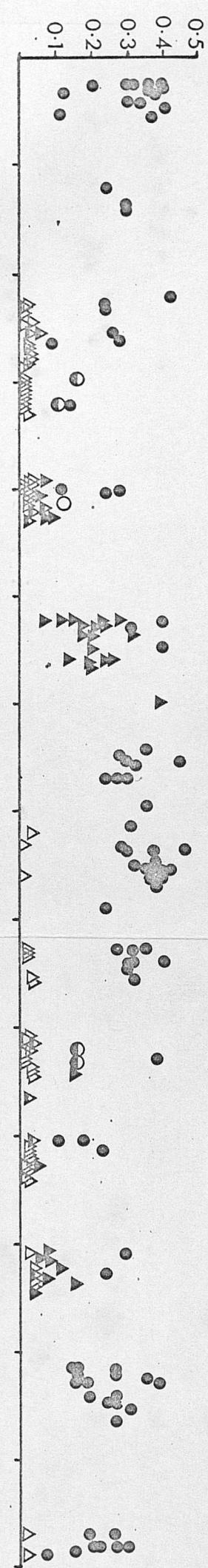
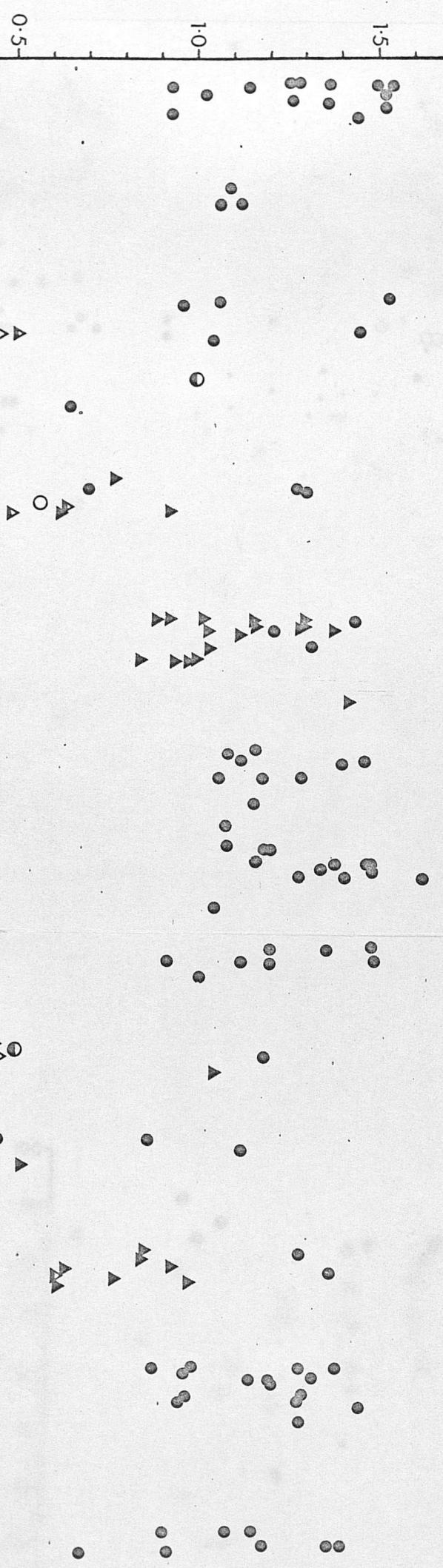
Fig. 38 - Distribution of the clean body-weights of 209 male Mastomys natalensis throughout the year. • sperm rating (0); + sperm ratings ($\frac{1}{4}$) and ($\frac{1}{2}$); ● sperm ratings ($\frac{3}{4}$) and (1).

Weights in gm.

Testes

Epididymides

Seminal vesicles



A M J J A S O N D J F M A M

Fig. 39 - Distribution of the weights of the testes, epididymides, and seminal vesicles throughout the year. Circles represent the adult population which has passed through at least one breeding season; triangles represent the 'juvenile' population which is less than 6 months old. O Asperm rating (0); \bullet Asperm ratings ($\frac{1}{4}$) and ($\frac{1}{2}$); \blacklozenge Asperm ratings ($\frac{3}{4}$) and (1).

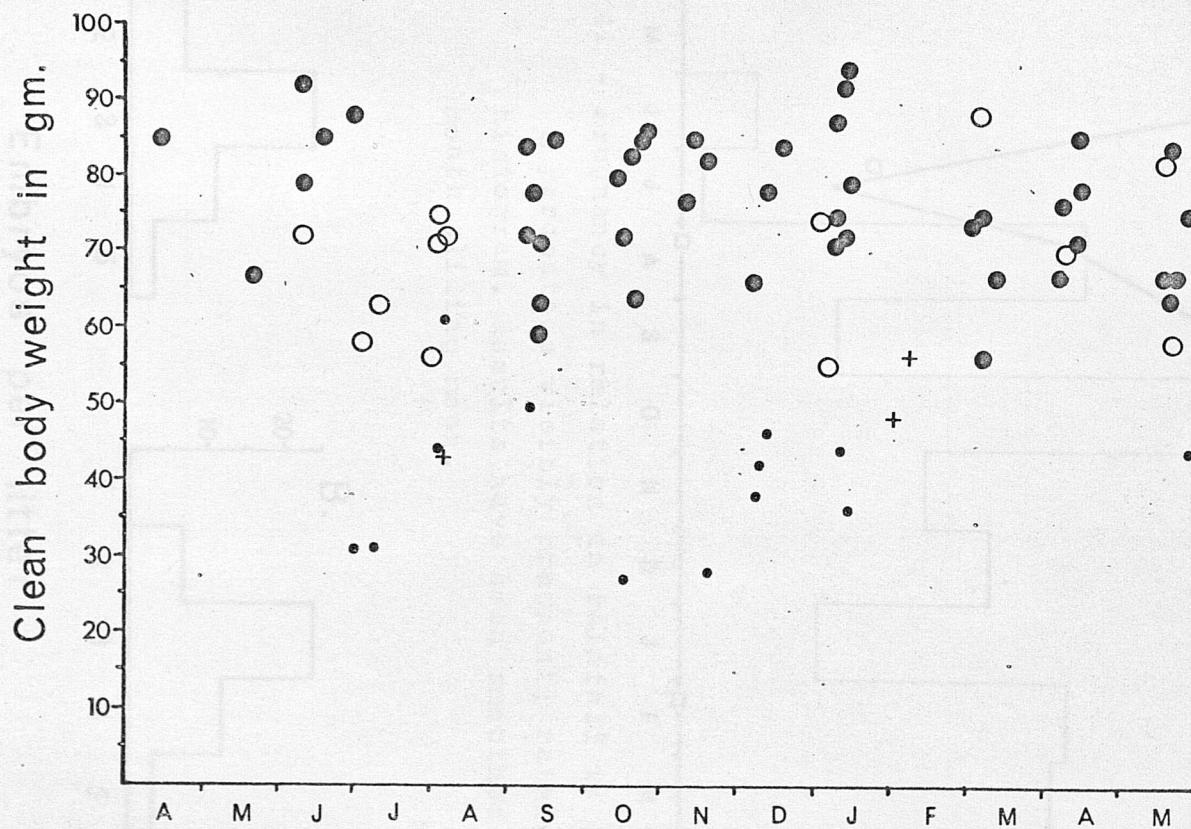


Fig. 40 - Distribution of the clean body-weights of 74 female Lophuromys sikapusi throughout the year. • immature animals; + mature non-parous non-pregnant animals; O parous non-pregnant animals; ● visibly pregnant animals.

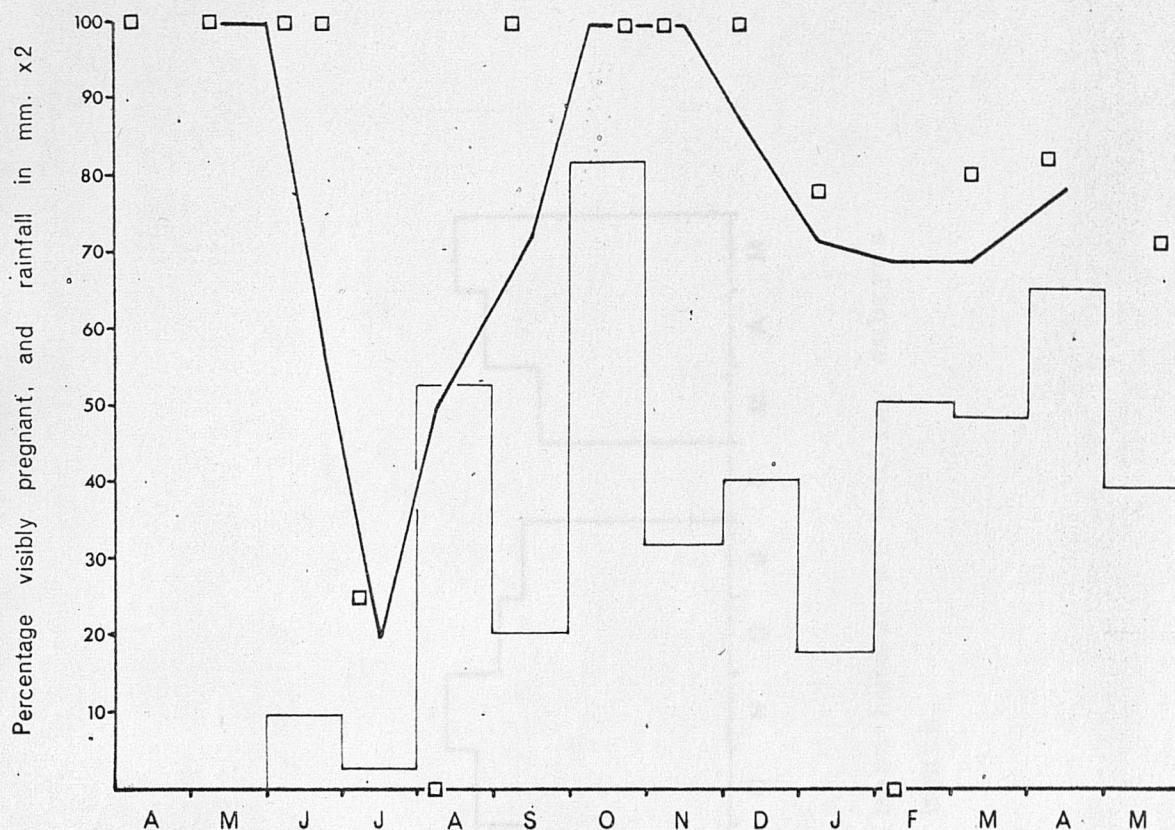


Fig. 41 - Pregnancy in relation to rainfall in 1965-66.

□ percentage visibly pregnant; rainfall as histogram. Results have been smoothed by a 3-month sliding mean.

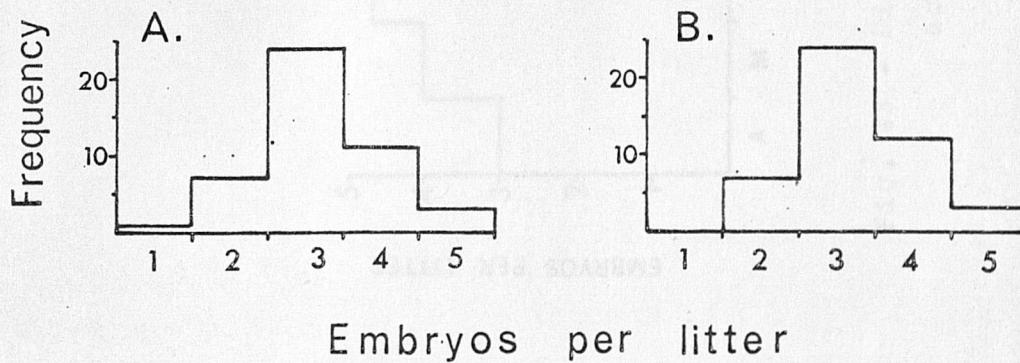


Fig. 42 - Frequency polygons illustrating size of litter as shown by A. - number of live embryos, and B. - total number of embryos in utero in a litter.

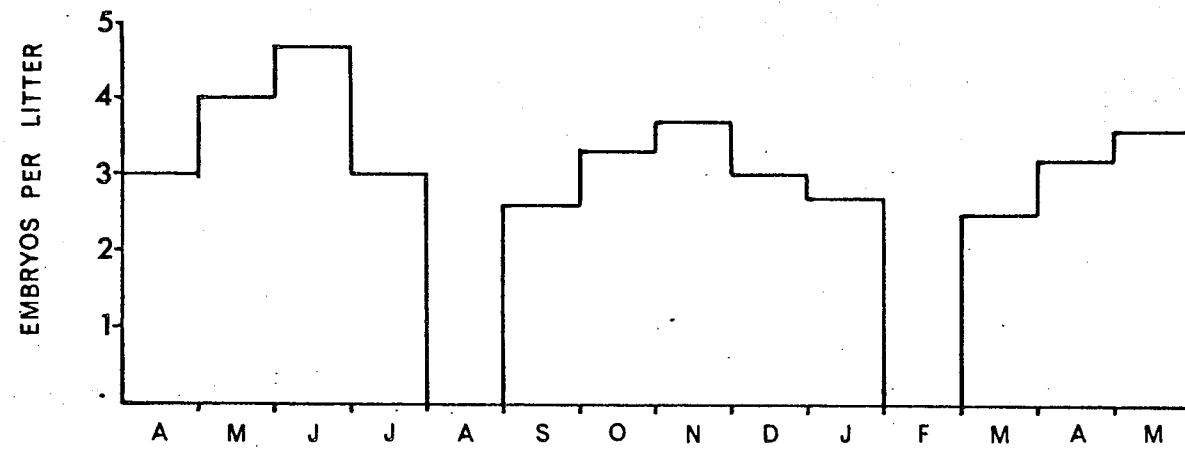


Fig. 43 - Histogram of the mean number of healthy embryos according to the month.

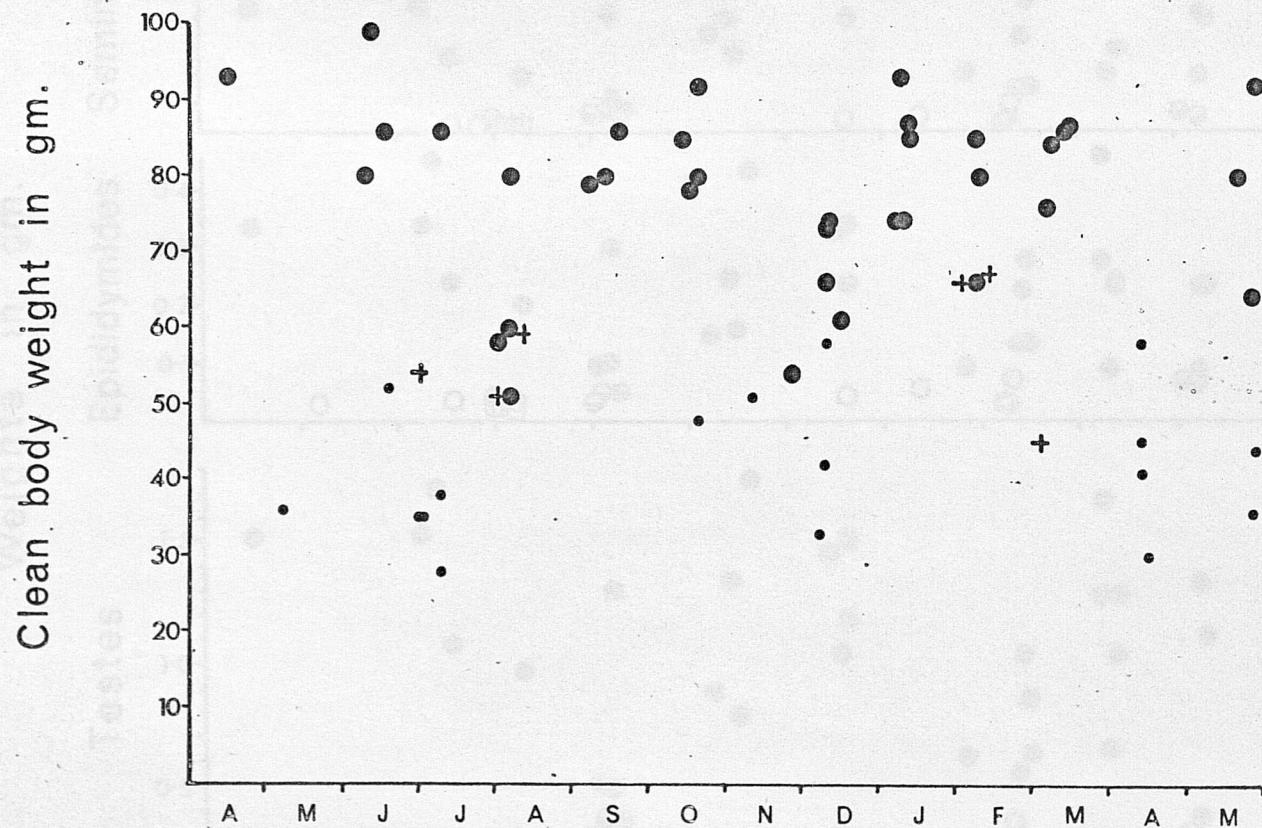


Fig. 44 - Distribution of the clean body-weights of 59 male Lophuromys sikapusi throughout the year. • sperm rating (0); + sperm ratings ($\frac{1}{4}$) and ($\frac{1}{2}$); ● sperm ratings ($\frac{3}{4}$) and (1).

Weights in gm.

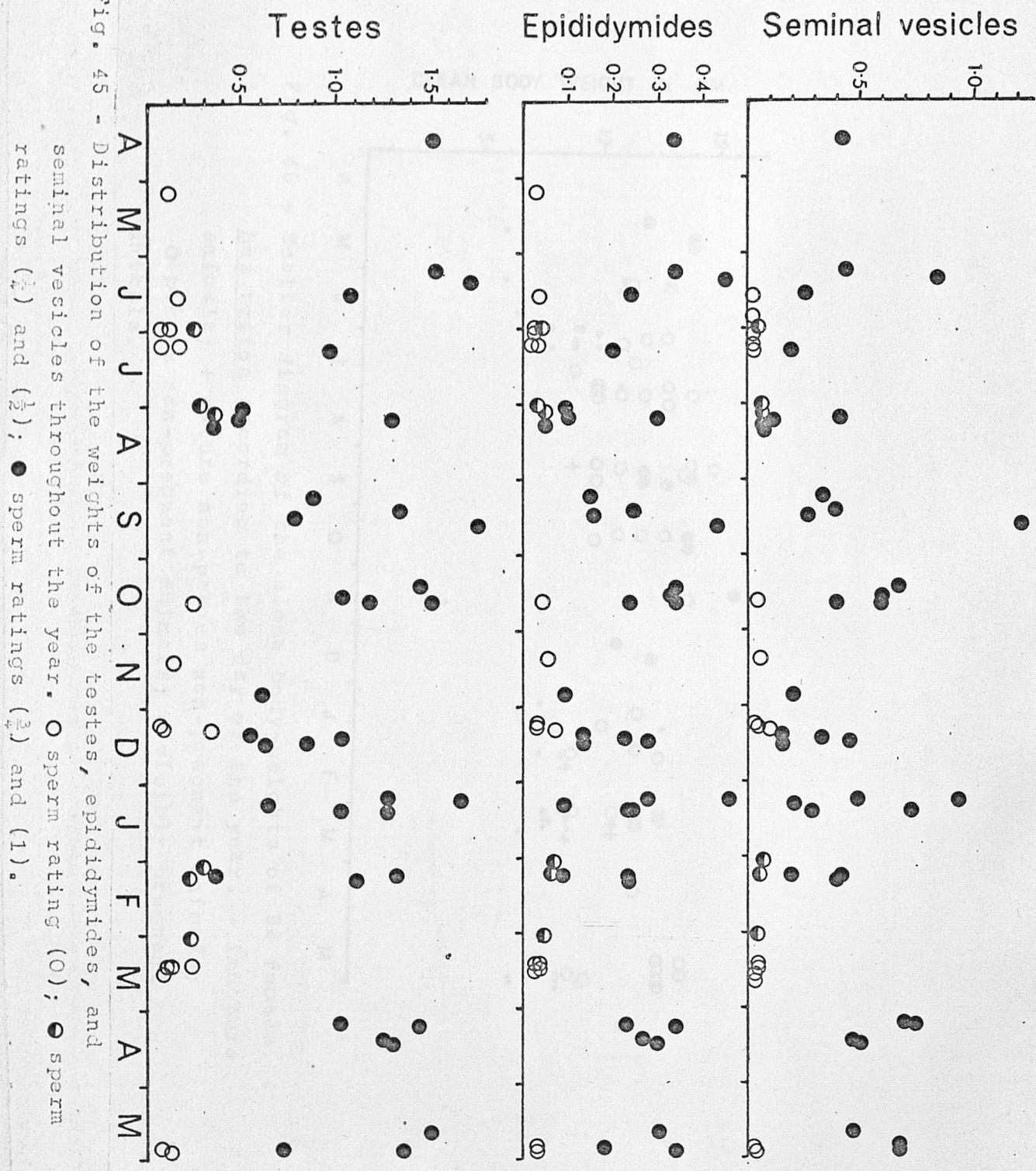


Fig. 45. - Distribution of the weights of the testes, epididymides, and seminal vesicles throughout the year. O sperm rating (0); ● sperm ratings ($\frac{1}{4}$) and ($\frac{1}{2}$); ○ sperm ratings ($\frac{3}{4}$) and (1).

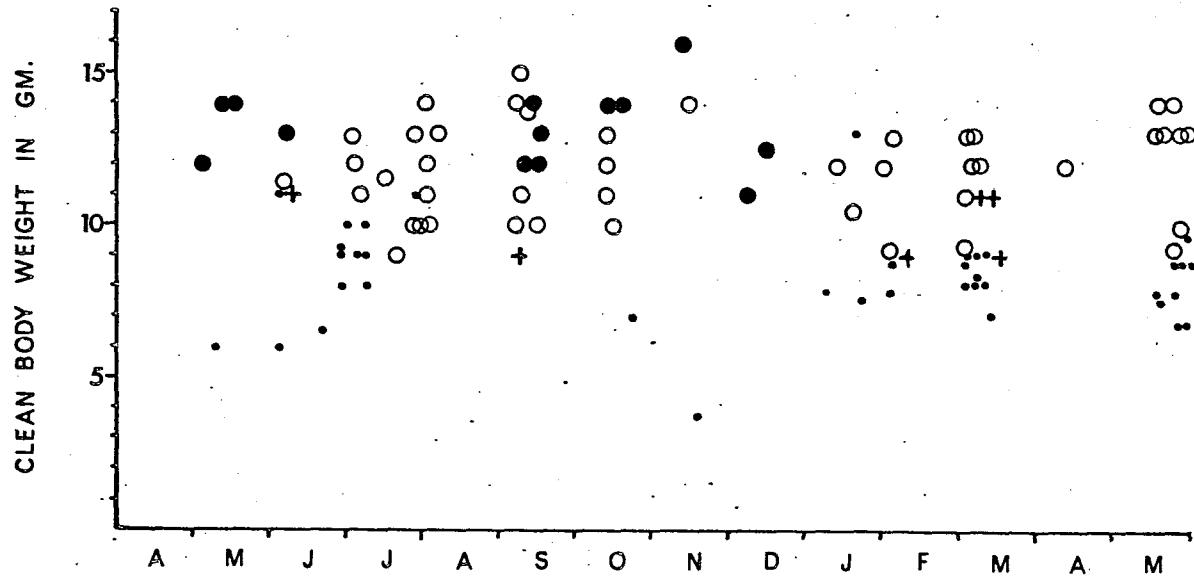


Fig. 46 - Scatter diagram of the clean body-weights of 96 female *Mus triton* according to the day of the year. • immature animals; + mature non-parous non-pregnant animals; ○ parous non-pregnant animals; ● visibly pregnant animals.

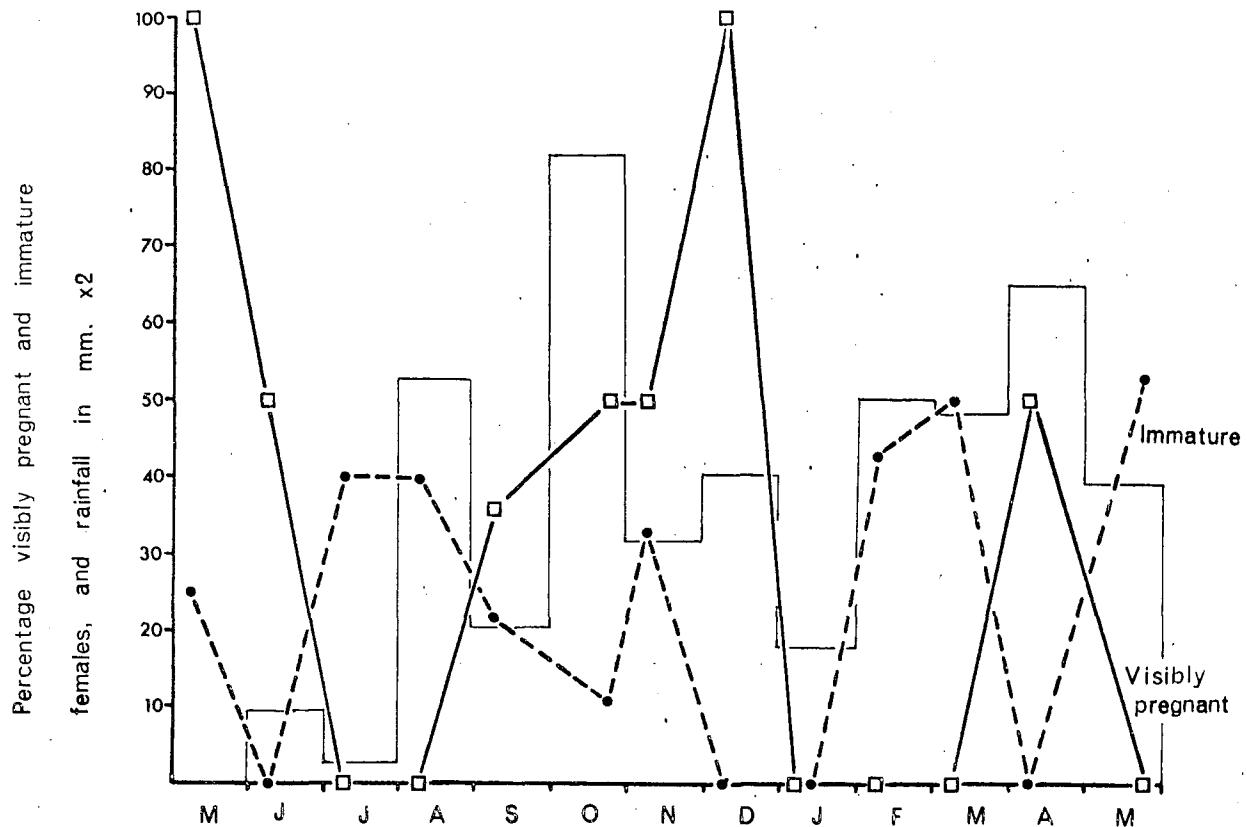


Fig. 47 - Pregnancy and number of juveniles in relation to rainfall in 1965-66. □ percentage visibly pregnant; • percentage immature females; rainfall as histogram.

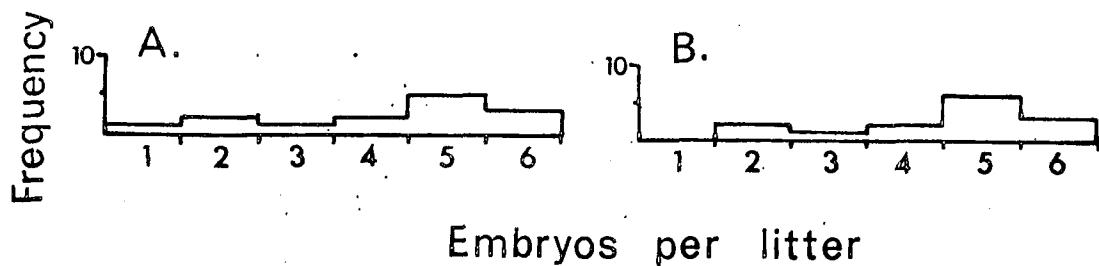


Fig. 48 - Frequency polygons illustrating size of litter as shown by A. - number of live embryos; B. - total number of embryos in utero in a litter.

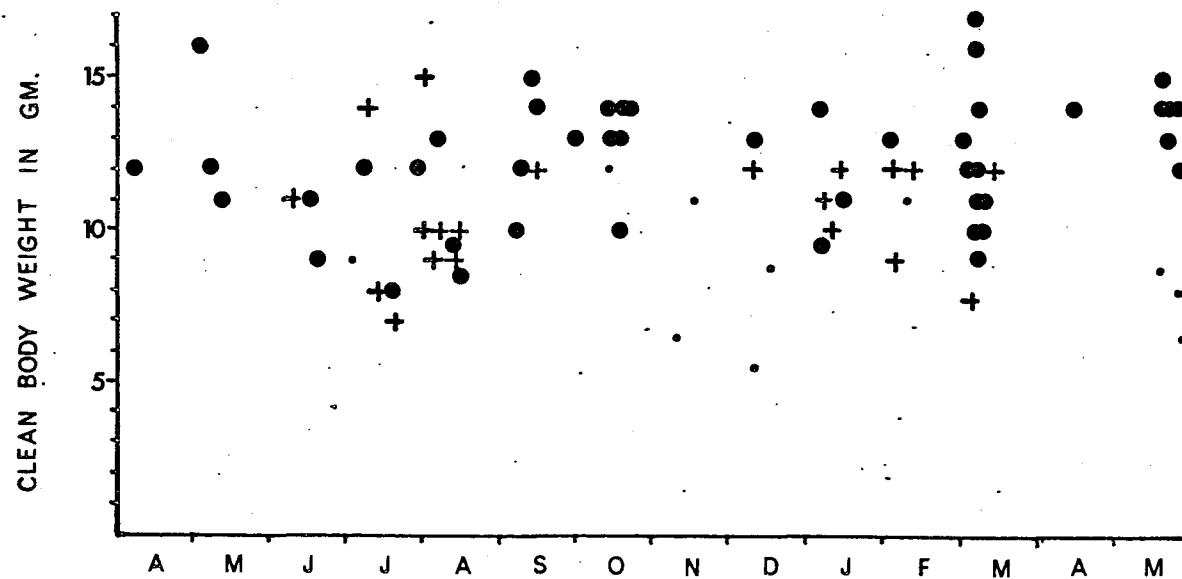
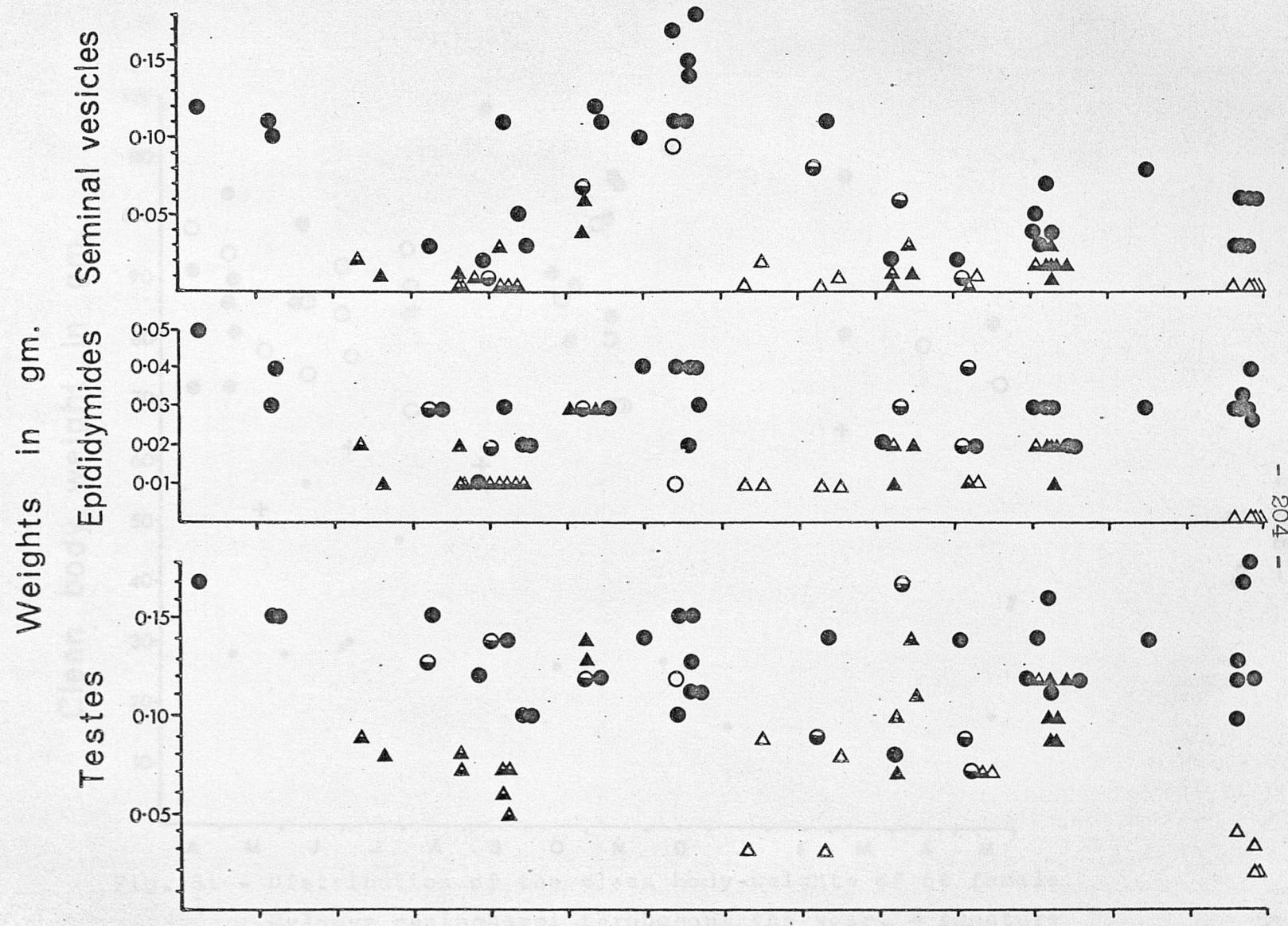


Fig. 49 - Distribution of the clean body-weights of 73 male Mus triton throughout the year. • sperm rating (0); + sperm ratings ($\frac{1}{4}$) and ($\frac{1}{2}$); ● sperm ratings ($\frac{3}{4}$) and (1).



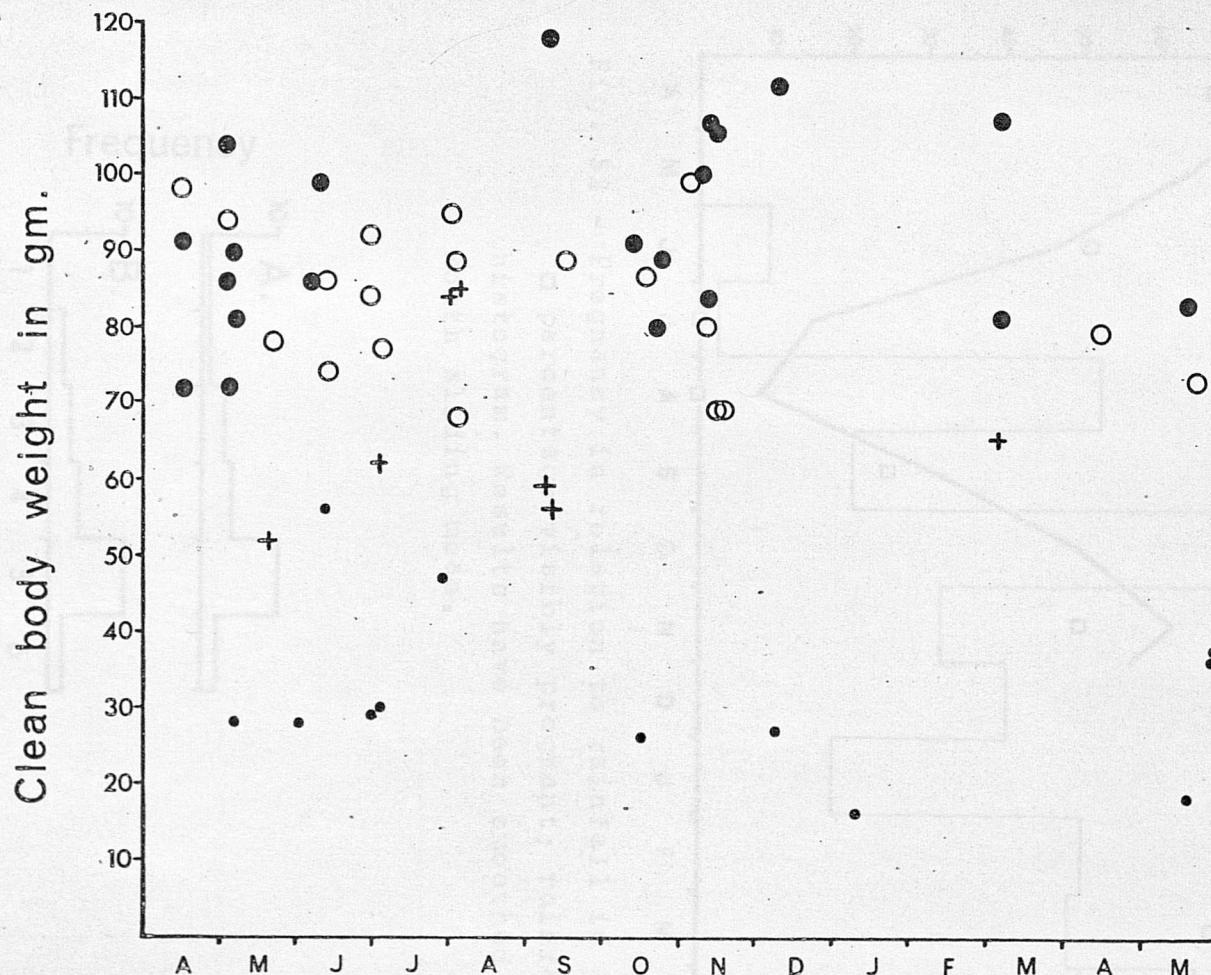


Fig. 51 - Distribution of the clean body-weights of 59 female *Mylomys cuninghamaei* throughout the year. • immature females; + mature non-parous non-pregnant animals; ○ parous non-pregnant animals; ● visibly pregnant animals.

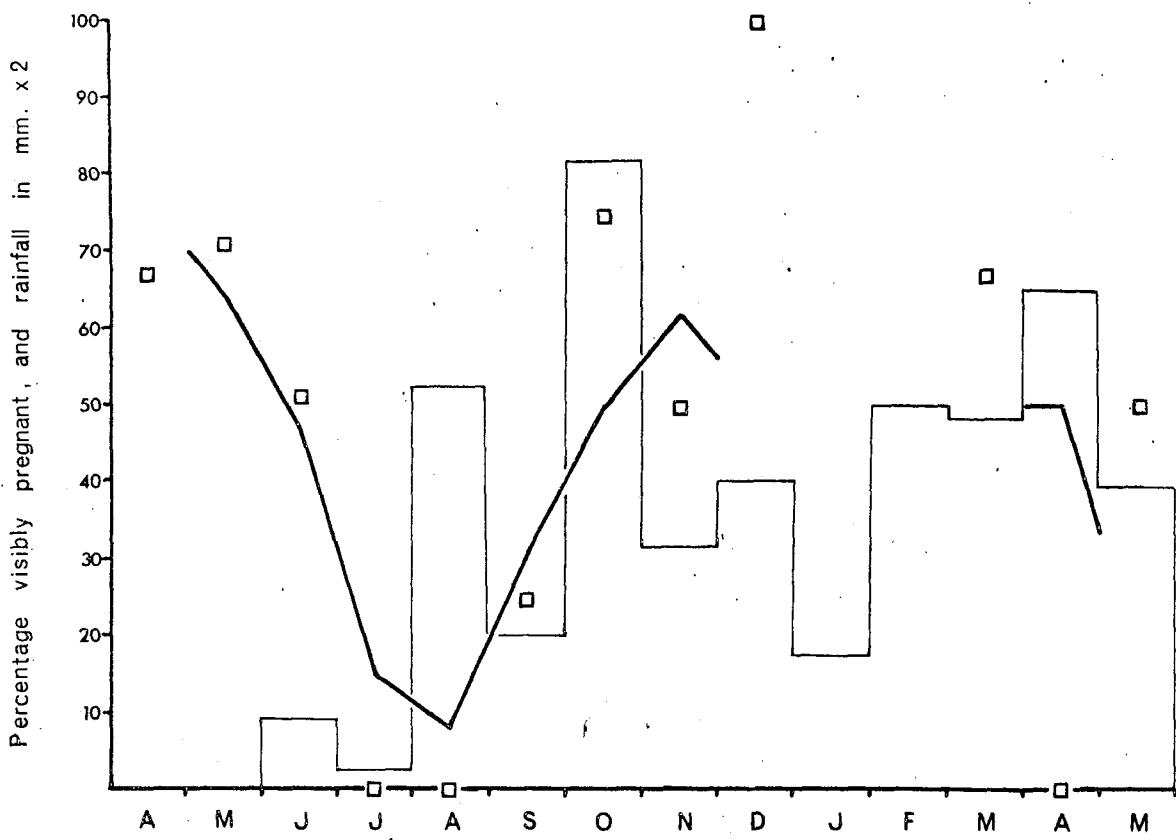


Fig. 52 - Pregnancy in relation to rainfall in 1965-66.

□ percentage visibly pregnant; rainfall as histogram. Results have been smoothed by a 3-month sliding mean.

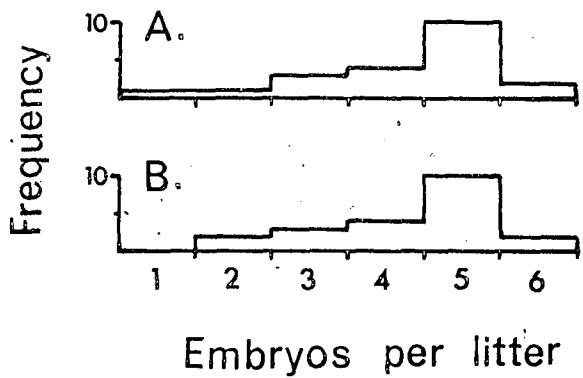


Fig. 53 - Frequency polygons illustrating size of litter as shown by A. - number of live embryos; B. - total number of embryos in utero in a litter.

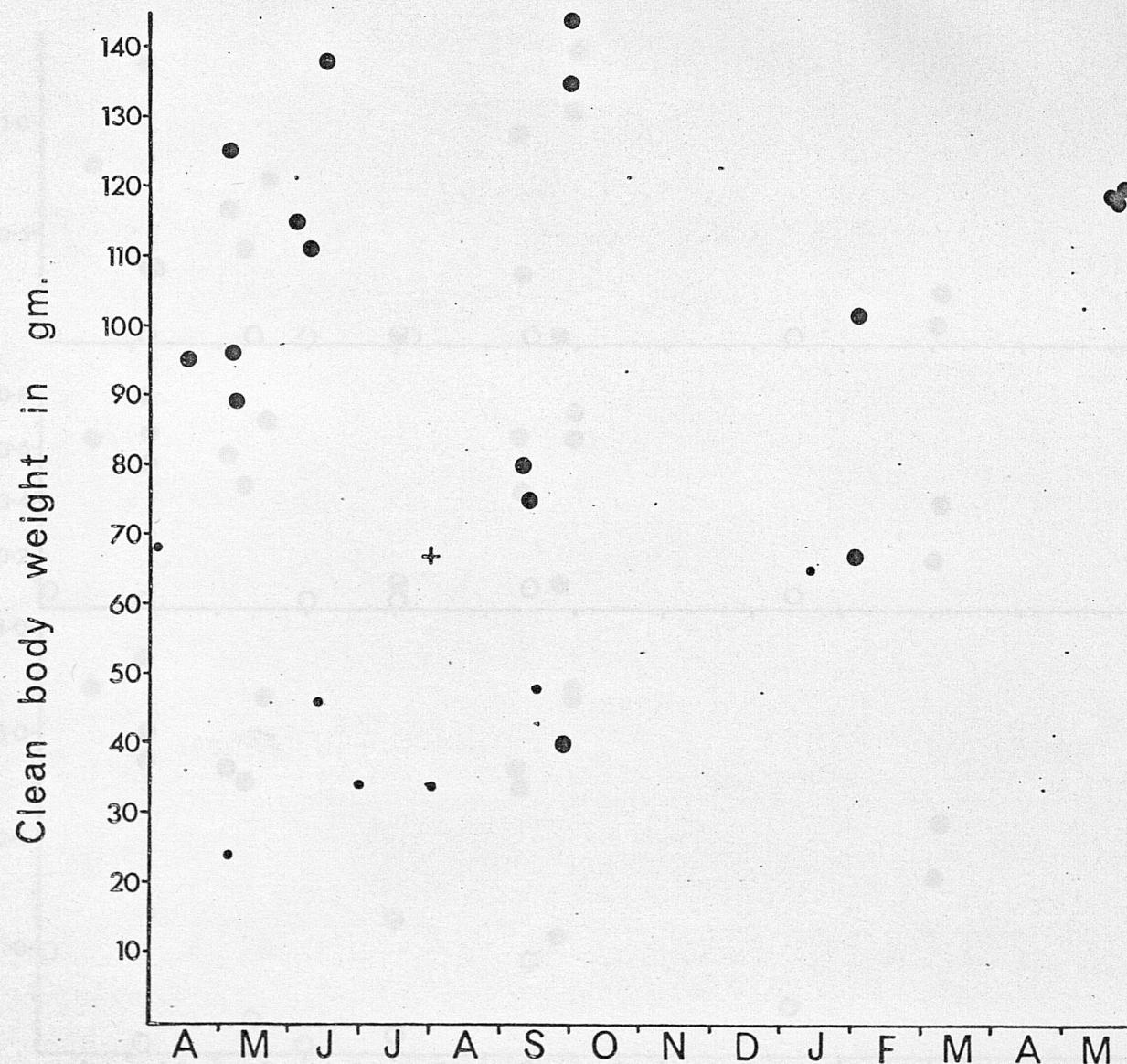


Fig. 54 - Scatter diagram of the clean body-weights of 26 males according to the days of the year. • sperm rating (0); + sperm ratings ($\frac{1}{4}$) and ($\frac{1}{2}$); ● sperm ratings ($\frac{3}{4}$) and (1).

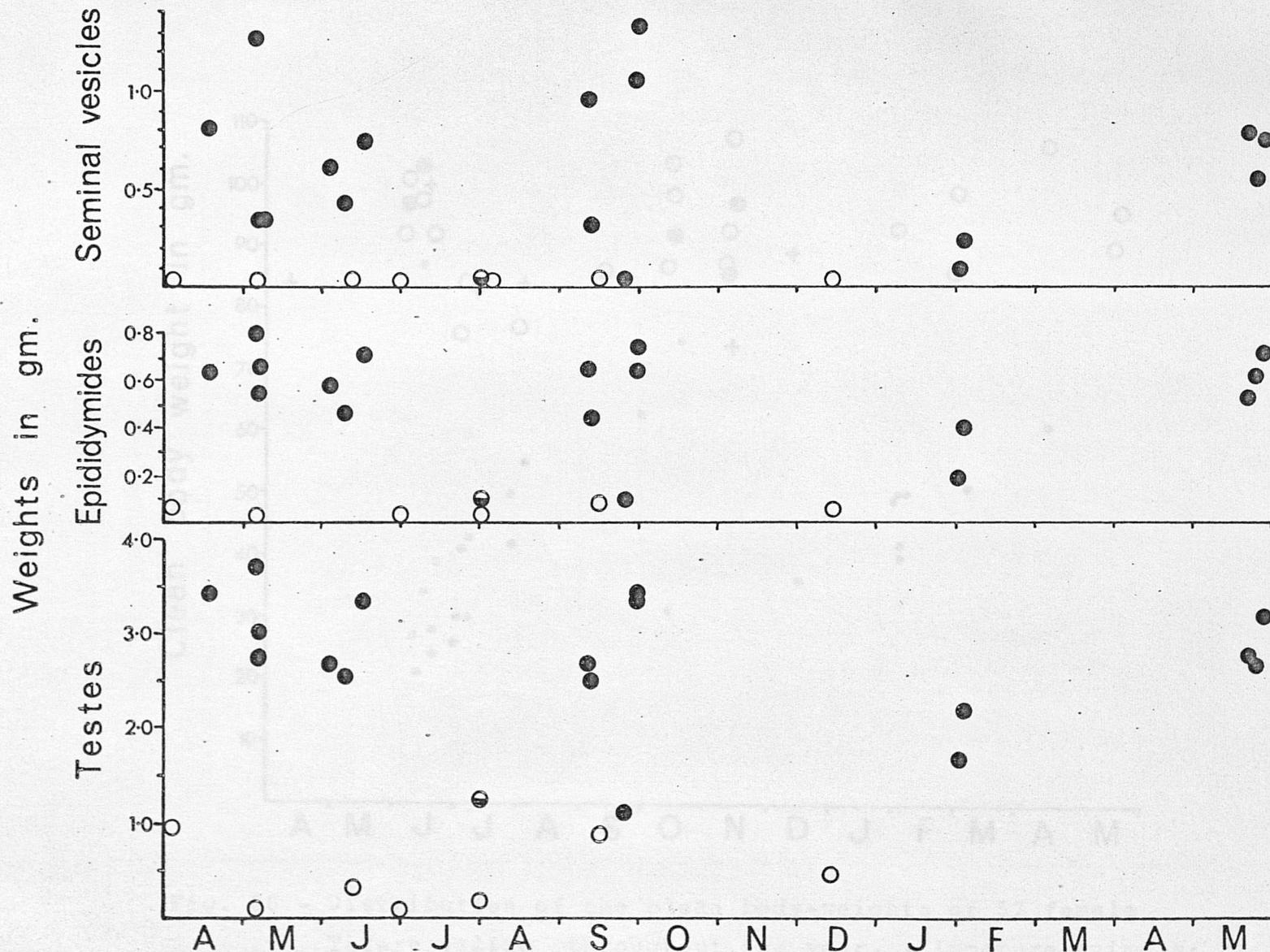


Fig. 55 - Distribution of the weights of the testes, epididymides, and seminal vesicles throughout the year. O sperm rating (0); \bullet sperm rating ($\frac{1}{4}$) and ($\frac{1}{2}$); \bullet sperm ratings ($\frac{3}{4}$) and (1).

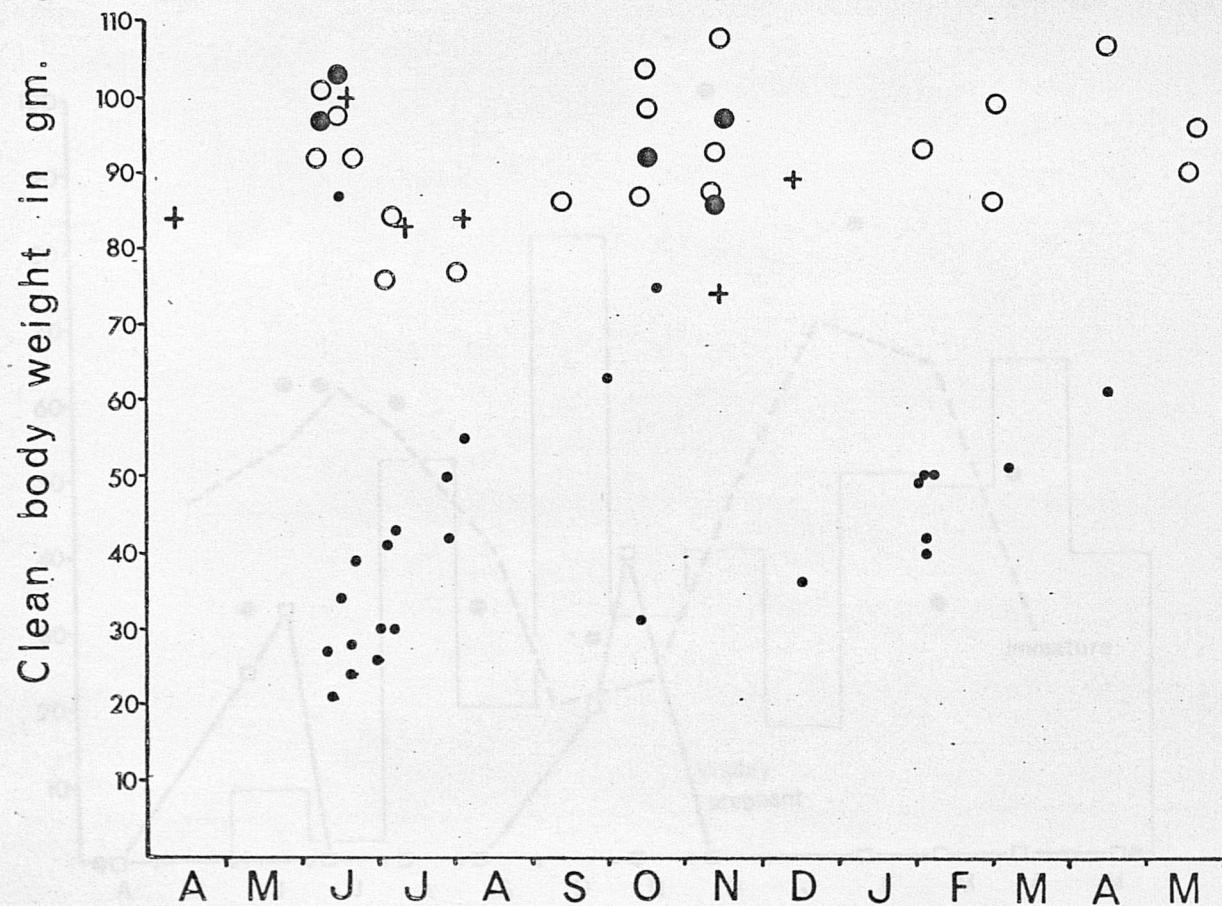


Fig. 56 - Distribution of the clean body-weights of 57 female *Tatera valida* throughout the year. • immature animals; + mature non-parous non-pregnant animals; ○ parous non pregnant animals; ● visibly pregnant animals.

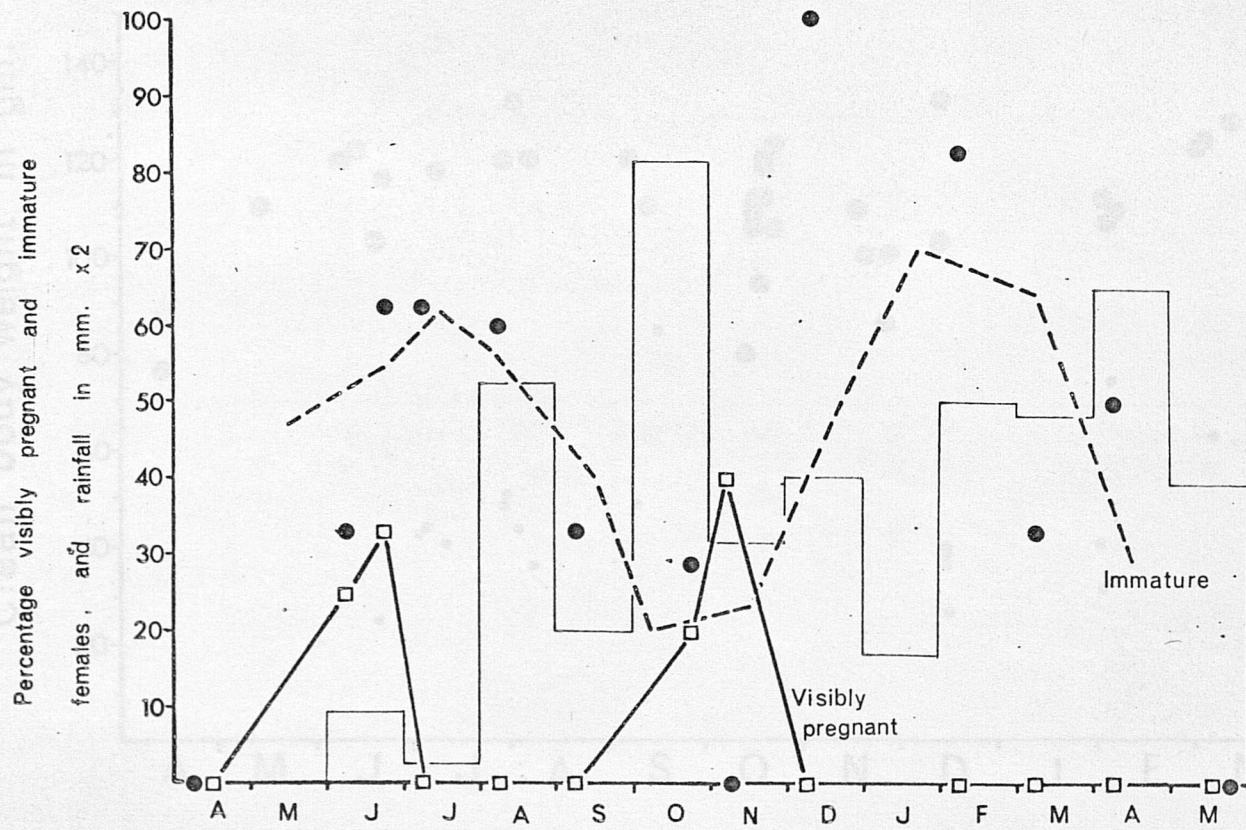


Fig 57 - Pregnancy and number of juveniles in relation to rainfall during 1965-66. □ percentage visibly pregnant; ● percentage immature females; rainfall as histogram. Curve of immature females has been smoothed by a 3-month sliding mean.

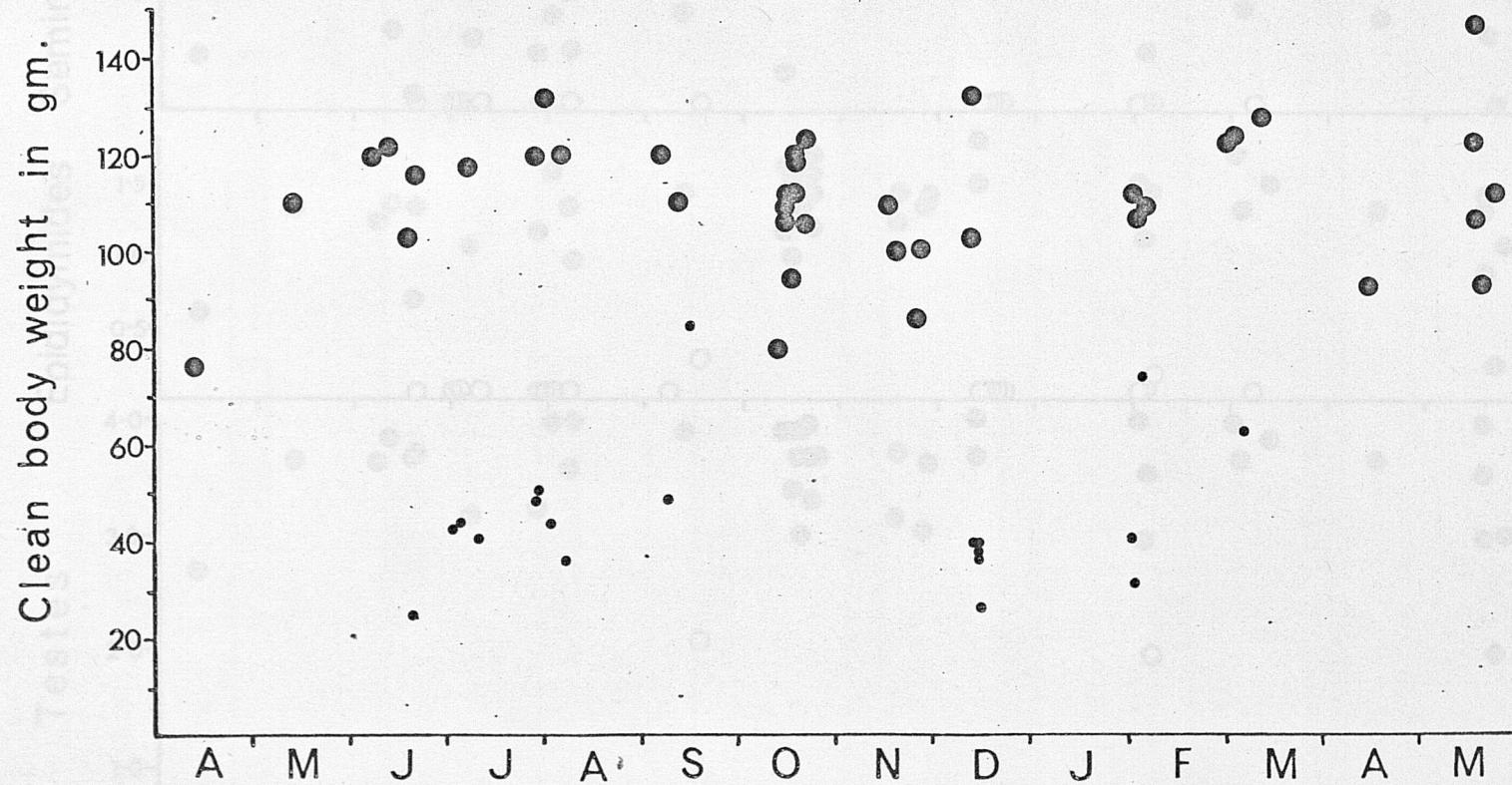


Fig. 58 - Distribution of the clean body-weights of 59 male Tatera valida according to the days of the year. • sperm rating (0); ● sperm ratings ($\frac{3}{4}$) and (1).

Weights in gm.

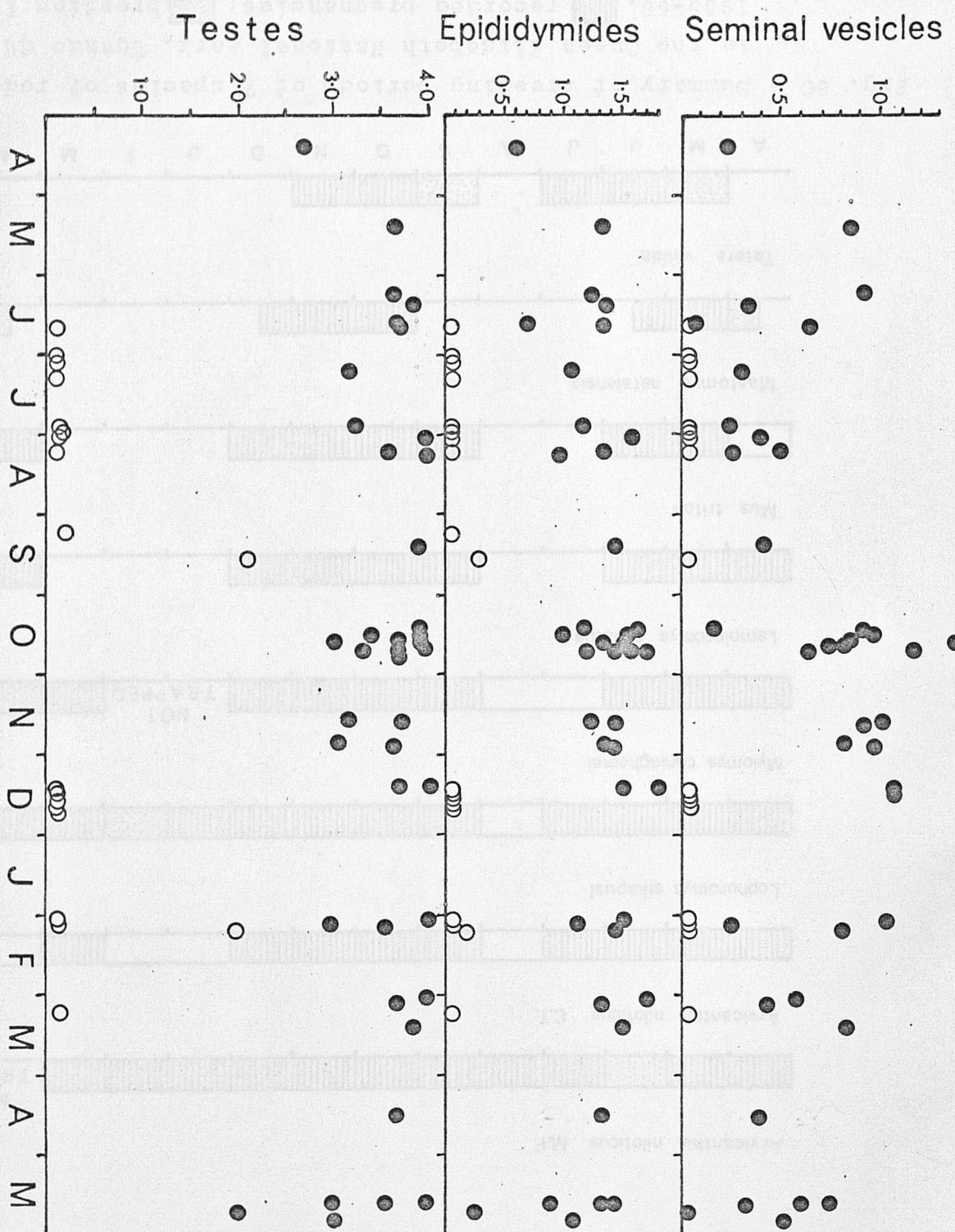
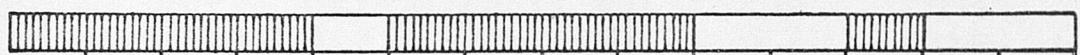


Fig. 59 - Distribution of the weights of the testes, epididymides, and seminal vesicles throughout the year. ○ sperm rating (0); ● sperm ratings ($\frac{1}{2}$) and (1).

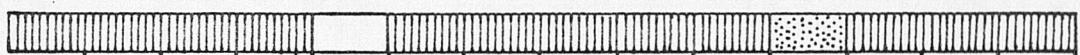
Arvicanthis niloticus M.P.



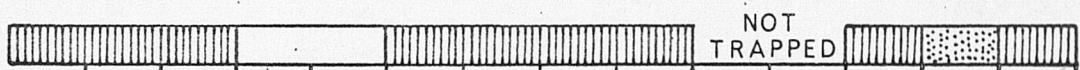
Arvicanthis niloticus C.T.



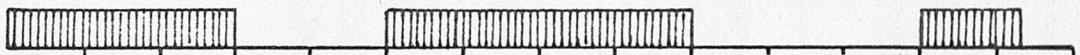
Lophuromys sikapusi



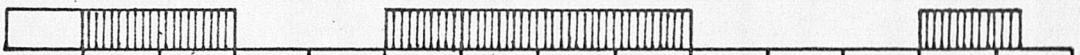
Myomys cuninghami



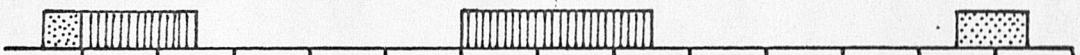
Lemniscomys striatus



Mus triton



Mastomys natalensis



Tatera valida

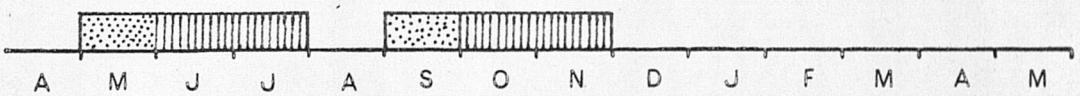
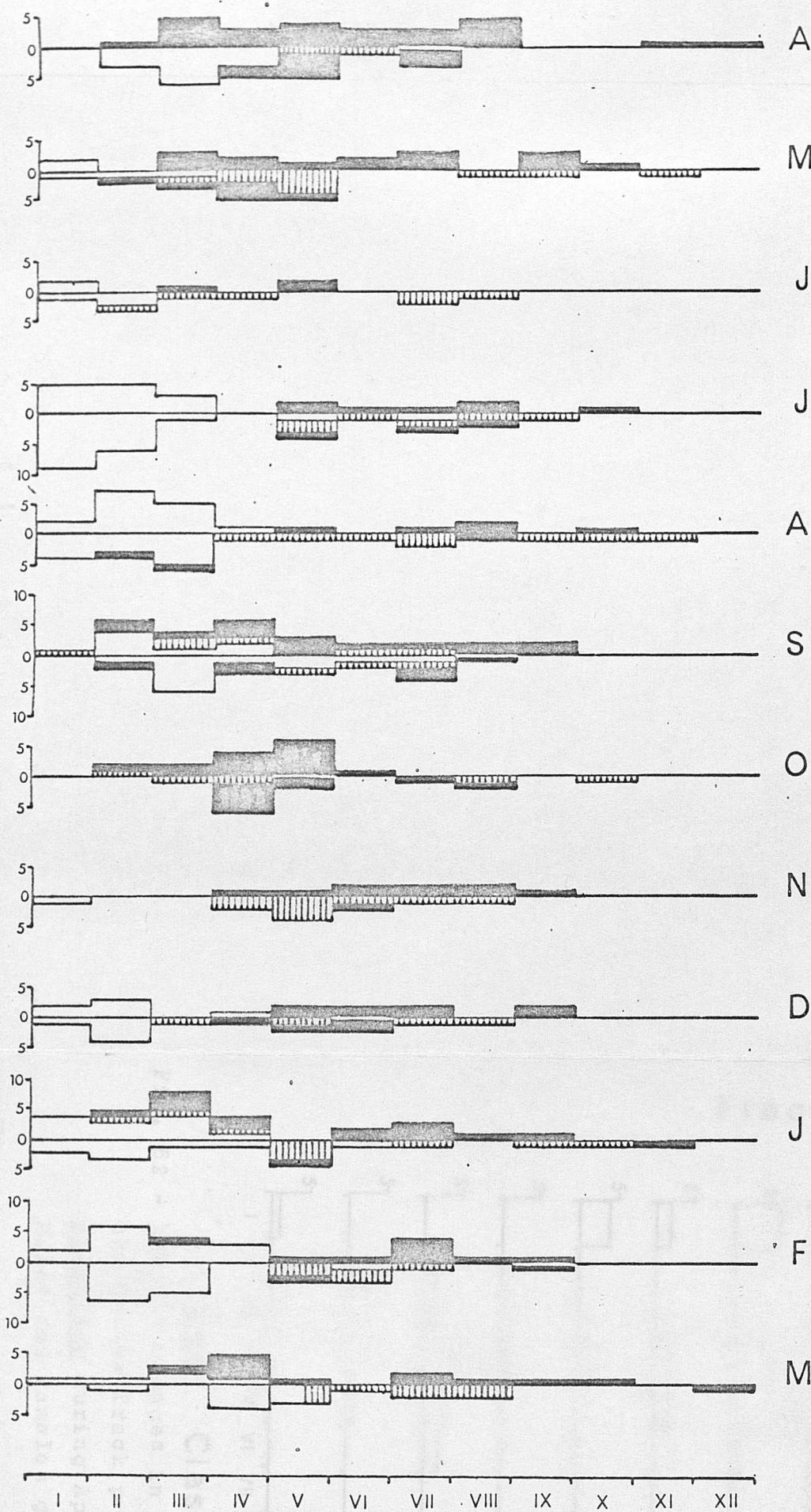


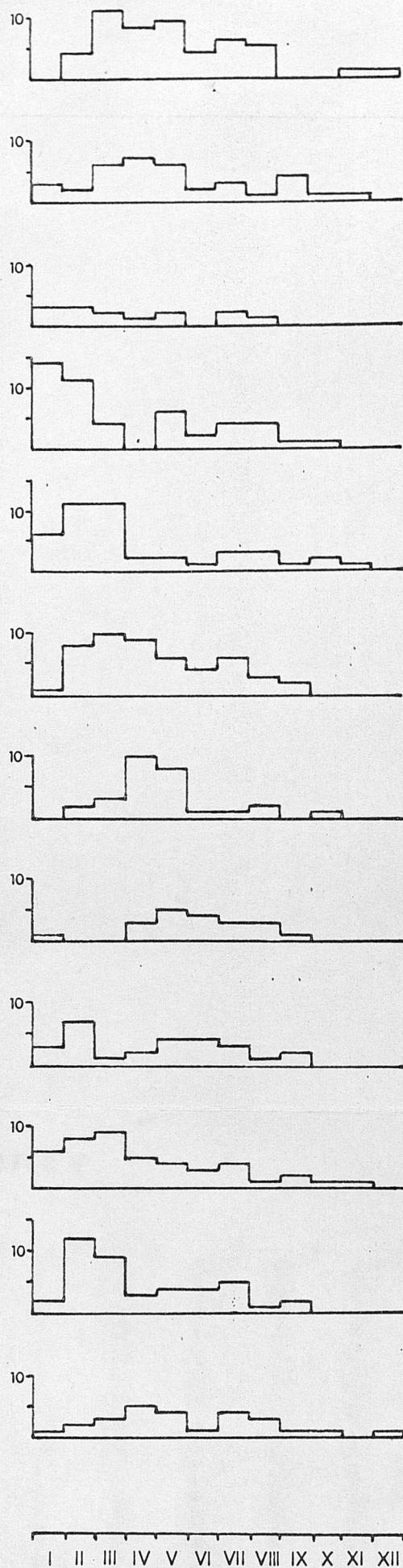
Fig. 60 - Summary of breeding periods of 7 species of rodents in the Queen Elizabeth National Park, Uganda during 1965-66. recorded pregnancies; breeding inferred from other reproductive data; breeding assumed with no evidence. M.P = Mweya Peninsula population, C.T. = Crater Track population.

Frequency

A.



B.



AGE CLASS

Fig. 61 - Monthly changes in the age composition of the Mweya Peninsula population of *Arvicantis niloticus* during April 1965 - March 1966.

A. - males and females separated, frequency of males above the horizontal axes and females below those axes. \square sperm rating (0), or non-parous non-pregnant females; \blacksquare sperm ratings ($\frac{1}{4}$) and ($\frac{1}{2}$), or parous non-pregnant females; \blacksquare sperm ratings ($\frac{3}{4}$) and (1), or visibly pregnant females.

B. - males and female frequencies grouped together.

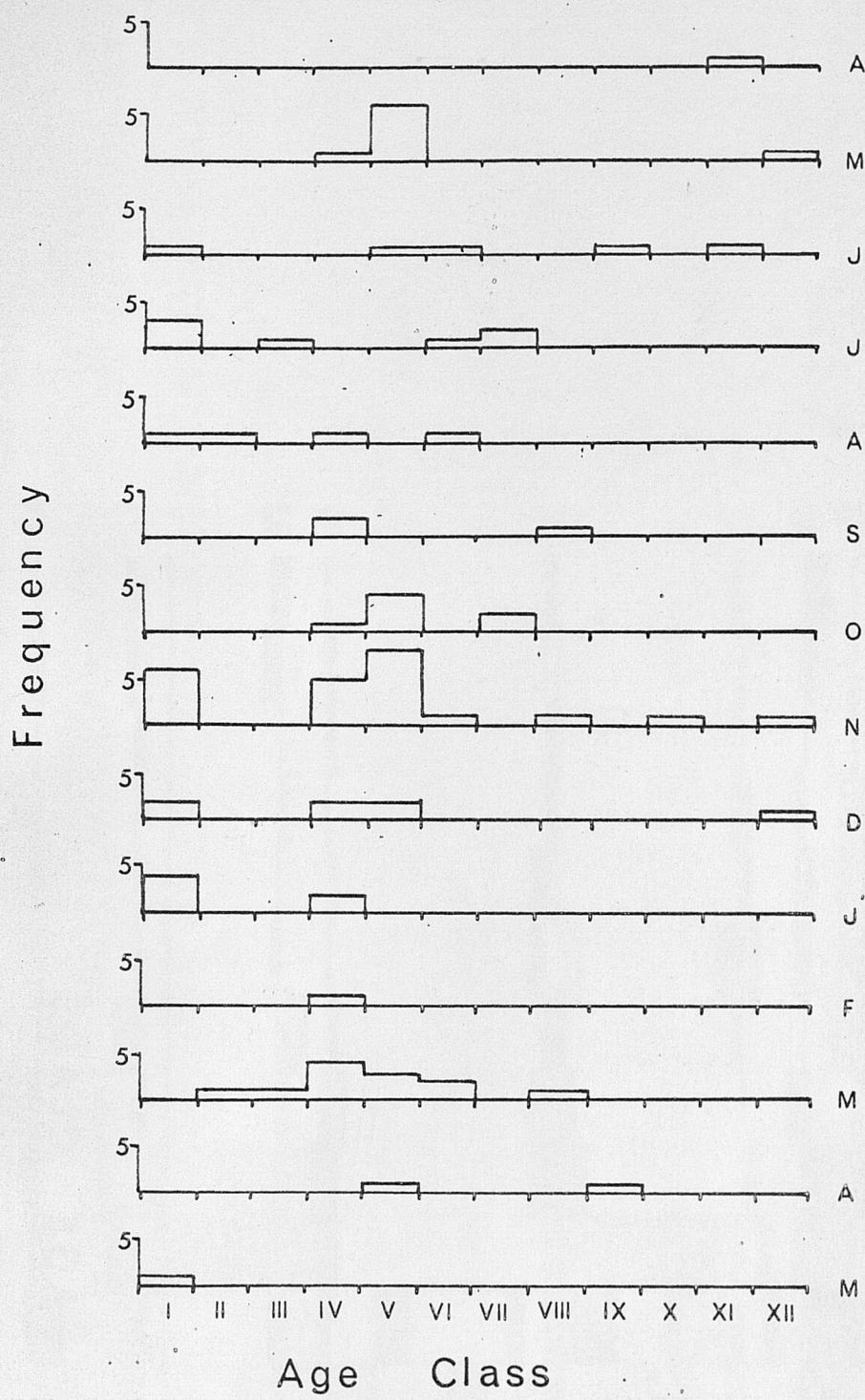


Fig. 62 - Monthly changes in the age composition of the Crater Track population of Arvicanthis niloticus during April 1965 - May 1966. Males and females grouped together.

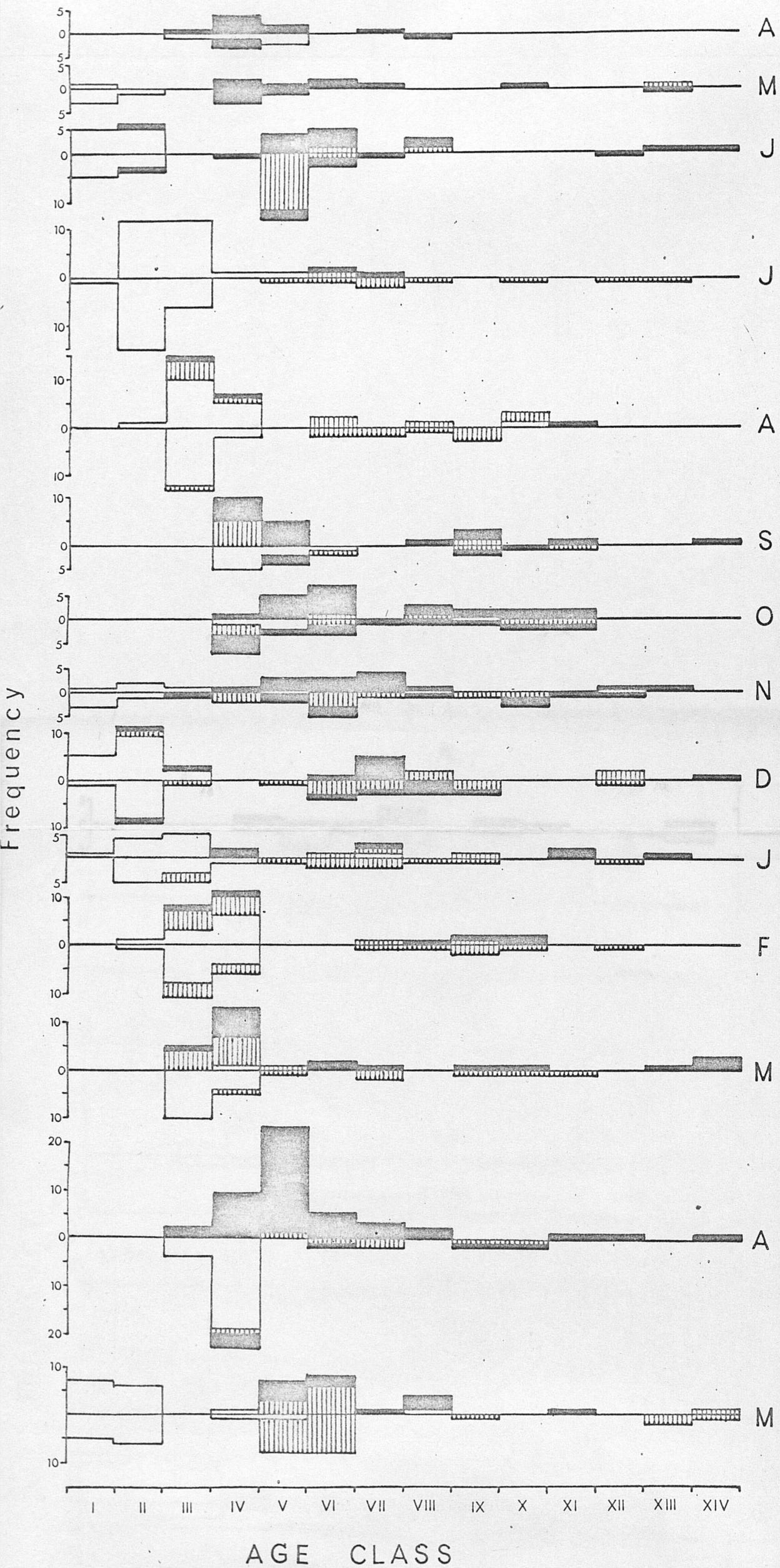
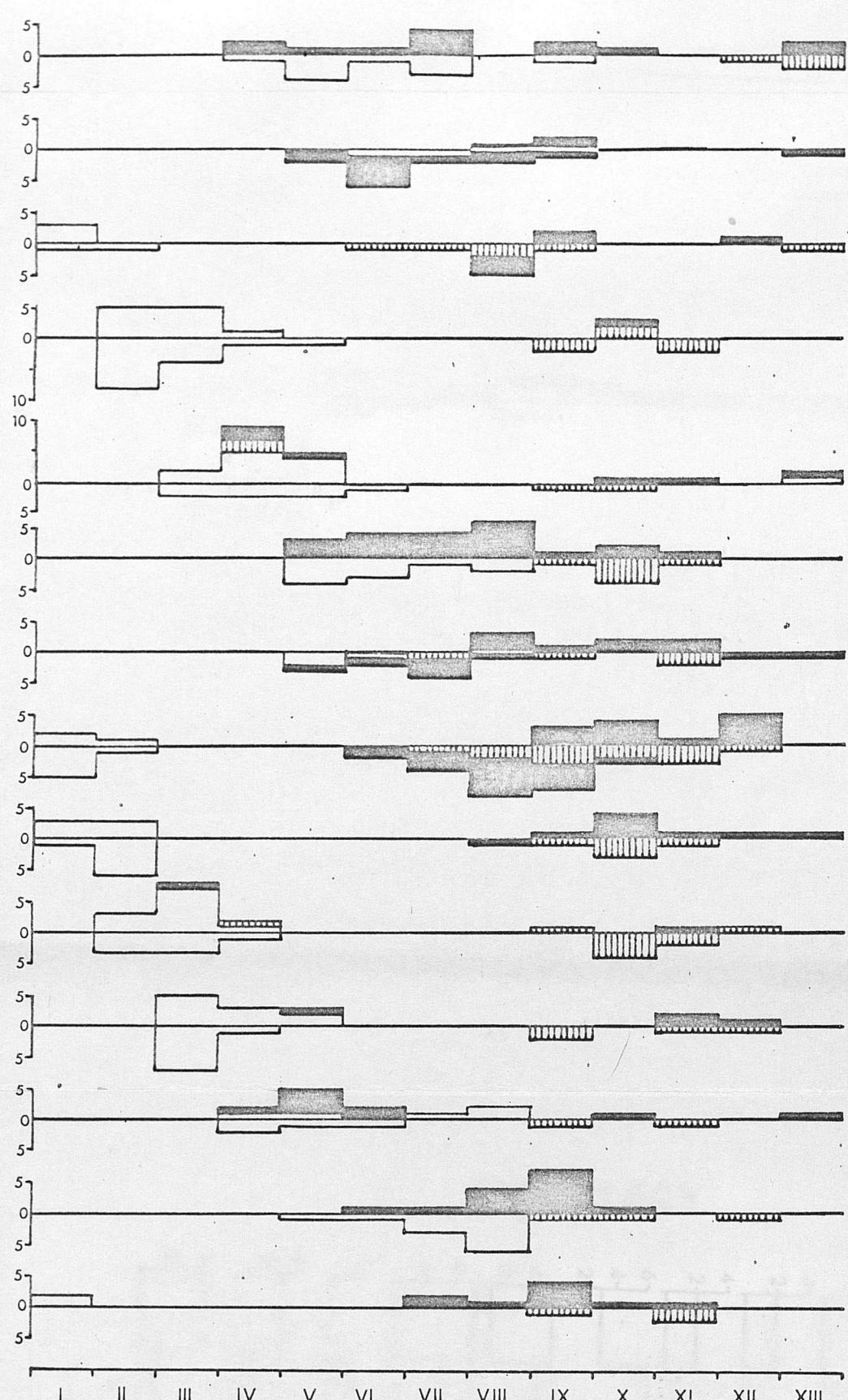


Fig. 63

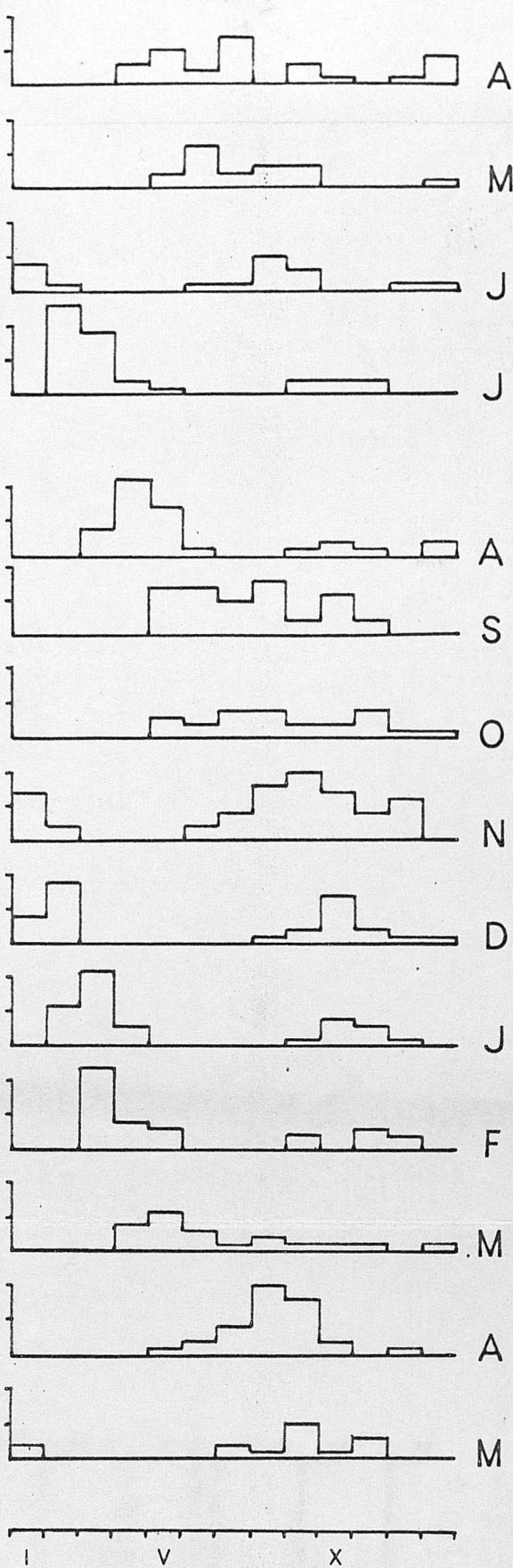
Monthly changes in the age composition of the Crater Track population of *Lemniscomys striatus* during April 1965 - May 1966. Frequency of males above the horizontal axes, and females below those axes. □ sperm rating (0), or non-parous non-pregnant females; ■ sperm ratings ($\frac{1}{4}$) and ($\frac{1}{2}$), or parous non-pregnant females; ■ sperm ratings ($\frac{3}{4}$) and (1), or visibly pregnant females.

FREQUENCY

A.



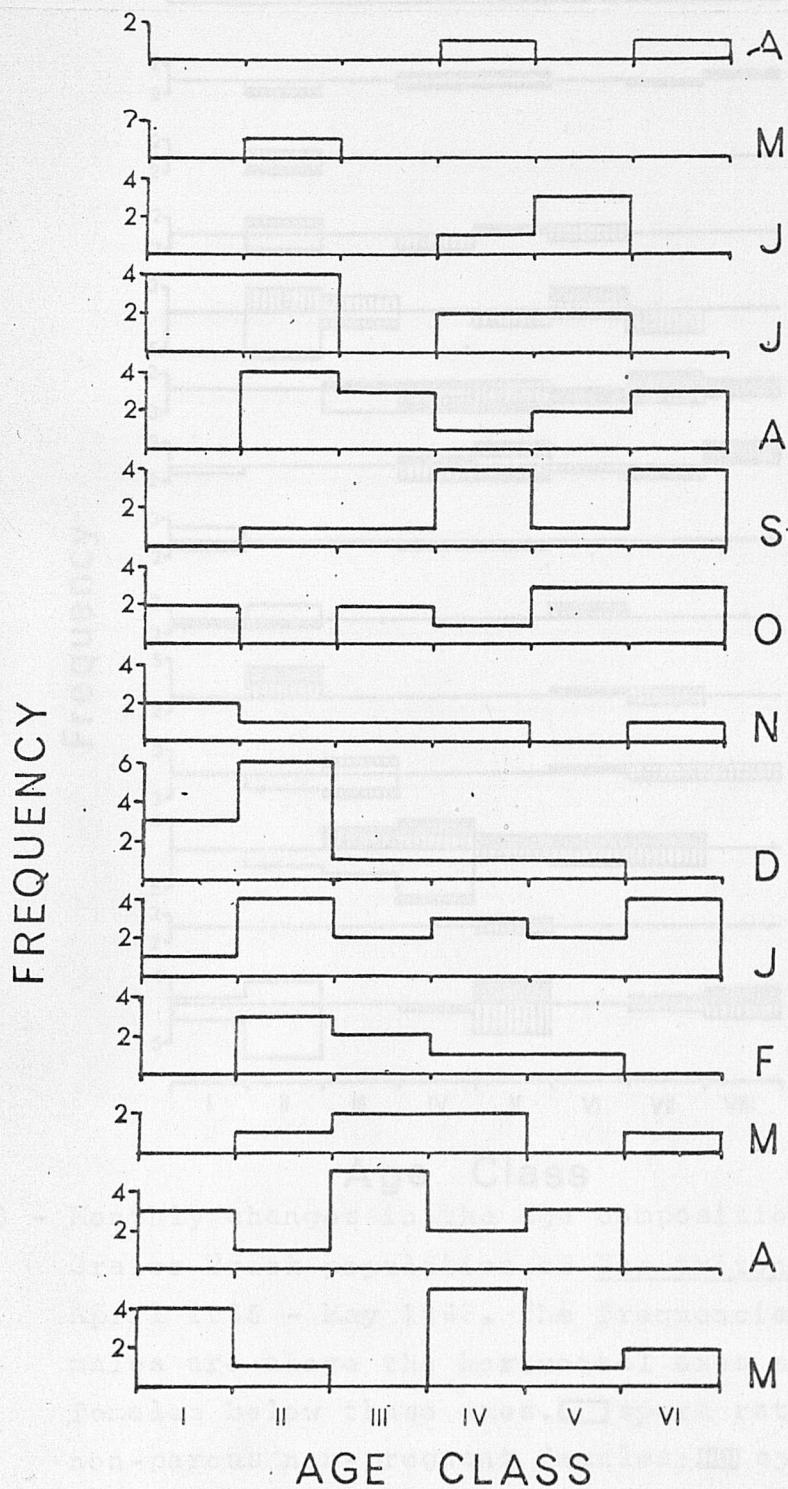
B.

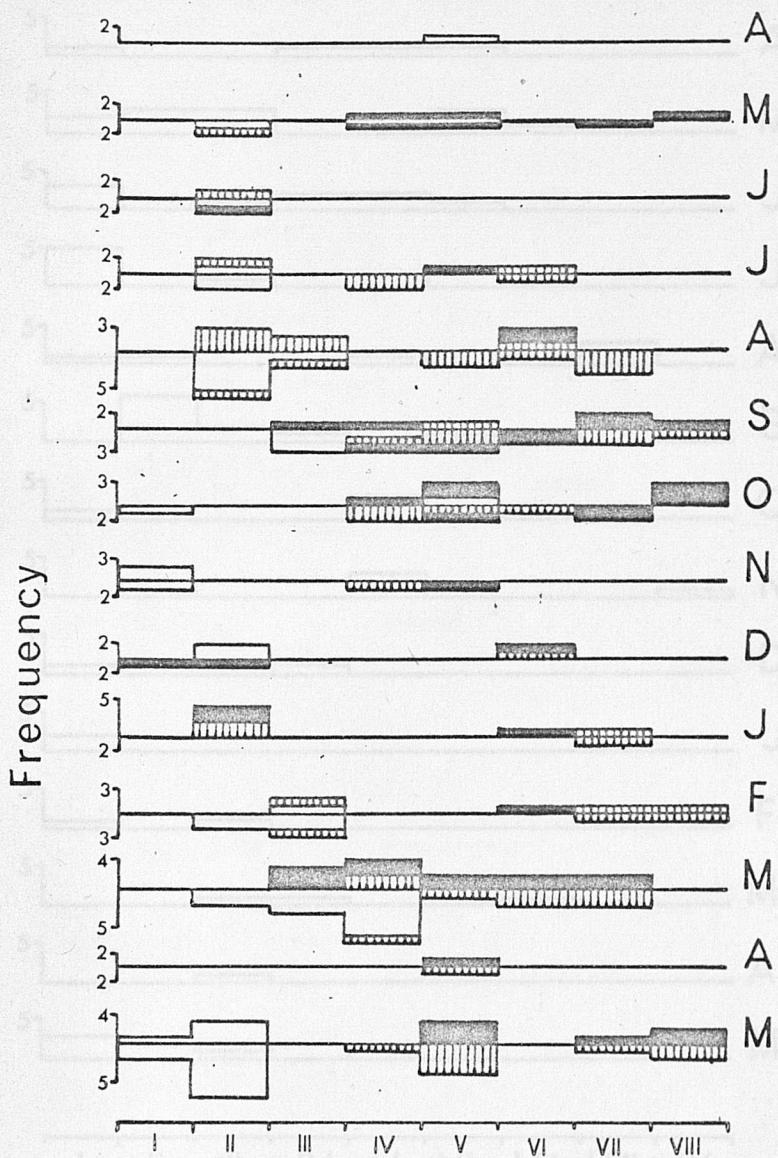


AGE CLASS

Fig. 64 - Monthly changes in the age composition of the Crater Track population of *Mastomys natalensis* during April 1965 - May 1966. A. - males and females separated, frequency of males above the horizontal axes and females below those axes. □ sperm rating (0), or non-parous non-pregnant females; ■ sperm ratings ($\frac{1}{4}$) and ($\frac{1}{2}$), or parous non-pregnant females; ▨ sperm ratings ($\frac{1}{2}$) and (1), or visibly pregnant females. B. - male and female frequencies grouped together.

Fig. 65 - Monthly changes in the age composition of the Crater Track population of Lophuromys sikapusi during April 1965 - May 1966. The frequencies of males and females are grouped together.





Age Class

Fig. 66 - Monthly changes in the age composition of the Crater Track population of Mus triton during April 1965 - May 1966. The frequencies of the males are above the horizontal axes and the females below those axes. \square sperm rating (0), or non-parous non-pregnant females; \blacksquare sperm ratings ($\frac{1}{2}$) and ($\frac{1}{2}$), or parous non-pregnant females; \blacksquare sperm ratings ($\frac{3}{4}$) and (1), or visibly pregnant females.

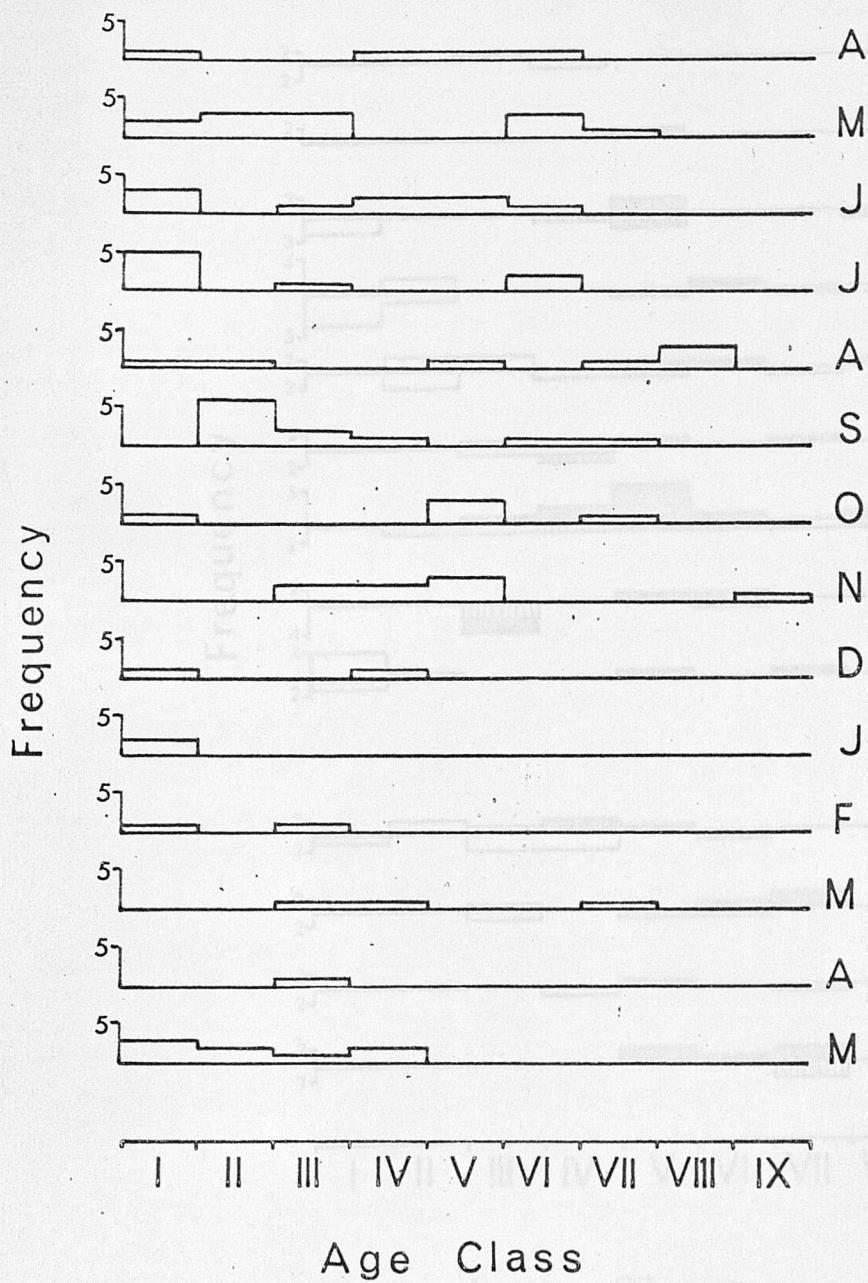


Fig. 67 - Monthly changes in the age composition of the Crater Track population of *Mylomys cuninghamaei* during April 1965 - May 1966. The frequencies of the males and females are grouped together.

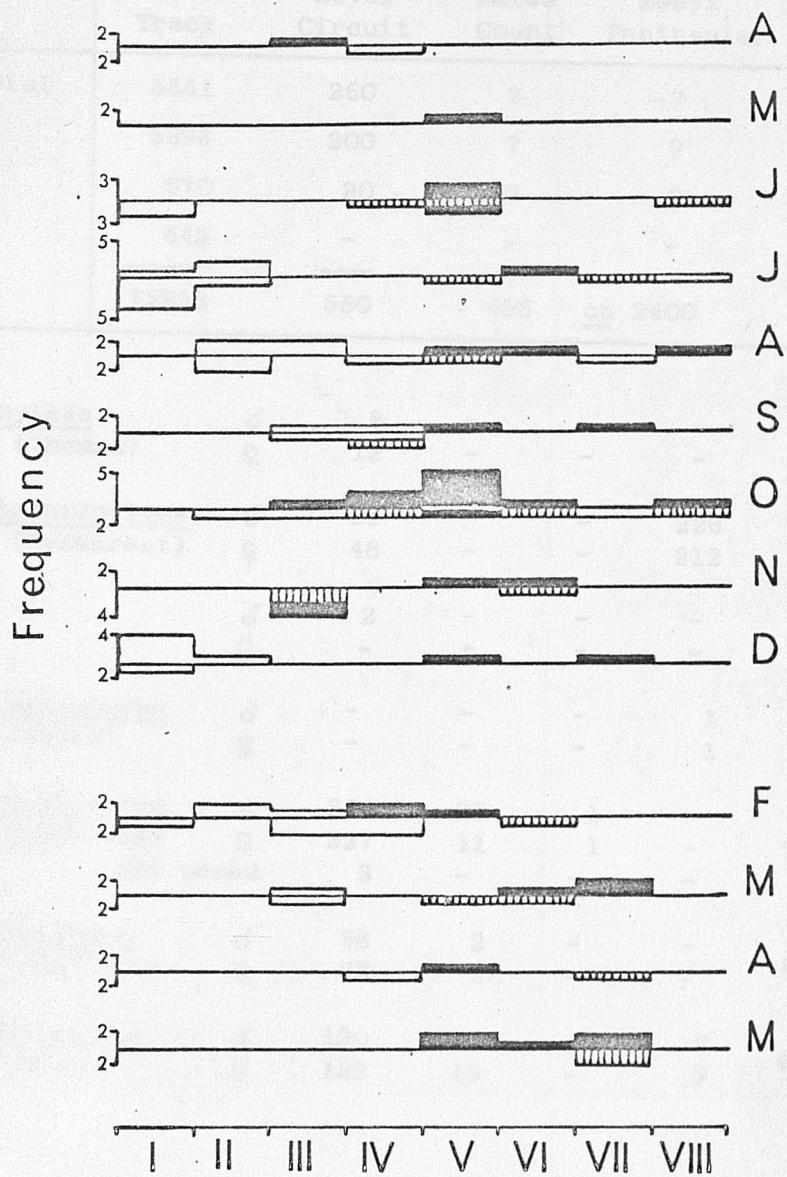


Fig. 68 - Monthly changes in the age composition of Taterra valida during April 1965 - May 1966. The frequencies of the males are above the horizontal axes and the females below.

□ sperm rating (0), or non-parous non-pregnant females;

▨ parous non-pregnant females; ■ sperm ratings (3/4) and (1), or visibly pregnant females.

TABLE 1

Small mammals trapped in grassland areas of the Queen Elizabeth National Park, Uganda. April 1965-May 1966.

Trap	Trap Nights					Total
	Crater Track	Royal Circuit	Katwe Count	Mweya Peninsular		
Museum Special	5541	260	?	?		
Reporter	5398	200	?	?		
Giljotin	670	90	?	?		
Havahart	649	-	-	-		
	<hr/>	<hr/>	<hr/>	<hr/>	<hr/>	
	12258	550	498	ca 2400		15706

Catch:

<u>Aethomys nyikae</u> (Thomas)	♂	8	-	-	-	27
	♀	19	-	-	-	
<u>Arvicanthis niloticus</u> (Desmarest)	♂	39	-	-	226	
	♀	48	-	-	212	525
<u>Dendromus</u> sp.	♂	2	-	-	-	2
	♀	-	-	-	-	
<u>Grammomys dolichurus</u> (Smuts)	♂	-	-	-	1	2
	♀	-	-	-	1	
<u>Lemniscomys striatus</u> (Linnaeus)	♂	364	23	1	-	
	♀	327	11	1	-	730
	not sexed	3	-	-	-	
<u>Lophuromys sikapusi</u> (Temminck)	♂	58	2	-	-	134
	♀	73	1	-	-	
<u>Mastomys natalensis</u> Smith	♂	190	21	4	7	447
	♀	199	19	-	7	
<u>Mus minutoides</u> Smith	♂	17	1	-	2	36
	♀	15	-	-	1	
<u>Mus triton</u> (Thomas)	♂	76	-	-	-	
	♀	107	-	-	-	184
	not sexed	1	-	-	-	
<u>Myomys cunicinghamei</u> Thomas	♂	24	1	-	-	
	♀	59	-	-	-	85
	not sexed	1	-	-	-	
<u>Otomys irroratus</u> (Brants)	♂	6	-	-	-	10
	♀	4	-	-	-	
<u>Rattus rattus</u> (Linnaeus)	♂	-	-	-	3	8
	♀	-	-	-	5	
<u>Zelotomys hildegardae</u> (Thomas)	♂	8	-	-	-	12
	♀	4	-	-	-	
<u>Tatera valida</u> (Bocage)	♂	56	3	-	-	116
	♀	49	8	-	-	
<u>Crocidura</u> sp.	♂	41	-	-	2	69
	♀	26	-	-	-	
<u>Suncus megalura</u>	♂	1	-	-	-	2
	♀	1	-	-	-	
<hr/>						
Total		1826	90	6	467	2390*

*The combined total includes 1 Graphiurus murinus not included in the table.
The number of traps set on Mweya peninsular is an approximation.

Table 2. Numbers of animals per 1000 traps of each species, caught in the different types of vegetation in the burnt and unburnt areas. An = Aethomys nyikae; A = Arvicanthis niloticus; D = Dendromus sp; Lst = Lemniscomys striatus; Ls = Lophuromys sikapusi, Ma = Mastomys natalensis; Mm = Mus minutoides; Mt = Mus triton; My = Myomys cuninghamei; O = Otomys irroratus; Z = Zelotomys hildegardeae; Tv = Tatera valida.

Vegetation	No. of traps	SPECIES											
		An	A	D	Lst	Ls	Ma	Mm	Mt	My	O	Z	Tv
UNBURNED													
<u>Cymbopogon</u>	363	-	-	-	33	19	6	-	6	8	6	-	3
<u>Themeda</u>	1951	0.5	18	-	55	9	29	1.5	11	3.6	0.5	0.5	6.7
<u>Imperata</u>	2019	2	4	0.5	36	27	23	-	19	12	0.5	1.5	15
Bush	270	31	3.5	-	70	-	115	-	-	-	-	-	3.5
<u>Hyparrhenia</u>	53	-	57	-	57	-	38	-	19	-	-	19	19
BURNED													
<u>Cymbopogon</u>	257	-	-	-	167	4	35	-	19	-	4	4	4
<u>Themeda</u>	599	-	3.3	1.7	114	6.7	37	3.3	6.7	1.7	-	1.7	5
<u>Imperata</u>	1782	1.1	7.3	-	103	19	46	3.4	35	9	-	2.2	17
Bush	89	34	22	-	124	-	112	-	-	-	-	-	-
<u>Hyparrhenia</u>	125	8	-	-	144	-	48	-	8	-	-	-	-

Table 3. Numbers of animals caught, in unburnt areas, of each species immediately before and after burning in the Crater Track Area. Abbreviation of species as Table 2.

Day	No. of traps	SPECIES										Total number of animals/100 traps	
		A	Lst	Ls	Ma	Mm	Mt	My	O	Z	Tv		
1. June 28	70	1	10	5	4	-	-	4	-	-	1	37	
2. June 29	50	1	4	1	3	-	-	-	-	-	1	20	
3. June 30	50	2	3	-	3	-	-	-	-	-	1	18	
4. July 1	50	-	2	-	2	-	2	2	1	-	-	18	
5. July 2	50	-	7	-	3	-	1	-	-	-	4	32	
6. July 3	59	1	8	-	1	1	-	1	-	-	-	20	
Total		5	34	7	16	1	3	7	1	-	7	Before Burn	
No./1000 traps		15	103	21	49	3	9	21	3	-	21		
7. July 4	30	-	10	-	-	-	-	-	-	-	-	33	
8. July 5	35	-	5	-	4	-	1	-	-	-	2	34	
9. July 6	29	-	3	-	2	-	1	-	-	-	-	21	
10. July 7	33	2	5	3	1	-	-	1	-	-	-	36	
11. July 8	34	-	3	2	3	-	-	-	-	1	1	29	
Total		2	26	5	10	-	2	1	-	1	3	After Burn	
No./1000 traps		12	161	31	62	-	12	6	-	6	19		

Table 4. Numbers of animals caught, in burnt areas, of each species immediately after burning in the Crater Track Area. Abbreviation of species as Table 2.

Day	No. of traps	SPECIES					Total number of animals/100 traps
		Lst	Ma	Mt	O	Tv	
7. July 4	29	3	1	-	1	1	21
8. July 5	25	2	2	-	-	1	20
9. July 6	30	1	1	-	-	-	7
10. July 7	26	-	2	1	-	-	12
11. July 8	25	-	3	-	-	-	12
Total		6	9	1	1	2	
No./1000 traps		44	67	7	7	15	

Table 5. Activity of Small Rodents. Number of captures of different species during the day and night in the live trap study area, from June 1965 to January 1966.
 % is percentage nocturnal; N is nocturnal activity; D is diurnal activity.
 Abbreviation of species as Table 2.

MONTH	ACTIVITY	A		Lst		Ls		Ma		Mt		Mm		My		Z		Tv	
		Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%
JUNE	N	-		69	44	2	50	45	80	13	93	-		5	45	1	100	-	
	D	-		88		2		11		1		-		6		0		-	
JULY	N	-		12	63	-		21	91	30	88	-		-		-		-	
	D	-		7		-		2		4		-		-		-		-	
AUG.	N	-		19	56	-		21	100	21	84	13	87	-		1	33	-	
	D	-		15		-		0		4		2		-		2		-	
SEPT.	N	-		65	51	-		33	97	4	100	18	95	-		1	100	12	100
	D	-		62		-		1		0		1		-		0		0	
OCT.	N	-		52	38	-		28	97	2	100	3	100	-		-		6	100
	D	-		85		-		1		0		0		-		-		0	
NOV.	N	0	0	92	46	3	75	15	88	12	86	-	-	-		2	100	19	79
	D	1		127		1		2		2		-	-	-		0		5	
JAN.	N	0	0	62	41	1	100	22	92			2	100	1	50	-		4	100
	D	2		89		0		2				0	1		-		0		

Table 6. Reproductive condition of female Arvicantis niloticus (Mweya Peninsula population) according to the clean body weight.

Table 7. Number of females of Arvicanthis niloticus (Mweya Peninsula population) examined each month and their reproductive condition.

MONTH	TOTAL	PREGNANT		NO. LACTATING	PAROUS			NON PAROUS			IMMATURE	
		NO.	%		ANOESTROUS	ACTIVE	OESTROUS	ANOESTROUS	ACTIVE	OESTROUS	NO.	%
APRIL	24	9	43	1	1	-	-	2	1	7	3	12½
MAY	20	6	32	6	1	3	1	-	1	1	1	5
JUNE	9	0(1)	-	-	2	2	1	-	1	1	1	11
JULY	27	3(1)	23	3	3	-	-	3	-	-	14	52
AUG.	24	1(1)	7	2	7	1	-	-	-	1	11	49
SEPT.	21	5	36	-	2	-	2	2	2	1	7	33
OCT.	13	9	69	3	-	1	-	-	-	-	-	-
NOV.	11	1	10	3	5	-	1	-	-	-	1	9
DEC.	13	3	38	1	4	-	-	-	-	-	5	38
JAN.	16	3	30	-	5	-	1	1	-	-	6	37½
FEB.	20	2	25	-	3	1	1	1	-	-	12	60
MAR.	14	1(1)	10	-	2	2	-	1	1	2	4	29
TOTAL	212	43(4)		19	35	10	7	9	6	13	66	

(Numbers in parentheses refer to pregnant females with all embryos resorbing).

Table 8. Number of implanted embryos of Arvicanthis niloticus (Mweya Peninsula population) according to the clean body-weight of the parent.

NO. EMBRYOS	CLEAN BODY-WEIGHT (gms.)				
	40-49	50-59	60-69	70-79	80+
1	-	-	-	-	-
2	-	-	-	-	-
3	1	1	2	3	-
4	2	1	4	5	3
5	1	1	4	3	2
6	-	-	2	3	-
7	-	-	-	-	1
8	-	-	1	-	-
9	-	-	-	-	-
10	-	-	-	-	1
MEAN	4.0	4.0	4.8	4.4	5.6

Table 9. Reproductive condition of male Arvicanthis niloticus (Mweya Peninsula population) according to the clean body-weight.

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CLEAN BODY-WEIGHT (GMS.)	SPERMATOZOA RATINGS		
	(0)	($\frac{1}{4}$) & ($\frac{1}{2}$)	($\frac{3}{4}$) & (1)
10-19	3	-	-
20-29	10	-	-
30-39	14	1	-
40-49	24	2	2
50-59	20	1	7
60-69	5	4	21
70-79	-	1	27
80-89	-	-	46
90-99	-	1	23
100+	-	1	12
TOTAL	76	11	138

Table 10. Reproductive condition of male Arvicanthis niloticus (Mweya Peninsula population) in monthly collections.

MONTH	TOTAL NO.	SPERMATOZOA RATINGS		
		(0)	($\frac{1}{4}$) & ($\frac{1}{2}$)	($\frac{3}{4}$) & (1)
APR.	29	-	-	29
MAY	18	2	1	15
JUNE	5	2	-	3
JULY	20	13	-	7
AUG.	21	14	-	7
SEPT.	29	7	7	15
OCT.	15	-	1	14
NOV.	9	-	-	9
DEC.	14	6	-	8
JAN.	28	13	2	13
FEB.	23	14	-	9
MAR.	15	5	-	10
TOTAL	226	76	11	139

Table 11. Reproductive condition of female Arvicanthis niloticus (Crater Track population) according to the clean body-weight.

CLEAN WEIGHT (GMS.)	TOTAL NO.	IMMATURE		FECUND NOT PAROUS		PREGNANT		PAROUS	
		NO.	%	NO.	%	NO.	%	NO.	%
10-19	5	5	100	-	-	-	-	-	-
20-29	4	4	100	-	-	-	-	-	-
30-39	5	4	80	1	20	-	-	-	-
40-49	8	1	12½	1	12½	-	-	6	75
50-59	17	-	-	-	-	10	59	7	41
60-69	6	-	-	-	-	3	50	3	50
70-79	4	-	-	-	-	2	50	2	50
TOTAL	49								

Table 12. Number of females of Arvicanthis niloticus (Crater Track population) examined each month and their reproductive condition.

MONTH	TOTAL	PREGNANT		NO. LACTATING	PAROUS		NON PAROUS		IMMATURE	
		NO.	%		ANOESTROUS ACTIVE	ANOESTROUS ACTIVE	NO.	%	NO.	%
APRIL	1	1	100	-	-	-	-	-	-	-
MAY	4	2	50	1	-	1	-	-	-	-
JUNE	5	2	50	1	-	1	-	-	1	20
JULY	6	1	33	1	1	-	-	-	3	50
AUG.	2	-	-	-	-	-	-	-	2	100
SEPT.	1	1	100	-	-	-	-	-	-	-
OCT.	3	2	67	-	1	-	-	-	-	-
NOV.	12	3	37½	3	2	-	-	-	4	33
DEC.	4	1	33	-	1	-	1	-	1	25
JAN.	2	-	-	1	-	-	-	-	1	50
FEB.	1	-	-	-	-	-	-	1	-	-
MARCH	5	2	50	-	2	-	-	-	1	20
APRIL	2	-	-	-	1	1	-	-	-	-
MAY	1	-	-	-	-	-	-	-	1	100
TOTAL	49	15		7	8	3	1	1	14	

Table 13. Reproductive condition of male Arvicanthis niloticus (Crater Track population) according to the clean body-weight.

234

CLEAN BODY-WEIGHT (GMS.)	SPERMATOZOA RATINGS		
	(0)	($\frac{1}{4}$) & ($\frac{1}{2}$)	($\frac{3}{4}$) & (1)
10-19	3	-	-
20-29	3	-	-
30-39	2	-	-
40-49	3	1	1
50-59	-	3	9
60-69	1	-	7
70-79	-	-	3
80-89	-	-	1
TOTAL	12	4	21

Table 14. Reproductive condition of female Lemniscomys striatus according to the clean body-weight.

CLEAN WEIGHT (GMS.)	TOTAL NO.	IMMATURE		FECUND NOT PAROUS		PREGNANT		PAROUS	
		NO.	%	NO.	%	NO.	%	NO.	%
5-9	8	8	100	-	-	-	-	-	-
10-14	31	30	97	-	-	1	3	-	-
15-19	42	38	90	3	7	-	-	1	2
20-24	98	31	31 $\frac{1}{2}$	25	25 $\frac{1}{2}$	12	12 $\frac{1}{2}$	30	30 $\frac{1}{2}$
25-29	89	6	7	7	8	14	16	62	70
30-34	52	1	2	1	2	23	44	27	52
35+	12	-	-	-	-	7	58	5	42
TOTAL	332								

Table 15. Number of females of Lemniscomys striatus examined each month and their reproductive condition.

MONTH	TOTAL	PREGNANT		LACTATING		PAROUS			NON PAROUS			IMMATURE	
		NO.	%	NO.	%	ANOESTROUS	ACTIVE	OESTROUS	ANOESTROUS	ACTIVE	OESTROUS	NO.	%
APRIL	7	3	60	-	-	-	-	-	-	1	1	2	29
MAY	11	7	87½	1	12½	-	-	-	-	-	-	3	27
JUNE (1-15)	30	8	36	9	41	5	-	-	-	-	-	8	27
JUNE (15-22)	12	1	12½	-	-	7	-	-	-	-	-	4	33
JULY	31	-	-	-	-	8	-	-	-	-	-	23	74
AUG.	25	-	-	-	-	9	-	-	-	-	-	16	64
SEPT.	15	4	40	-	-	2	1	1	1	1	-	5	33
OCT.	20	12	60	4	20	-	1	-	-	2	1	-	-
NOV.	22	10	56	3	17	3	1	1	-	-	-	4	18
DEC.	26	6	35	8	47	1	2	-	-	-	-	9	35
JAN.	19	-	-	4	33	6	-	-	2	-	-	7	37
FEB.	24	-	-	-	-	11	-	-	1	-	-	12	50
MAR.	21	-	-	-	-	7	-	-	2	-	-	12	57
APR.	35	6	18	-	-	2	2	2	3	11	8	1	3
MAY	33	-	-	11	52	10	-	-	-	-	-	12	36
TOTAL	332	58	40			71	7	4	9	15	10	118	

Table 16. Number of implanted embryos of Lemniscomys striatus according to the clean body-weight of the parent.

- 227 -

NO. EMBRYOS	CLEAN BODY-WEIGHT (gms.)			
	UNDER 24 GM.	25-29	30-34	35+
1	-	-	-	-
2	-	-	-	-
3	-	1	5	-
4	5	3	2	1
5	6	5	8	3
6	2	3	6	2
7	-	2	1	1
8	-	-	1	-
MEAN	4.8	5.14	4.96	5.43

Table 17. Monthly variation in mean number of healthy embryos of Lemniscomys striatus.

MONTH	NO. PREGNANT	NO. HEALTHY EMBRYOS	AVERAGE NO. EMBRYOS PER LITTER
APRIL	3	13	4.3
MAY	7	35	5.0
JUNE	9	46	5.1
JULY	-	-	-
AUG.	-	-	-
SEPT.	4	19	4.75
OCT.	12	53	4.4
NOV.	10	50	5.0
DEC.	6	31	5.2
JAN.	-	-	-
FEB.	-	-	-
MAR.	-	-	-
APR.	6	27	4.5
MAY	-	-	-

Table 18. Reproductive condition of male Lemniscomys striatus according to the clean body-weight.

632

CLEAN BODY-WEIGHT (GMS.)	SPERMATOZOA RATINGS		
	(0)	($\frac{1}{4}$) & ($\frac{1}{2}$)	($\frac{3}{4}$) & (1)
5-9	8	-	-
10-14	20	-	-
15-19	31+(4)	-	-
20-24	12+(11)	9+(1)	22+(4)
25-29	6+(6)	16+(1)	50+(15)
30-34	4+(1)	10+(2)	58+(8)
35+	2	6	13+(1)
TOTAL	83+(22)	41+(4)	143+(28)

The spermatozoa ratings have been assumed for those figures in parentheses.

Table 19. Reproductive condition of male Lemniscomys striatus in monthly collections.

MONTH	SPERMATOZOA RATINGS		
	(0)	($\frac{1}{4}$) & ($\frac{1}{2}$)	($\frac{3}{4}$) & (1)
APR.	-	-	-+(8)
MAY	1	1	7
JUNE (1-15)	10	2	13
JUNE (15-22)	8	9	5
JULY	21+(3)	2	2
AUG.	7+(15)	2+(1)	2
SEPT.	-	6	14+(1)
OCT.	-	2	18+(2)
NOV.	2	-	14+(3)
DEC.	12+(1)	5+(1)	8+(1)
JAN.	8	6+(1)	6
FEB.	8+(2)	2	6
MAR.	1+(1)	3	14+(2)
APR.	-	2	29+(10)
MAY	14	8+(1)	10+(1)
TOTAL	84+(22)	41+(4)	143+(28)

The spermatozoa ratings have been assumed for those figures in parentheses.

Table 20. Reproductive condition of female Mastomys natalensis according to the clean body-weight.

CLEAN WEIGHT (GMS.)	TOTAL NO.	IMMATURE		FECUND NOT PAROUS		PREGNANT		PAROUS	
		NO.	%	NO.	%	NO.	%	NO.	%
5-9	6	6	100	-	-	-	-	-	-
10-14	24	24	100	-	-	-	-	-	-
15-19	36	36	100	-	-	-	-	-	-
20-24	23	18	78	4	17	-	-	1	4
25-29	17	9	53	6	35	-	-	2	12
30-34	18	2	11	5	28	3	16½	8	44½
35-39	40	-	-	1	2½	16	40	23	57½
40-44	30	-	-	-	-	8	27	22	73
45-49	13	-	-	-	-	7	54	6	46
50+	10	-	-	-	-	7	70	3	30
TOTAL	217								

Table 21. Number of females of Mastomys natalensis examined each month (excluding live trap study specimens) and their reproductive condition.

MONTH	TOTAL	PREGNANT		LACTATING		PAROUS			NON PAROUS			IMMATURE	
		NO.	%	NO.	%	ANOESTROUS	ACTIVE	OESTROUS	ANOESTROUS	ACTIVE	OESTROUS	NO.	%
APR.	14	-	-	-	-	-	1	2	3	1	2	5	36
MAY	14	12	86	-	-	-	-	-	-	2	-	-	-
JUNE (1-15)	11	3	33	1	11	5	-	-	-	-	-	2	18
JUNE (15-22)	19	-	-	1	25	2	-	-	1	-	-	15	79
JULY	19	-	-	-	-	5	1	-	-	-	-	13	68 $\frac{1}{2}$
AUG.	9	-	-	-	-	1	1	-	-	-	-	7	78
SEPT.	16	-	-	-	-	6	-	-	-	-	-	1	56
OCT.	15	9	64	-	-	1	1	1	-	-	1	1	7
NOV.	34	16	57	5	18	6	1	-	-	-	-	6	18
DEC.	13	1	17	1	17	3	1	-	-	-	-	7	54
JAN.	14	-	-	1	17	3	2	-	-	-	-	8	57
FEB.	12	-	-	-	-	4	-	-	-	-	-	8	67
MAR.	6	-	-	-	-	2	-	-	-	-	-	4	67
APR.	14	-	-	-	-	2	-	-	-	2	2	8	57
MAY	3	-	-	1	33	2	-	-	-	-	-	-	-
TOTAL	213	41		10		42	8	3	4	6	6	93	

Table 22. Number of implanted embryos of Mastomys natalensis according to the clean body-weight of the parent.

243

NO. EMBRYOS	CLEAN BODY-WEIGHT (gms.)				
	30-34	35-39	40-44	45-49	50+
6	-	-	-	-	-
7	1	-	-	-	-
8	1	-	-	-	-
9	-	3	1	1	-
10	-	1	1	-	1
11	-	1	1	1	1
12	1	5	1	1	1
13	-	1	1	2	1
14	-	2	1	-	-
15	-	-	-	-	1
16	-	1	-	-	2
17	-	1	1	2	-
18	-	1	-	-	-
19	-	-	1	-	-
MEAN	9.0	12.5	13.1	13.3	13.3

Table 23. Reproductive condition of male Mastomys natalensis according to the clean body-weight.

244

CLEAN BODY-WEIGHT (GMS.)	SPERMATOZOA RATINGS		
	(0)	($\frac{1}{4}$) & ($\frac{1}{2}$)	($\frac{3}{4}$) & (1)
5-9	5	-	-
10-14	21	-	-
15-19	24+(2)	1	-
20-24	19+(1)	4	2
25-29	4	3	12+(1)
30-34	-	1	17+(2)
35-39	-	-	14+(2)
40-44	1	1	20+(1)
45-49	-	2	16+(4)
50-54	-	1	17+(2)
55-59	-	-	4+(2)
60-64	-	-	4
65-69	-	-	1
TOTAL	74+(3)	11	107+(14)

The spermatozoa ratings have been assumed for those figures in parentheses.

Table 24. Reproductive condition of male Mastomys natalensis in monthly collections.

245

MONTH	SPERMATOZOA RATINGS		
	(0)	($\frac{1}{4}$) & ($\frac{1}{2}$)	($\frac{3}{4}$) & (1)
APR.	-	-	-+(14)
MAY	-	-	3
JUNE	20	3	6
JULY	11	1	1
AUG.	11	3	7
SEPT.	-	-	21
OCT.	-	-	9
NOV.	2+(1)	-	14
DEC.	4+(2)	-	8
JAN.	11	4	2
FEB.	9	1	4
MAR.	4	1	9
APR.	-	-	14
MAY	2	-	9
TOTAL	74+(3)	11	107+(14)

Table 25. Reproductive condition of female Lophuromys sikapusi according to the clean body-weight.

CLEAN WEIGHT (GMS.)	TOTAL NO.	IMMATURE		FECUND NOT PAROUS		PREGNANT		PAROUS	
		NO.	%	NO.	%	NO.	%	NO.	%
25-29	2	2	100	-	-	-	-	-	-
30-34	2	2	100	-	-	-	-	-	-
35-39	2	2	100	-	-	-	-	-	-
40-44	5	4	80	1	20	-	-	-	-
45-49	2	1	50	1	50	-	-	-	-
50-54	-	-	-	-	-	-	-	-	-
55-59	7	-	-	1	14	2	29	4	57
60-64	5	1	20	-	-	3	60	1	20
65-69	6	-	-	-	-	6	100	-	-
70-74	12	-	-	-	-	7	58	5	42
75-79	11	-	-	-	-	10	91	1	9
80-84	7	-	-	-	-	6	86	1	14
85-89	10	-	-	-	-	9	90	1	10
90-94	3	-	-	-	-	3	100	-	-
TOTAL	74	12		3		46		13	

Table 26. Number of females of Lophuromys sikapusi examined each month and their reproductive condition.

MONTH	TOTAL	PREGNANT		NO. LACTATING	PAROUS			IMMATURE	
		NO.	%		ANOESTROUS	ACTIVE	ANOESTROUS	NO.	%
APRIL	1	1	100	-	-	-	-	-	-
MAY	1	1	100	-	-	-	-	-	-
JUNE (1-15)	2	2	100	-	-	-	-	-	-
JUNE (15-22)	1	1	100	-	-	-	-	-	-
JULY	6	1	25	1	1	1	-	2	33
AUG.	7	-	-	-	1	3	1	2	29
SEPT.	7	7	100	-	-	-	-	-	-
OCT.	7	6	100	-	-	-	-	1	14
NOV.	4	3	100	-	-	-	-	1	25
DEC.	6	3	100	-	-	-	-	3	50
JAN.	11	7	78	2	-	-	-	2	18
FEB.	2	-	-	-	-	-	2	-	-
MAR.	5	4	80	1	-	-	-	-	-
APRIL	6	5	83	1	-	-	-	-	-
MAY	8	5	71	2	-	-	-	1	12 $\frac{1}{2}$
TOTAL	74	46		7	2	4	3	12	

Table 27. Number of implanted embryos of Lophuromys sikapusi according to the clean body-weight of the parent.

NO. EMBRYOS	CLEAN BODY-WEIGHT (gms.)			
	55-64	65-74	75-84	85-94
1	-	-	-	-
2	2	4	1	-
3	1	7	8	8
4	2	2	6	2
5	-	-	1	2
MEAN	3.0	2.8	3.4	3.5

Table 28. Reproductive condition of male Lophuromys sikapusi according to the clean body-weight.

CLEAN BODY-WEIGHT (GMS.)	SPERMATOZOA RATINGS		
	(0)	($\frac{1}{4}$) & ($\frac{1}{2}$)	($\frac{3}{4}$) & (1)
25-29	1	-	-
30-34	2	-	-
35-39	5	-	-
40-44	3	-	-
45-49	2	1	-
50-54	2	2	2
55-59	1+(1)	1	1
60-64	-	-	3
65-69	-	2	2
70-74	-	-	4
75-79	-	-	3
80-84	-	-	7
85-89	-	1	9
90-94	-	-	3+(1)
95-100	-	-	1
TOTAL	16+(1)	6	35+(1)

The spermatozoa ratings have been assumed for those figures in parentheses.

Table 29. Reproductive condition of male Lophuromys sikapusi in monthly collections.

MONTH	SPERMATOZOA RATINGS		
	(0)	($\frac{1}{4}$) & ($\frac{1}{2}$)	($\frac{3}{4}$) & (1)
APR.	-	-	(1)
MAY	1	-	-
JUNE	1	-	3
JULY	4	1	1
AUG.	-	2	4
SEPT.	-	-	4
OCT.	1	-	4
NOV.	1	-	1
DEC.	2+(1)	-	4
JAN.	-	-	5
FEB.	-	2	3
MAR.	-	1	-
APR.	4	-	4
MAY	2	-	3
TOTAL	16+(1)	6	36+(1)

The spermatozoa ratings have been assumed for those figures in parentheses.

Table 30. Reproductive condition of female *Mus triton* according to the clean body-weight.

Table 31. Number of females of Mus triton examined each month (excluding live trap study specimens) and their reproductive condition.

MONTH	TOTAL	PREGNANT		NO. LACTATING	PAROUS			NON PAROUS		IMMATURE	
		NO.	%		ANOESTROUS	ACTIVE	OESTROUS	ANOESTROUS	NO.	NO.	%
APR.	-	-	-	-	-	-	-	-	-	-	-
MAY	4	3	100	-	-	-	-	-	1	25	
JUNE	4	2	50	1	-	-	-	1	-	-	
JULY	5	-	-	-	3	-	-	-	2	40	
AUG.	15	-	-	-	9	-	-	-	6	40	
SEPT.	14	4	36	-	5	-	1	1	3	21 $\frac{1}{2}$	
OCT.	9	4	50	-	2	1	1	-	1	11	
NOV.	3	1	50	-	1	-	-	-	1	33	
DEC.	2	2	100	-	-	-	-	-	-	-	
JAN.	1	-	-	-	1	-	-	-	-	-	
FEB.	7	-	-	-	3	-	-	1	3	43	
MAR.	18	-	-	-	6	-	-	3	9	50	
APR.	2	1	50	-	1	-	-	-	-	-	
MAY	17	-	-	1	7	-	-	-	9	53	
TOTAL	101	17		2	38	1	2	6	35		

Table 32. Reproductive condition of male Mus triton according to the clean body-weight.

253

CLEAN BODY-WEIGHT (GMS.)	SPERMATOZOA RATINGS		
	(0)	($\frac{1}{4}$) & ($\frac{1}{2}$)	($\frac{3}{4}$) & (1)
4-5 $\frac{1}{2}$	1	-	-
6-7 $\frac{1}{2}$	1+(1)	-+(1)	-
8-9 $\frac{1}{2}$	4	3+(1)	5+(1)
10-11 $\frac{1}{2}$	2	5+(1)	7
12-13 $\frac{1}{2}$	1	5+(1)	15+(2)
14-15 $\frac{1}{2}$	-	2	8+(3)
16-17 $\frac{1}{2}$	-	-	3
TOTAL	9+(1)	15+(4)	38+(6)

The spermatozoa ratings have been assumed for those figures in parentheses.

Table 33. Reproductive condition of male Mus triton in monthly collections.

MONTH	SPERMATOZOA RATINGS		
	(0)	($\frac{1}{4}$) & ($\frac{1}{2}$)	($\frac{3}{4}$) & (1)
APR.	-	-	-+(1)
MAY	-	-	3
JUNE	-	1	1
JULY	-	2+(1)	2
AUG.	-	4+(2)	3+(1)
SEPT.	-	1	3+(2)
OCT.	1	-	5+(1)
NOV.	1+(1)	-	-
DEC.	2	-+(1)	1
JAN.	-	3	3
FEB.	1	3	1
MAR.	-	1	9+(2)
APR.	-	-	1
MAY	4	-	6
TOTAL	9+(1)	15+(4)	38+(7)

The spermatozoa ratings have been assumed for those figures in parentheses.

Table 34. Reproductive condition of female Myomys cuninghamei according to the clean body-weight.

CLEAN WEIGHT (GMS.)	TOTAL NO.	IMMATURE		FECUND NOT PAROUS		PREGNANT		PAROUS	
		NO.	%	NO.	%	NO.	%	NO.	%
10-19	2	2	100	-	-	-	-	-	-
20-29	5	5	100	-	-	-	-	-	-
30-39	3	3	100	-	-	-	-	-	-
40-49	1	1	100	-	-	-	-	-	-
50-59	4	1	25	3	75	-	-	-	-
60-69	5	-	-	2	40	-	-	3	60
70-79	7	-	-	-	-	2	29	5	71
80-89	16	-	-	2	12 $\frac{1}{2}$	8	50	6	37 $\frac{1}{2}$
90-99	9	-	-	-	-	4	44	5	56
100-109	5	-	-	-	-	5	100	-	-
110-119	2	-	-	-	-	2	100	-	-
TOTAL	59								

Table 35. Number of females of Myomys cuninghamaei examined each month (excluding live trap study specimens) and their reproductive condition.

MONTH	TOTAL	PREGNANT		LACTATING		PAROUS		NON PAROUS			IMMATURE	
		NO.	%	NO.	%	ANOESTROUS	ACTIVE	ANOESTROUS	ACTIVE	OESTROUS	NO.	%
APR.	3	2	67	1	33	-	-	-	-	-	-	-
MAY	8	5	71	1	14	1	-	-	-	-	1	12 $\frac{1}{2}$
JUNE	6	2	50	-	-	1	1	-	-	-	2	33
JULY	6	-	-	-	-	2	1	2	-	-	2	33
AUG.	5	-	-	-	-	3	-	-	2	-	-	-
SEPT.	4	1	25	-	-	-	1	-	-	1	1	-
OCT.	5	3	75	1	25	-	-	-	-	-	1	20
NOV.	8	4	50	1	12 $\frac{1}{2}$	3	-	-	-	-	-	-
DEC.	2	1	100	-	-	-	-	-	-	-	1	50
JAN.	1	-	-	-	-	-	-	-	-	-	1	100
FEB.	-	-	-	-	-	-	-	-	-	-	-	-
MAR.	3	2	67	-	-	-	-	-	-	1	-	-
APR.	1	-	-	1	100	-	-	-	-	-	-	-
MAY	5	1	50	1	50	-	-	-	-	-	3	60
TOTAL	57	21		6		10	3	2	4	1	11	-

Table 36. Reproductive condition of male Myomys cunninghamei according to the clean body-weight.

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CLEAN BODY-WEIGHT (GMS.)	SPERMATOZOA RATINGS		
	(0)	($\frac{1}{4}$) & ($\frac{1}{2}$)	($\frac{3}{4}$) & (1)
20-29	1	-	-
30-39	2	-	-
40-49	3	-	1
50-59	-	-	-
60-69	2	1	1
70-79	-	-	1
80-89	-	-	2
90-99	-	-	2
100-109	-	-	1
110-119	-	-	4
120-129	-	-	2
130-139	-	-	2
140-149	-	-	1
TOTAL	8	1	17

Table 37. Reproductive condition of female Tatera valida according to the clean body-weight.

CLEAN WEIGHT (GMS)	TOTAL NUMBER	IMMATURE		FECUND NOT PAROUS		PREGNANT		PAROUS	
		NO.	%	NO.	%	NO.	%	NO.	%
20-29	5	5	100	-	-	-	-	-	-
30-39	6	6	100	-	-	-	-	-	-
40-49	6	6	100	-	-	-	-	-	-
50-59	5	5	100	-	-	-	-	-	-
60-69	2	2	100	-	-	-	-	-	-
70-79	4	1	25	1	25	-	-	2	50
80-89	11	1	9	4	36	1	9	5	46
90-99	12	-	-	-	-	3	25	9	75
100-109	6	-	-	1	17	1	17	4	67
TOTAL	57								

Table 38. Number of female Tatera valida examined each month and their reproductive condition.

MONTH	TOTAL NO.	PREGNANT		LACTATING		PAROUS			NON PAROUS			IMMATURE		
		NO.	%	NO.	%	ANOESTRUS	ACTIVE OESTRUS	ANOESTRUS	ACTIVE OESTRUS	NO.	%	NO.	%	
APRIL	1	-	-	-	-	-	-	-	-	1	-	-	-	
MAY	-	-	-	-	-	-	-	-	-	-	-	-	-	
JUNE (1-15)	6	1	25	2	50	1	-	-	-	-	-	2	33	
JUNE (15-22)	8	1	33	-	-	1	-	-	-	1	-	5	62 $\frac{1}{2}$	
JULY	8	-	-	1	33	1	-	-	-	-	1	-	5	62 $\frac{1}{2}$
AUG.	5	-	-	-	-	1	-	-	-	1	-	3	60	
SEPT.	3	-	-	-	-	1	-	-	-	1	-	1	33	
OCT.	7	1	20	1	20	-	1	1	-	-	-	1	29	
NOV.	5	2	40	2	40	1	-	-	-	-	-	-	-	
DEC.	1	-	-	-	-	-	-	-	-	-	-	1	100	
JAN.	-	-	-	-	-	-	-	-	-	-	-	-	-	
FEB.	6	-	-	-	-	-	1	-	-	-	-	5	83	
MAR.	3	-	-	-	-	2	-	-	-	-	-	1	33	
APRIL	2	-	-	-	-	-	1	-	-	-	-	1	50	
MAY	2	-	-	-	-	2	-	-	-	-	-	-	-	
TOTAL	57	5	6	10	3	1	3	2	1	26				

Table 39. Reproductive condition of male Tatera valida according to the clean body-weight.

CLEAN BODY-WEIGHT (GMS.)	SPERMATOZOA RATINGS	
	(0)	(1)
20-29	2	-
30-39	6	-
40-49	7	-
50-59	1	-
60-69	1	-
70-79	1	1+(1)
80-89	1	1
90-99	-	3
100-109	-	10
110-119	-	11
120-129	-	10
130-139	-	2
140-149	-	1
TOTAL	19	40

The spermatozoa ratings have been assumed for those figures in parentheses.

Table 40. Reproductive condition of male Tatera valida in monthly collections.

MONTH	SPERMATOZOA RATINGS	
	(0)	(1)
APR.	-	-+(1)
MAY	-	1
JUNE	1	4
JULY	3	1
AUG.	4	3
SEPT.	2	2
OCT.	-	10
NOV.	-	4
DEC.	5	2
JAN.	-	-
FEB.	3	3
MAR.	1	3
APR.	-	1
MAY	-	5
TOTAL	19	39+(1)

The spermatozoa ratings have been assumed for those figures in parentheses.

APPENDIX

TRAP SELECTION

(A) Introduction

The small mammal fauna of Africa includes a large number of species covering an appreciable size range. Pirlot and Van den Bulcke (1952), and Delany (1964a,b) have stressed the importance of using different sized traps in order to obtain representative collections. Unfortunately, there is little information on the selection of different species and sizes of animals by the various traps. Delany (1964a) compared the success of five traps and found that certain traps caught the smaller, and other traps the larger individuals, but he made no distinction between the different species of small mammals.

In the present study, the catches of two traps from the Crater Track area, the Reporter and Museum Special, were analysed in an attempt to discover what factors play an important part in the selection of animals. These traps were analysed because they caught most of the animals from this area and they were set in exactly the same way.

(B) Weight Selection of Traps

The distribution of the weights of animals of each species caught by the two traps (fig. A1) shows that for most species the catches of the two traps were very different. The difference was very marked for some species, such as Myomys and Arvicanthis.

The weights of animals caught by the two traps of each species were analysed by a computer programmed to convert the data into natural logarithms, and then calculate the (log.) mean, the sum, and the sum of squares about the mean. The log. transformation was used because it was expected (and found) that this made the variance within the species much more homogeneous. The relevant results for the subsequent statistical analyses are summarized in table A1.

The percentage of animals of each species caught by the Reporter Trap (table A1 and fig. A2) varies from 11 to 87 per cent. Both figs. A1 and A2 show that the Museum Special catches the smaller, and the Reporter the larger individuals and species. The total mean (log_e) difference in weight between the catches of the Reporter and Museum Special = 3.7168 (table A1). The mean trap difference = 3.7168/12 = 0.3097. Anti-log_(e) 0.3097 = 1.36. Thus, the Reporter catches animals of the same species 36 per cent heavier, on average, than the Museum Special. However, the mean trap difference varies considerably from species to species, which suggests that the species behave in different ways towards the two traps.

(1) The Test for Interaction or Heterogeneity of Data

To test if the suggested interaction (i.e. each species behaving differently) was significant, the $R \times 2$ table with disproportionate subclass numbers was used. The analysis is explained in Snedecor (1946, p. 291, table 11.24).

<u>Source of variation</u>	<u>d.f.</u>	<u>Sum of squares</u>	<u>Mean square</u>
Interaction	11	8.79	0.80
Individuals	1559	234.02	0.15

$$\underline{F} = 0.80/0.15 = 5.3, \underline{d.f.} = 11 \text{ and } 1559, \underline{F}_{.001} = \underline{\text{ca}} 3$$

The interaction is very large and highly significant. The species, therefore, behave in different ways towards the two traps.

(2) Analysis of Variance

To analyse the variation in the catches between the two traps, allowance must be made for the heterogenous data. The analysis of variance has been calculated from the data presented in table 41, following Snedecor (1946 pp. 291-292, table 11.25).

Completed Analysis of Variance

<u>Source of variation</u>	<u>Degrees of freedom</u>	<u>Sum of squares</u>	<u>Mean square</u>
Species	11	274.64	24.97
Traps	1	5.88	5.88
Interaction	11	8.79	0.80
Individuals	1559		0.15

The traps difference is based on one comparison so Student's t-test may be used to test its significance.

$$t_{11} = \sqrt{5.88/0.80} = 2.71$$

The probability of this arising by chance is about 2 per cent, therefore, the difference in weight selection by the traps is very significant. The completed analysis of variance shows that most of the variation in the weights of animals caught by the two traps is due to the species, then the trap selection, with very little variation due to the individuals.

(3) Analysis of Interaction

Although the species behave in different ways towards the two traps, there is a possibility that as the mean weight of the species increases, the difference in the mean weight of animals caught by the two traps also increases in a predictable way. To find if this was the case, the coefficient of regression of the difference of the mean $\log_{(e)}$ weights (column D, table A1) between the traps on the mean $\log_{(e)}$ weight of the species was calculated. Each point was weighted in the calculation, using the weighting factor, W , from table A1. The regression coefficient (fig. 71) was calculated to be 0.0932. The significance of the regression coefficient is calculated by testing the mean square of regression against the residual mean square of interaction (Mather, 1946, pp. 113-118).

Analysis of Variance of Interaction

<u>Source of variation</u>	<u>Degrees of freedom</u>	<u>Sum of squares</u>	<u>Mean square</u>
Regression	1	0.6	0.6
Residual	10	8.19	0.82
Total (Interaction)	11	8.79	

The regression is based on one comparison so Student's t-test may be used to test its significance.

$$t_{10} = \sqrt{0.6/0.82} = 0.85$$

The probability of this arising by chance is more than 40 per cent, therefore, the coefficient of regression cannot be regarded as being significantly different from zero.

The regression analysis is very insensitive, as the two overwhelmingly most numerous species (Lemniscomys and Mastomys) are close to the overall mean. Larger numbers of the extremely heavy or light species might have revealed a significant regression. Nevertheless, it is clear that weight differences could, at most, be only a minor factor in the behavioural differences of the various species towards the two traps.

(C) Discussion

It is clear that the traps used are far from satisfactory because a random sample is not achieved, and the trap selection varies from species to species. This must limit the conclusions that can be drawn from the results of the material collected. Earlier workers on small African mammals have largely ignored the question of trap selection, although the traps they used were probably just as unsatisfactory. This throws doubt on some of the conclusions drawn, such as estimates of the weights at weaning or attainment of sexual maturity. In future, it is suggested that some attention should be given to the design of traps for use in such animal populations.

(D) Summary

(1) The Reporter and Museum Special traps have different selections for each species.

(2) The Reporter trap catches animals of heavier weight than the Museum Special, for every species except Mus minutoides. This exception is based on a small sample and cannot be regarded as significant. On average, the Reporter catches animals of the same species 36 per cent heavier than the Museum Special.

(3) The weight difference is not a significant factor in the behavioural differences of the various species towards the two traps.

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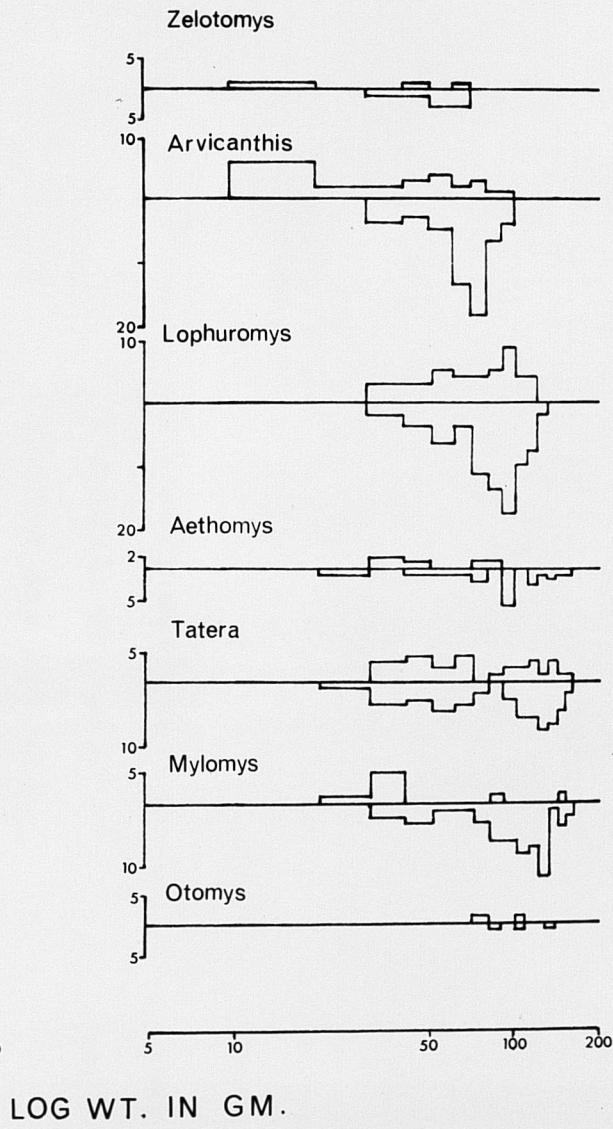
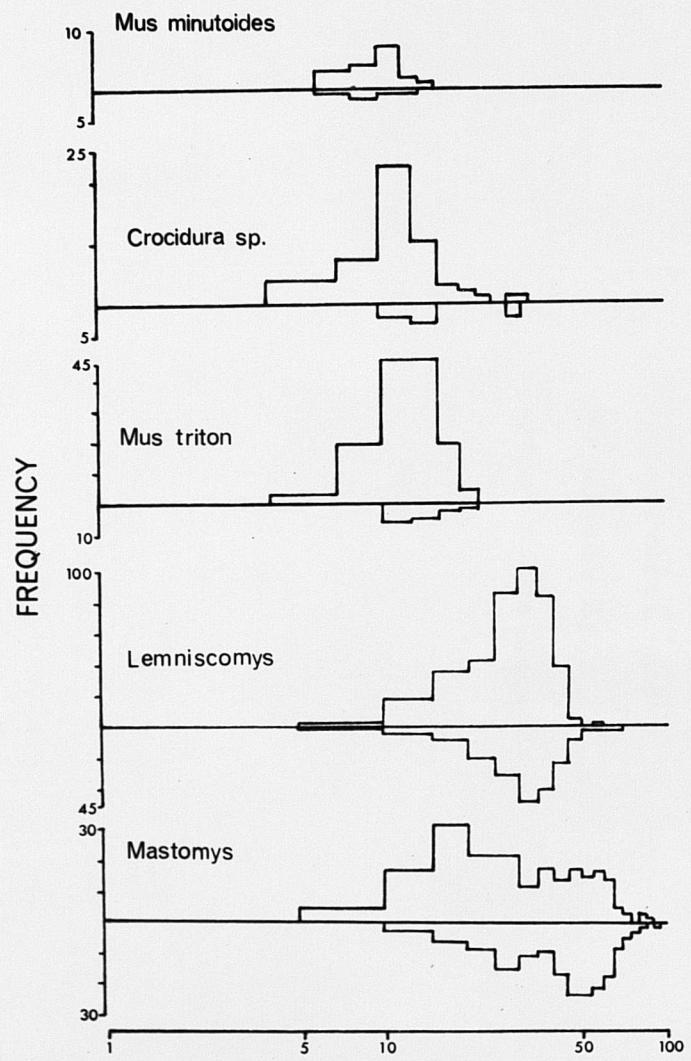


Fig. A1. Frequency distribution of the weights of animals caught by two traps, the Reporter and Museum Special. The distribution above the axis is for the Museum Special, and below the axis for the Reporter trap.

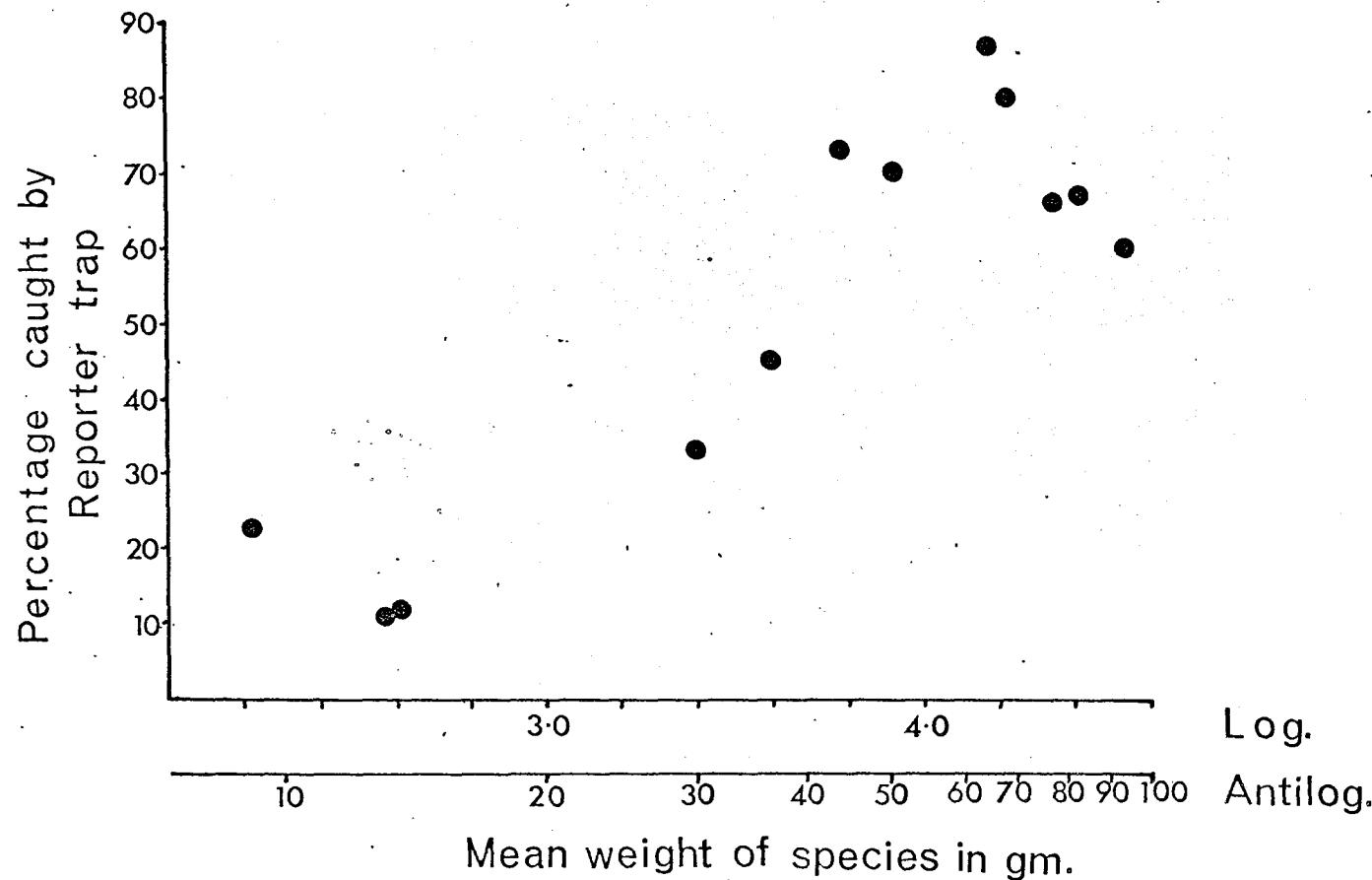


Fig. A2 - Percentage of animals caught by the Reporter trap according to the log mean weight of the species.

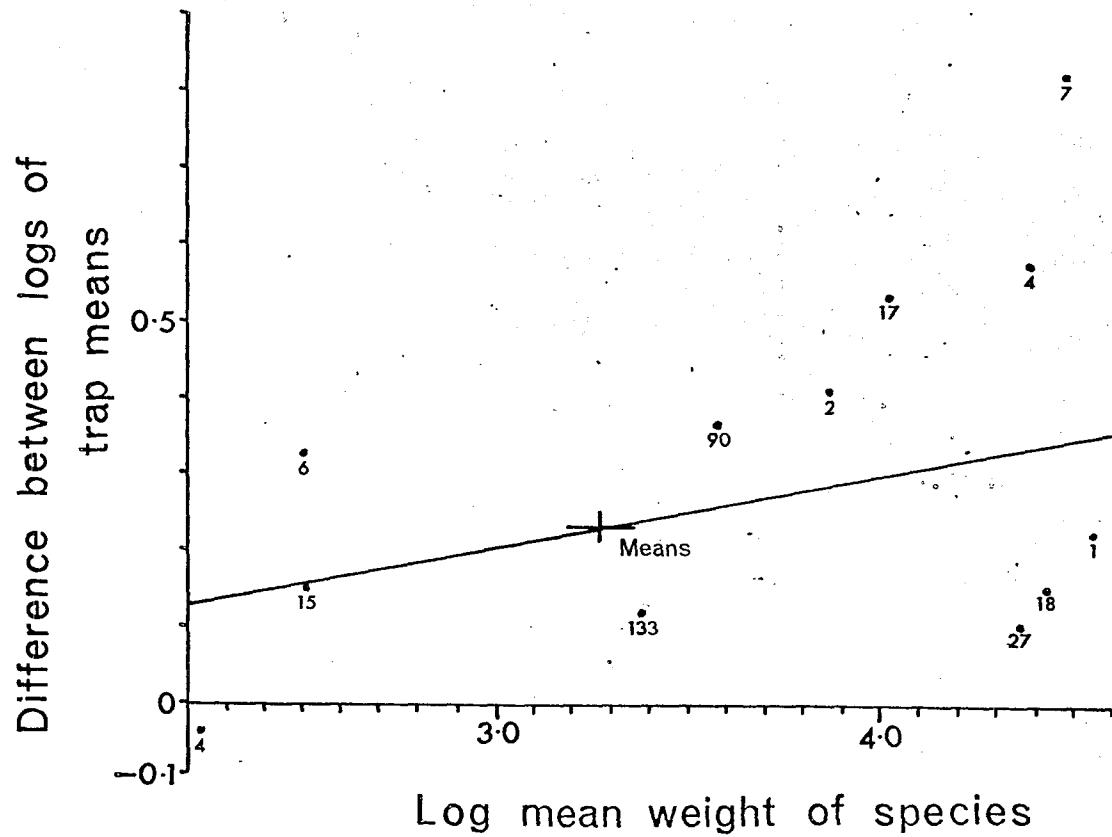


Fig. A3 - Scatter diagram and regression line of the difference between logs of the trap means on the log mean weight of the species.

Table Al. Number and mean log weight of 1,583 individuals of 12 species caught April 1965 - May 1966 in the Crater Track Area. (e) Species arranged in order of their mean weights.

Species	Reporter trap n ₁	mean ₁	Museum n ₂	Special mean ₂	$\frac{n_1 n_2}{n_1 + n_2}$ = W	mean ₁ - mean ₂ = D	(mean ₁ + mean ₂)/2 As Log. Antilog.	% caught by Reporter
<u>Mus minutoides</u>	5	2.1947	17	2.2388	3.86	-0.0440	2.2168	9.2g
<u>Mus triton</u>	17	2.6442	131	2.4976	15.05	0.1466	2.5709	13.1g
<u>Crocidura</u> sp.	7	2.7819	51	2.4578	6.16	0.3241	2.6199	13.7g
<u>Lemniscomys striatus</u>	197	3.4534	406	3.3374	132.64	0.1160	3.3954	29.8g
<u>Mastomys natalensis</u>	166	3.7739	199	3.4144	90.50	0.3596	3.5942	36.4g
<u>Zelotomys hildegardeae</u>	8	3.9809	3	3.5741	2.18	0.4067	3.7775	43.7g
<u>Arvicanthis niloticus</u>	55	4.1875	24	3.6568	16.71	0.5307	3.9222	50.5g
<u>Myomys cuninghamei</u>	55	4.5836	8	3.7563	6.98	0.8273	4.1699	64.7g
<u>Aethomys nyikae</u>	20	4.5064	5	3.9329	4.00	0.5739	4.2195	68.0g
<u>Lophuromys sikapusi</u>	80	4.3990	41	4.2975	27.11	0.1015	4.3482	77.3g
<u>Tatera valida</u>	56	4.4923	27	4.3401	18.22	0.1523	4.4162	82.8g
<u>Otomys irroratus</u>	3	4.6490	2	4.4268	1.20	0.2222	4.5379	93.5g
					324.61	3.7168	43.7886	

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INTRODUCTION

ALTHOUGH Uganda has an exceptionally rich mammal fauna, there has up to the present time been very little work published on the systematics and biology of these animals. Apparently, the only check list of Uganda mammals was that given by Oldfield Thomas in 1902 and published in Sir Harry Johnston's *The Uganda Protectorate*. The present work restricts itself to a review of the existing information on the murid rodents of Uganda. Thomas gave sixteen species occurring in the same general area (Uganda's boundaries have been changed since 1902) whereas the present list numbers forty-four. Even so, it is uncertain that this list is complete particularly in view of the fact that as recently as 1961 a new genus (*Delanymys*) was discovered in the south-west of the country and in 1963 a previously unrecorded genus (*Zelotomys*) was collected in Ankole. The main sources of information have been the collections in the British Museum (Natural History), the Coryndon Museum, Nairobi, published and unpublished literature and the collections made by Delany in 1961 and 1963. Of the unpublished, Hopkins manuscript entitled *The Known Wild Rodents of Uganda* has been particularly useful.

Descriptions of genera and species are given with keys to their identification. As we found it possible to identify almost every species without reference to cranial morphology or internal anatomy it has been decided to base the descriptions entirely on external characters. Such features as grooving of the incisors are included as their examination does not necessitate dissecting the animal in any way. Only in the identification of the species of *Otomys* has it been necessary to refer to other than external characters. All the measurements given in the text have been obtained from animals collected in Uganda. Animals that from their external measurements are obviously very young have been omitted.

The systematics include the reference to the original description of the genus and the name of the type species. The reference to the original description of each species is given together with the type locality. If the latter is outside Uganda the location follows the place name; if it is in Uganda then the location appears in the

gazetteer. Synonyms based on material collected in Uganda are also included. We have not attempted any revisions of the systematics although in several cases they are clearly required. Subgeneric names have been avoided. Whether forms such as *Grammomys*, *Praomys*, *Myomys*, *Mastomys* or *Hylomyscus* are genera or subgenera seems a matter of constant debate. We have given them generic status in accordance with fairly general usage, but we fully appreciate that future and more extensive studies may show them to be of lower taxonomic rank. Furthermore, the paucity of information on the variation shown by individual species has prompted us to omit any reference to subspecies. Only very much more collecting from the whole country can reveal the nature of the subspecies, clines and variability that may be present.

In the following account we have used Simpson's (1945) definition of the Muridae. His classification of the Myomorph rodents recognizes three superfamilies. They are, the Muroidea which includes the rats, mice, voles, gerbils and lemmings; the Gliroidea containing the dormice, and the Dipodoidea containing the jumping "mice" and the jerboas. None of the third group occur in Uganda whilst the Gliroidea are represented by the genus *Graphiurus* Smuts. The dormice are easily recognized by their small size and very bushy tail; although normally grey in colour, brown and buff forms also occur.

The Muroidea are split into four families; the Muridae which are being considered in the present account, the Spalacidae or mole rats of the Mediterranean region, the Rhizomyidae which has only one species recorded from Uganda (*Tachyoryctes ibeanus* Thomas) and the Cricetidae in which group are included the gerbils. *Tachyoryctes*, one of the African mole rats, is easily recognized and not readily confused with the murids. It is highly adapted for burrowing. The limbs are very short and the front legs broad and slightly flattened for digging; external ears are almost completely absent and the eyes are very small. The fur is long, soft and dense and usually brown to black in colour. The tail is very short.

The gerbils are the forms most likely to be confused with the murids and can only be separated from them by a combination of several characters. The hind limbs are long in proportion to the fore limbs (not so obvious in *Tatera*), the feet have long claws, the fur is soft and dorsally sandy or buff in colour. The belly fur and the backs of the hands and feet are pure white and a patch of short white hairs occurs behind the ear. The tail is long and hairy and often tufted. The upper incisors are grooved but on occasion the grooving is so shallow as to make it hardly perceptible. Two genera (*Tatera* and *Taterillus*) have been recorded from Uganda.

Petter (1964) has recently suggested that the genera *Cricetomys* and *Saccostomus* should be placed in the Cricetidae.

In the sections on distribution the locality from which animals have been obtained is given with the District except in Buganda where the reference is to the Kingdom. The latitude and longitude of each locality appears in the gazetteer. In addition the distributions have been mapped; the location of Buganda and the Districts outside this Kingdom are shown in Text-fig. 1. The distribution records are undoubtedly inadequate as almost every species probably has a wider and more continuous distribution than is suggested from the maps. This can only be remedied by

considerably more collecting. Some distribution records are very vague and may refer to no more than a District ; in which case the District is given in quotation marks. Various parts of Uganda appear to have been more rigorously collected than others with particularly large gaps occurring in Acholi, Busoga, east Toro and Ankole and in the north along the length of the Sudan border.

There is not a great deal of information available on the biology and breeding. Some data have been included from outside Uganda. However, there seemed little reason for including times of breeding of animals outside the country as this pheno-



FIG. 1. Map of Uganda showing the location of the Kingdom of Buganda and the Districts outside the Kingdom (underlined).

menon is probably influenced by local climatic conditions. As these vary considerably from one part of Africa to another (as well as in Uganda itself) the inclusion of times of breeding from elsewhere could give an erroneous picture of when breeding took place in Uganda.

We are particularly indebted for the very considerable help Mr. R. W. Hayman of the British Museum (Natural History) has given us with this work. We are grateful to the Royal Geographical Society for assistance in tracing some of the localities. The collecting trips made by M. J. D. in 1961 and 1963 were financed by grants from the Royal Society, the Percy Sladen Memorial Fund and the University of Southampton.

ABBREVIATIONS

The following abbreviations have been used in the text :—

cm.	centimetres	Mt.	Mount
Co.	County	N.	North
E.	East	Q.E.P.	Queen Elizabeth National Park
g.	grams	S.	South
h. & b.	head-and-body length	strm.	stream
h. f.	hind foot length	W.	West
meas.	measured	wt.	weight
M.N.P.	Murchison Falls National Park	♂	male
m.	metre(s)	♀	female
mm.	millimetres		

Months have been abbreviated to their first three letters.

The number of records of the number of foetuses have been indicated in brackets ; thus (2 x 1) signifies that two animals each had one foetus.

KEY TO THE GENERA OF UGANDA MURIDS

1	Large size (h. & b. 300–450 mm.). Long tail, distal portion white, proximal portion dark	<i>CRICETOMYS</i> (p. 338)
	Smaller with tail not showing this pattern of coloration	2
2	Dorsal fur either spiny or very bristly	3
	Dorsal fur neither spiny nor very bristly	6
3	Fur modified into distinct spines along dorsal surface	<i>ACOMYS</i> (p. 334)
	Fur bristly but not spiny	4
4	Dorsal fur chestnut, bristly and stiff; tail about 1.5 times h. & b.	<i>DEOMYS</i> (p. 343)
	Dorsal fur stiff and brush-like, reddish-brown; tail approximately equal to or less than h. & b.	5
5	Backs of hands and feet brown or black; belly red-brown or buff	<i>LOPHUROMYS</i> (p. 331)
	Backs of hands and feet white, belly white	<i>URANOMYS</i> (p. 336)
6	Either upper and lower incisors grooved or just the upper ones	7
	Neither upper nor lower incisors grooved	11
7	Both upper and lower incisors deeply grooved; fur long and soft; tail appreciably shorter than h. & b.	<i>OTOMYS</i> (p. 345)
	Upper incisors at least faintly grooved; lower incisors not grooved	8

8	Large forms (h. & b. over 100 mm.)	9
	Small forms (h. & b. under 100 mm.)	10
9	Fur coarse and harsh; belly hairs dirty yellow-grey	PELOMYS (p. 310)
	Fur thick and soft; belly hairs white at the tips and sharply demarcated from those at the flanks	MYLOMYS (p. 305)
10	Tail very short, less than 40 mm.	STEATOMYS (p. 342)
	Tail appreciably longer, over 60 mm.	DENDROMUS (p. 339)
11	With red tip to snout in sharp contrast to rest of body	OENOMYS (p. 305)
	Colour of snout neither bright red nor in sharp contrast with rest of body	12
12	Fur with metallic iridescent lustre	13
	Fur without metallic iridescent lustre	14
13	Fur rough and shaggy looking	DASYMYS (p. 307)
	Fur closely applied to the body	AETHOMYS (p. 317)
14	With at least one dorsal stripe	15
	Without stripes	17
15	A single black mid-dorsal stripe	HYBOMYS (p. 316)
	Several stripes present	16
16	Four black stripes along back; mid-dorsal line pale	RHABDOMYS (p. 315)
	Numerous pale stripes along back (may be composed of lines of spots); mid-dorsal line dark	LEMNISCOMYS (p. 313)
17	Tail considerably longer than h. & b.	18
	Tail approximately equal to h. & b. or shorter	23
18	Tip of tail with small but distinct pencil of hairs	19
	Tip of tail without pencil of hairs	20
19	Hind foot relatively broad	THAMNOMYS (p. 302)
	Hind foot not broadened	GRAMMOMYS (p. 304)
20	Very small (h. & b. less than 60 mm.); tail relatively long (about 100 mm.)	DELANYMYS (p. 343)
	H. & b. over 60 mm.; tail relatively not so long	21
21	Medium size (h. & b. 105 to 138 mm.)	PRAOMYS (p. 321)
	Smaller size (h. & b. 71 to 107 mm.)	22
22	Hairs of belly with white tips and grey bases	HYLOMYSCUS (p. 322)
	Hairs of belly pure white	MYOMYS (p. 324)
23	Medium size (h. & b. 127 to 160 mm.); tail $\frac{1}{3}$ to $\frac{1}{2}$ h. & b.	SACCOSTOMUS (p. 337)
	Small or medium size; if the latter tail is not short	24
24	Hairs coarse, strongly annulated black on buff, producing a "pepper and salt" effect; tail shorter than h. & b. but never less than $\frac{2}{3}$ h. & b. length; ears hairy	ARVICANTHIS (p. 309)
	Without "pepper and salt" effect	25
25	Medium size (h. & b. 133 to 171 mm.); tail about h. & b. length; hind feet very large (35 to 40 mm.)	MALACOMYS (p. 327)
	Variable size but with appreciably smaller hind feet	26
26	Upper incisors pro-odont (projecting forwards)	ZELOTOMYS (p. 327)
	Upper incisors not pro-odont	27
27	Small size (h. & b. less than 93 mm.)	MUS (p. 329)
	Larger size (h. & b. over 90 mm.)	28
28	Texture of fur very soft; flanks brown, belly grey with clear demarcation between the two	MASTOMYS (p. 325)
	Texture of fur coarse, dorsally brown to grey with a gradual transition in colour from back to belly with no sharp line of demarcation between flanks and belly	RATTUS (p. 319)

SYSTEMATIC ACCOUNT

Family MURIDAE Gray

1821. Muridae Gray, *London Med. Reposit.* **15** : 303.

Subfamily MURINAE Murray

1866. Murinae Murray, *The Geographic Distribution of Mammals* : 359.

Genus **THAMNOMYS** Thomas. Thicket Rats

1907. *Thamnomys* Thomas, *Ann. Mag. nat. Hist.*, (7) **19** : 121. Genotype *Thamnomys venustus* Thomas.

The genera *Thamnomys* and *Grammomys* are very similar. The tail is very long in both and with a pencil of hairs at its tip. The same is true of the gerbils but they can be separated from these two genera on other characters (p. 298). The hind foot of *Thamnomys* is broader than in *Grammomys*. Examination of the Uganda material shows differences in the colour of the belly fur in the two genera. In *Grammomys* the belly is pure white whilst in *Thamnomys* it is whitish washed with buff, or greyish with white tips. This character has not been found to hold good for all the specimens examined from other parts of Africa. We have recognized *T. kempi* as conspecific with *T. venustus*.

Hairs of belly white to bases, washed with buff	<i>T. rutilans</i>
Hairs of belly grey with white tips	<i>T. venustus</i>

***Thamnomys rutilans* (Peters)**

1876. *Mus rutilans* Peters, *Monatsb. K. preuss. Akad. Wiss., Berlin* **1876** : 478. Lambarene, Gaboon [$0^{\circ} 45' S.$ $10^{\circ} 15' E.$].

DESCRIPTION. Only specimen examined from Uganda has a rich suffusion of buff to the white hairs of the belly.

DISTRIBUTION. Zika Forest, Buganda. Text-fig. 2.

MEASUREMENTS. One ♂ h. & b. 145 mm. ; tail 172 mm. ; h. f. 25 mm. ; ear 17 mm. ; weight 54 g.

BREEDING. No information available.

HABITAT. Typically a forest species.

BIOLOGY. No information available.

***Thamnomys venustus* Thomas**

1907. *Thamnomys venustus* Thomas, *Ann. Mag. nat. Hist.*, (7) **19** : 122. Mubuku Valley, Toro.

1911. *Thamnomys kempi* Dollman, *Ann. Mag. nat. Hist.*, (8) **8** : 658. Buhamba, near Lake Kivu, Congo [$1^{\circ} 32' S.$ $29^{\circ} 19' E.$].

DESCRIPTION. Tips of belly hairs white, bases grey. Fur thicker and softer texture than *T. rutilans*.

DISTRIBUTION. Echuya Forest, Impenetrable Forest, Kigezi; Mihunga Swamp, Mubuku Valley, Toro. Text-fig. 2.

MEASUREMENTS. One ♂ h. & b. 125 mm.; tail 181 mm.; h. f. 25 mm.; ear 18 mm. Three ♀ h. & b. 151 mm., 131 mm., 141 mm.; tail 183 mm., 162 mm., 184 mm.; h. f. 26 mm., 26 mm., 28 mm.; ear 19 mm., 20 mm., 19 mm.; weights 66 g., 51 g., 56 g.

BREEDING. No information available.



FIG. 2. Distribution of *Thamnomys rutilans*, *T. venustus* and *Grammomys dolichurus*.

HABITAT. High altitude (including moist montane) forest.

BIOLOGY. Arboreal. Nocturnal (Allen & Loveridge, 1942).

Genus **GRAMMOMYS** Thomas. Tree Rats

1915. *Grammomys* Thomas, *Ann. Mag. nat. Hist.*, (8) **16** : 150. Genotype, by original designation, *Mus dolichurus* Smuts.

Separated, on external characters, from *Thamnomys* on the narrower hind foot. Long tail with a pencil of hairs at its tip. In the Uganda specimens examined the belly hairs are pure white without a buff suffusion. The dorsal fur is brown to grey-brown with, in some specimens, a buff line where flank and belly fur meet. Allen (1939) includes *Grammomys* as a subgenus of *Thamnomys*.

***Grammomys dolichurus* (Smuts)**

1832. *Mus dolichurus* Smuts, *Enumerat. Mamm. Capens.* : 38. Type locality given as "near Cape Town", South Africa but this is of uncertain accuracy (see Ellerman, Morrison-Scott & Hayman, 1953).
 1907. *Thamnomys dryas* Thomas, *Ann. Mag. nat. Hist.*, (7) **19** : 123. Mubuku Valley, Toro.
 1907. *Thamnomys macmillani* Wroughton, *Ann. Mag. nat. Hist.*, (7) **20** : 504. Wouida, north of Lake Rudolf, Ethiopia.
 1908. *Thamnomys surdaster* Thomas & Wroughton, *Proc. zool. Soc. Lond.* **1908** : 550. Zomba, Malawi [$15^{\circ} 22' S.$ $35^{\circ} 22' E.$].
 1910. *Thamnomys discolor* Thomas, *Ann. Mag. nat. Hist.*, (8) **5** : 283. Kakamega Forest, Kisumu, Kenya [$0^{\circ} 19' N.$ $34^{\circ} 51' E.$].

DESCRIPTION. As for genus.

DISTRIBUTION. Maramagambo Forest, Ankole ; Kalule, Kampala, Lialo, Nkyanuna, Buganda ; Salalira, "south Bugisu", Bugisu ; "Bukedi" ; Kotido, Lotome, Moroto, Karamoja ; Echuya Forest, Kumba, Nyalusanje, Kigezi ; Serere, Teso ; Ilumia, Mihunga, Mubuku Valley, Mweya, Wasa River, Toro ; Rhino Camp, West Nile. Text-fig. 2.

MEASUREMENTS. Three ♂ h. & b. 120 mm., 98 mm., 126 mm. ; tail 165 mm., 134 mm., 183 mm. ; h. f. 23 mm., 22 mm., 27 mm. ; ear 15 mm., 14 mm., 17 mm. ; weights ?, 24 g., 51 g. ♀ h. & b. 113.9 mm. (8 meas., range 99 to 130 mm.) ; tail 173.7 mm. (8 meas., range 150 to 205 mm.) ; h. f. 23.6 mm. (8 meas., range 22 to 25 mm.) ; ear 16.2 mm. (8 meas., range 15 to 20 mm.) ; weight 41.2 g. (5 weighed, range 33 to 53 g.).

BREEDING. Foetuses (1×3), Mweya ; (2×3) Moroto, Nov. In Zambia (3×4) (Ansell, 1960). Watson (1950) reports usually 3 young in a litter.

HABITAT. Scrub, bush and various types of forest.

BIOLOGY. Arboreal ; nocturnal. Build nests in bushes and trees. Outer part of nest of coarse grass with a lining of finely chewed grass. Brown house snake (*Boaedon lineatus*) reported to prey on it (Allen & Loveridge, 1942). Vegetarian, including seeds.

Genus **OENOMYS** Thomas. Rusty-nosed Rats

1904. *Oenomys* Thomas, *Ann. Mag. nat. Hist.*, (7) **13** : 416. Genotype, by original designation, *Mus hypoxanthus* Pucheran.

Medium sized rats easily recognized by their rusty-red nose. Upper surface brown or grey often with tinge of olive, this colour produced by the hairs having long buff or rufous tips and dark grey bases. Rump suffused with rusty-red colour. Backs of hands and feet pale brown. Flanks paler than back sharply demarcated from white of underside. Belly hairs white to roots. Tail grey-brown above, much paler below.

Oenomys hypoxanthus (Pucheran)

1855. *Mus hypoxanthus* Pucheran, *Rev. Mag. Zool.* **2** : 206. Gaboon.

1910. *Oenomys bacchante* Thomas and Wroughton, *Trans. zool. Soc. Lond.* **19** : 509. Mubuku Valley, Toro.

DESCRIPTION. As for genus.

DISTRIBUTION. Kampala, Buganda; Bubungi, Buyobo, Sipi, Bugisu; Fadjao, Bunyoro; Impenetrable Forest, Kigezi; Benet, Sebei; Bundibugyo, Bundimali, Ilumia, Kilembe, Kyatwa, Mihunga, Mubuku Valley, Sara, Toro. Text-fig. 3.

MEASUREMENTS. H. & b. ♂ 142.4 mm. (11 meas., range 105 to 167 mm.), ♀ 143.2 mm. (13 meas., range 131 to 159 mm.); tail ♂ 172.6 mm. (11 meas., range 150 to 205 mm.), ♀ 170.5 mm. (13 meas., range 135 to 187 mm.); h. f. ♂ 29.9 mm. (11 meas., range 24 to 33 mm.), ♀ 29.7 mm. (13 meas., range 28.5 to 31 mm.); ear ♂ 19.2 mm. (11 meas., range 18 to 21 mm.), ♀ 18.8 mm. (13 meas., range 17 to 21 mm.); weight ♂ 70 g., 90 g., ♀ 57 g., 76 g. (only four weighed).

BREEDING. Foetuses (5 × 3, 4 × 4) Kampala (Hopkins MS.); (1 × 3) in Congo (Misonne, 1963). Litter of three blind nestlings in Congo (Allen & Loveridge, 1942).

HABITAT. Tall grass bordering marshes and streams; swamps amongst *Cyperus latifolius* and fern.

BIOLOGY. Climbs easily and makes nests in grass.

Genus **MYLOMYS** Thomas

1906. *Mylomys* Thomas, *Ann. Mag. nat. Hist.*, (7) **18** : 224. Genotype, by original designation, *Mylomys cuninghamei* Thomas.

Medium sized rats with the dorsal surface a bright olive-gold, heavily lined with black; flanks with less black but sharply demarcated from the white of the underside. Tail generally a little shorter than the head-and-body length, black above, yellow buff or whitish below. Grooved upper incisors.

Mylomys cuninghamei Thomas

1906. *Mylomys cuninghamei* Thomas, *Ann. Mag. nat. Hist.*, (7) **18** : 225. East of Aberdare Mountains, Kenya [approximately 0°-1° S. 36° 45' E.].

1915. *Mylomys lutescens* Thomas, *Ann. Mag. nat. Hist.*, (8) **16** : 149. Nyalasanje, Kigezi.

DESCRIPTION. As for genus.

DISTRIBUTION. Para, Acholi; Lutoto, north of Maramagambo Forest, Ankole; Kampala, Mabira Forest, Buganda; Walasi Bugisu; Budama, Kidoko, Mulanda, Bukedi; Kanaba, Kiduha, Nyalusanje, Kigezi; Serere, Teso; Butiti, Crater Track, Toro. Text-fig. 3.

MEASUREMENTS. H. & b. ♂ 154.3 mm. (20 meas., range 122 to 183 mm.), ♀ 153.1 mm. (21 meas., range 125 to 180 mm.); tail ♂ 141.4 mm. (20 meas., 104 to 180 mm.), ♀ 142.2 mm. (20 meas., range 119 to 156 mm.); h. f. ♂ 33.2 mm. (20 meas., range 29 to 36 mm.), ♀ 32.4 mm. (21 meas., range 30 to 35 mm.); ear ♂ 18.5 mm.

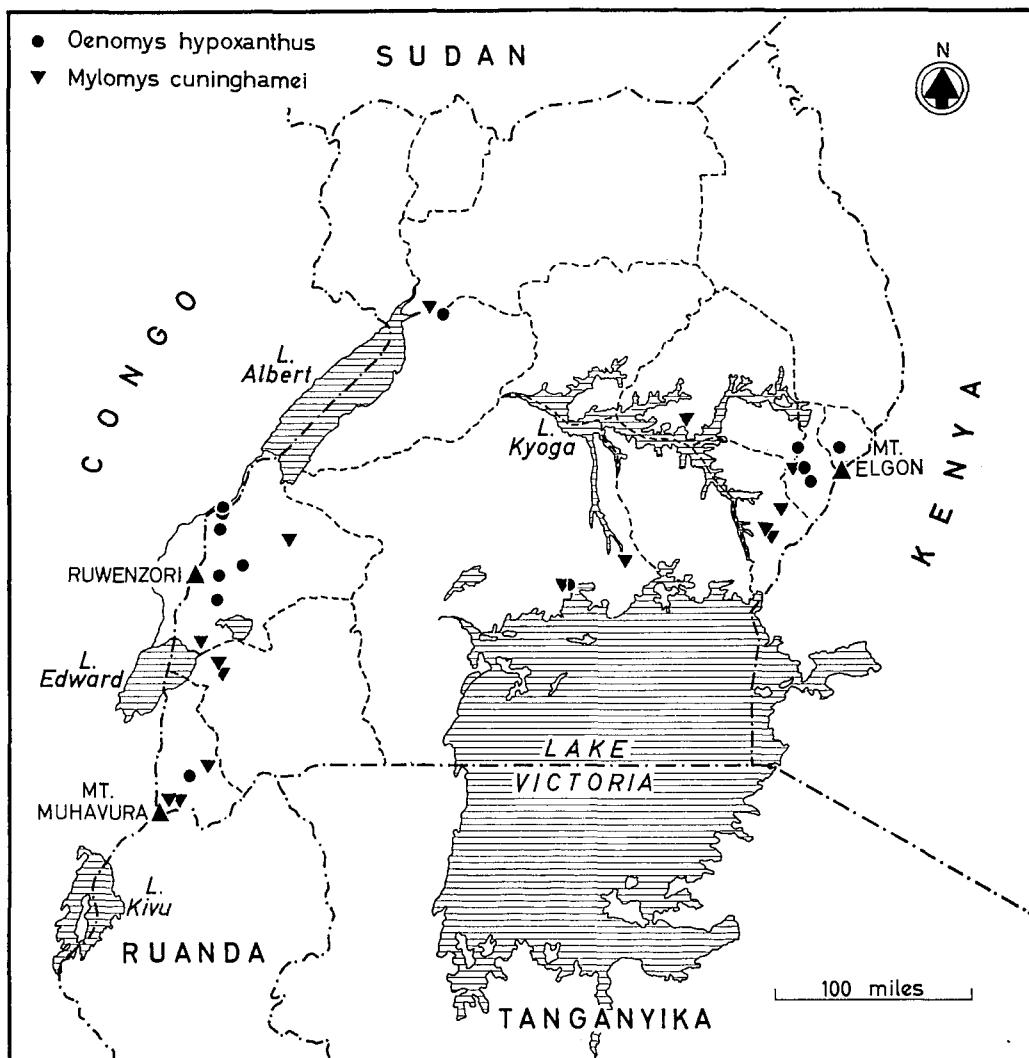


FIG. 3. Distribution of *Oenomys hypoxanthus* and *Mylomys cunninghamei*.

(17 meas., range 14 to 22 mm.), ♀ 18.8 mm. (20 meas., range 15 to 22 mm.) ; weight ♂ 103.1 g. (18 weighed, range 50 to 165 g.), ♀ 99.4 g. (20 weighed, range 46 to 160 g.).

BREEDING. Foetuses (1 × 3, wt. less than 1 g.), (1 × 5, wt. 18 g.) Jul. Crater Track. (1 × 5, wt. 1 g.), (1 × 4, wt. 4 g.) Aug. north of Maramagambo Forest. (1 × 3), (1 × 4 wt. 1 g.) Aug. Lutoto.

HABITAT. Typically thick grassland, heath and scrub.

BIOLOGY. Diurnal ? Herbivorous, eating grass leaves and stems.

Genus *DASYMYS* Peters. Shaggy Swamp Rats

1875. *Dasymys* Peters, *Mber. preuss. Akad. Wiss. Berl.* 1875 : 12. Genotype, by monotypy, *Dasymys gueinzii* Peters = *Mus incomitus* Sundevall.

Moderate sized rats with long, soft and untidy fur and sparsely haired tail. The animal has a flattened appearance. Dorsal hairs inconspicuously annulated black and buff giving the general effect of darkish grey tinged with brown or greyish brown. Backs of the hands and feet dark coloured, almost naked. Underside slaty grey with a greater or lesser amount of whitish admixture due to the pale tips of the hairs. Eyes small. Ears hairy. Ellerman (1941) and Hopkins (MS.) believe there is only one species of *Dasymys* in Uganda.

Dasymys incomitus (Sundevall)

1846. *Mus incomitus* Sundevall, *Övers. VetenskAkad. Förh. Stockh.* 3 : 120. "E. Caffraria prope Port Natal" (= Durban, Natal) [29° 53' S. 31° 00' E.]
 1875. *Dasymys gueinzii* Peters, *Mber. preuss. Akad. Wiss. Berl.* 1875 : 13. Interior of "Port Natal" (= Durban, Natal).
 1906. *Dasymys medius* Thomas, *Ann. Mag. nat. Hist.*, (7) 18 : 143. Mubuku Valley, Toro.
 1906. *Dasymys montanus* Thomas, *Ann. Mag. nat. Hist.*, (7) 18 : 143. Mubuku Valley, Toro.
 1911. *Dasymys orthos* Heller, *Smithson. misc. Coll.* 56 : 13. Butiaba, Bunyoro.

DESCRIPTION. As for genus.

DISTRIBUTION. Asuya, Gulu, Acholi ; near Kagambah, Lutoto, Ankole ; Kakumiro, Kampala, Mengo, Buganda ; Budama, Bukedi ; Butiaba, Bunyoro ; Echuya Swamp, Ingezi, Kiduha, Kumba, Nyalasanji, Kigezi ; Moyo, Madi ; Amuria, Serere, Teso ; Mihunga, Mubuku Valley, Toro ; Rhino Camp, West Nile. Text-fig. 4.

MEASUREMENTS. H. & b. ♂ 154.9 mm. (13 meas., range 146 to 166 mm.), ♀ 145.0 mm. (11 meas., range 130 to 170 mm.) ; tail ♂ 132.5 mm. (13 meas., range 111 to 150 mm.), ♀ 127.4 mm. (11 meas., range 105 to 150 mm.) ; h. f. ♂ 29.9 mm. (13 meas., range 26 to 32.5 mm.), ♀ 28.8 mm. (11 meas., range 27 to 31 mm.) ; ear ♂ 20.6 mm. (13 meas., range 19 to 23 mm.), ♀ 20.4 mm. (11 meas., range 17.5 to 25 mm.) ; one ♀ weighed 59 g.

BREEDING. Foetuses (1×4 , 1×5) in Zambia (Ansell, 1960); (3×2 , 3×3) Hopkins (MS.). Usually 2 to 4 in a litter in South West Africa (Shortridge, 1934).

HABITAT. Typically swamps, reed beds and river valleys. Occurs at various elevations; recorded from boggy moss covered ground between 12,500 and 14,000 feet on Ruwenzori. Misonne (1963) has found this species in mixed savanna in the Congo.

BIOLOGY. Vegetarian. Nests made of grass on surface of the ground.

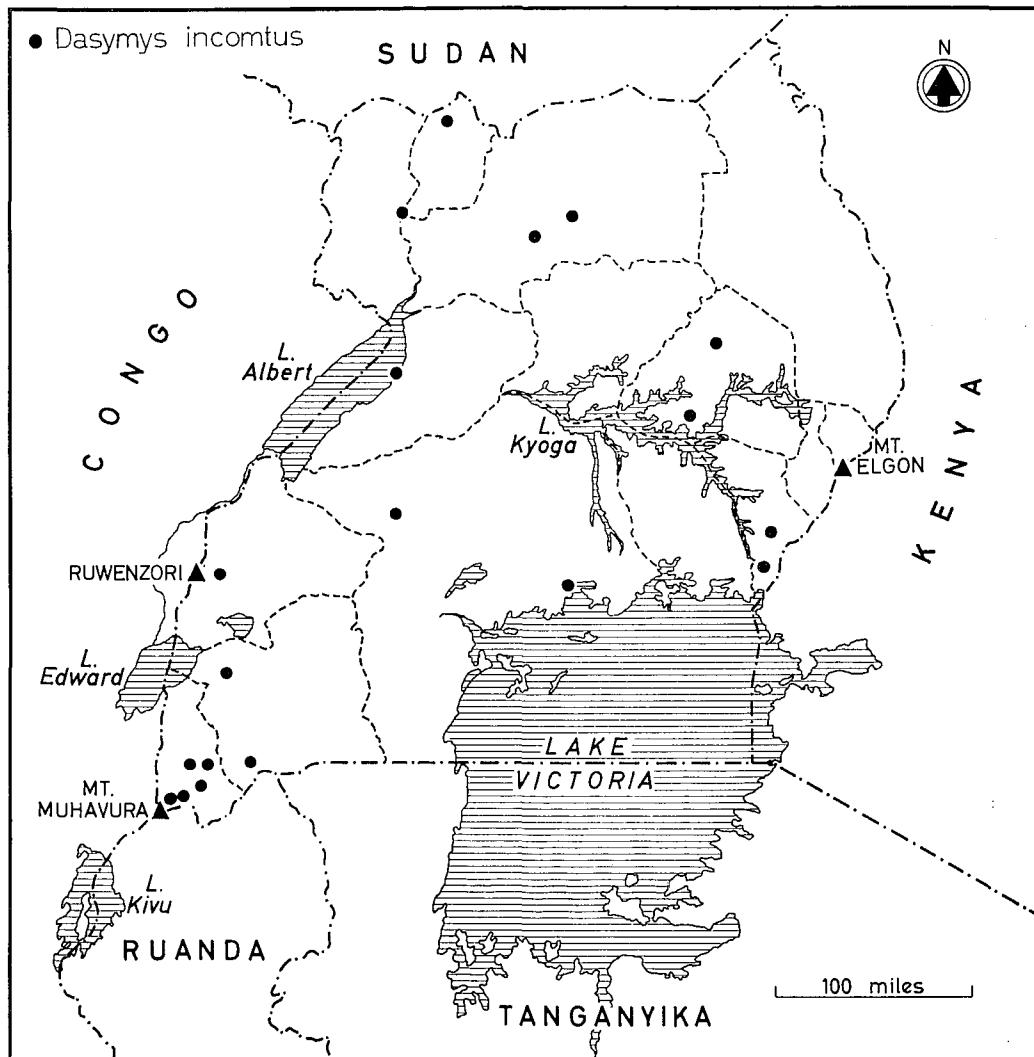


FIG. 4. Distribution of *Dasymys incomitus*.

Genus **ARVICANTHIS** Lesson. Unstriped Grass-mice

1842. *Arvicanthis* Lesson, *Nouv. Tabl. Regne Anim. Mammif.* : 147. Genotype, by monotypy and original designation, *Lemmus niloticus* Geoffroy, 1803 = *Hypudaeus variegatus* Lichtenstein, 1823 = *Arvicola niloticus* Desmarest, 1822.

1843. *Isomys* Sundevall, *K. svenska VetenskAkad. Handl.* 1842 : 219.

Medium sized animals, with fur composed of rather harsh hairs which are annulated with brown and buff in such a way as to produce a "pepper and salt" effect. The genus might be confused with *Myomys* but *Arvicanthis* has a grisly coloured under-surface and upper incisors without grooves. The tail is usually distinctly shorter than the head and body.

Arvicanthis niloticus (Desmarest)

1822. *Arvicola niloticus* Desmarest, *Mammalogie* 2 : 281. Egypt.

1842. *Mus abyssinicus* Rüppell, *Mus. Senckenbergianum* 3 : 104. Entschetqab, Simen Province, Ethiopia [13° 15' N. 38° 20' E.]

DESCRIPTION. As for genus.

DISTRIBUTION. Kitgum, Acholi; Congo Road, north of Maramagambo Forest, Burumba, Kagambah, Mbarara, Ankole; Buruli, Entebbe, Kakumiro, Kampala, Kisingo, Mabira Forest, near Masaka, Nalweyo, Buganda; Budongo Forest, Bulisa, Butiaba, Hoima, Kibiro, Masindi, Bunyoro; Amudat, Anamuget, Bokora, Kamchuru, Kotido, Locihotome, Moroto, Moruita, Nabilatuk, Karamoja; Nyakabande, Nyalusanje, Kigezi; Kibusi, Lango; Ajeluk, Amuria, Serere, Teso; Bugoye, Bundibugyo, Crater Track, Hakitengya, Ilumia, Kamulikwezi, Kilembe, Kimara, Makoga, Mpanga Forest, Mubuku Valley, Mweya, south-east Ruwenzori, Toro; Adropi, Arua, Offude, Rhino Camp, West Nile. Kibandama, Patong. Text-fig. 5.

MEASUREMENTS. H. & b. ♂ 146.3 mm. (54 meas., range 120 to 184 mm.), ♀ 141.6 mm. (59 meas., range 120 to 167 mm.); tail ♂ 110.8 mm. (54 meas., range 83 to 134 mm.), ♀ 109.7 mm. (58 meas.; range 86 to 129 mm.); h. f. ♂ 28.5 mm. (55 meas., range 23 to 32 mm.), ♀ 27.9 mm. (58 meas., range 25 to 32.5 mm.); ear ♂ 16.7 mm. (52 meas., range 13 to 20 mm.), ♀ 16.3 mm. (57 meas., range 13 to 20 mm.); weight ♂ 80.0 g. (23 weighed, range 57 to 120 g.), ♀ 77.5 g. (33 weighed, range 50 to 101 g.).

BREEDING. Foetuses (1 × 4) Aug. Congo Road, (1 × 4) Sep. Kamulikwezi. Watson (1950) reports a possible maximum breeding season towards the end of the rains as they are very numerous during the early months of the dry season.

HABITAT. Typically a grassland species but also common in bush and cultivated land. May be found in native huts and grain stores.

BIOLOGY. Nocturnal and diurnal. Herbivorous, eating leaves and stems, especially of *Ameranthus polygamus*. The black-shouldered kite (*Elanus coeruleus*) has been reported to prey on this species. It digs burrows in which it nests, often in banks or rubbish heaps or at the foot of bushes, with tunnels leading through the thick grass from them. They are made of fine grass and often placed four or five together, forming a warren. Surface nests also occur, as well as burrows, but it is not

known in what circumstances they are used. The underground nests are usually 8 inches to 2 feet deep. The surface nests are usually in a thick tussock of grass.

Genus **PELOMYS** Peters. Creek Rats

1852. *Pelomys* Peters, *Mber. preuss. Akad. Wiss. Berl.* 1852: 275. As a subgenus of *Mus* Linneaus; genotype, by monotypy, *Mus. (Pelomys) fallax* Peters.
 1910. *Desmomys* Thomas, *Ann. Mag. nat. Hist.*, (8) 5: 284. *Pelomys harringtoni* Thomas, valid as a subgenus.
 1924. *Komemys* de Beaux, *Ann. Mus. Stor. nat. Genova* 51: 207. *Komemys isseli* de Beaux, valid as a subgenus.



FIG. 5. Distribution of *Arvicanthis niloticus*.

The creek rats are medium sized rats. The colour of the dorsal surface rather resembles *Arvicanthis* from which they can be distinguished by the grooved upper incisors. They may or may not have a distinct dorsal stripe. The underside is dirty yellow, buff or greyish and not sharply demarcated from the dark coloured flanks. The relative length of the tail varies in the different species. *P. isseli* is included in the subgenus *Komemys* and the other two Uganda species in the subgenus *Pelomys*.

1	With very distinct black dorsal stripe	2
	Dorsal stripe absent	<i>P. fallax</i>
2	Tail about 1.5 times length of head and body	<i>P. isseli</i>
	Tail about as long as head and body	<i>P. hopkinsi</i>

Pelomys fallax (Peters)

1852. *Mus (Pelomys) fallax* Peters, *Mber. preuss. Akad. Wiss. Berl.* **1852** : 275. Caya District, Zambezi River, Portuguese East Africa = Sena, Mozambique [17° 20' S. 35° 10' E.].

DESCRIPTION. Golden-yellow above, the hairs heavily annulated with black, giving a "pepper and salt" effect as in *Arvicanthis*; no dark dorsal stripe. Underside olive buff. Tail just shorter than head-and-body length.

DISTRIBUTION. Kagambah, Mbarara, Ankole; Kiduha, Nyalasanje, Kigezi. Text-fig. 6.

MEASUREMENTS. H. & b. ♂ 142.3 mm. (6 meas., range 135 to 146 mm.), ♀ 147 mm. (1 meas.); tail ♂ 133.7 mm. (6 meas., range 127 to 137 mm.), ♀ 135 mm.; h. f. ♂ 29.7 mm. (6 meas., range 29 to 30 mm.), ♀ 29.5 mm.; ear ♂ 17.8 mm. (6 meas., range 17 to 18 mm.), ♀ 18 mm.; none weighed.

BREEDING. Foetuses, Ansell (1960) reports (1 × 9, 1 × 7); juveniles and subadults caught throughout the year suggests no fixed breeding season in Zambia.

HABITAT. Reported from swamps, reed beds, river banks and damp places.

BIOLOGY. Reported to be diurnal in South West Africa (Shortridge, 1934), but Ansell (1960) suggests that it is mainly nocturnal in Zambia. The South West African form of this species is reported to feed on reed shoots and other swamp vegetation, whilst in Tanzania it is stated to be destructive to grain crops. The species is a very able swimmer, and in Angola is reported to make deep burrows although no signs of any nests or holes have been found in other localities.

Pelomys isseli (de Beaux)

1924. *Komemys isseli* de Beaux, *Ann. Mus. Stor. nat. Genova* **51** : 207. Kome Island, Buganda.

DESCRIPTION. Upperside buff, sprinkled with black and with a very distinct black mid-dorsal stripe. Underside dirty whitish or buff. Tail nearly 1.5 times the length of the head and body.

DISTRIBUTION. Bugala Island, Kome Island, Buganda. Text-fig. 6.

MEASUREMENTS. Only two ♀ measured, h. & b. 100 and 106 mm.; tail 143 and 148.5 mm.; h. f. 29 and 29 mm.; ear 16 and 18.5 mm.; not weighed.

BREEDING. No information available.

HABITAT. No information available.

BIOLOGY. No information available.



FIG. 6. Distribution of *Pelomys* spp.

Pelomys hopkinsi Hayman

1955. *Pelomys hopkinsi* Hayman, *Rev. Zool. Bot. afr.* **52** : 323. Rwamachuchu, Kigezi.

DESCRIPTION. General appearance that of a small *Arvicanthis* with a distinct black mid-dorsal stripe. Underside generally buffy. Tail about as long as head and body.

DISTRIBUTION. Rwamachuchu, Kigezi. Text-fig. 6.

MEASUREMENTS. One ♂ meas., tail 135 mm. ; h. f. 32 mm.

BREEDING. No information available.

HABITAT. Edge of papyrus swamp.

BIOLOGY. No information available.

Genus *LEMNISCOMYS* Trouessart. Striped Grass-mice

1881. *Lemniscomys* Trouessart, *Bull. Soc. Sci. Angers* **10** : 124. As a subgenus of *Mus* Linnaeus ; genotype, by subsequent designation (Thomas, 1916, *Ann. Mag. nat. Hist.*, (8) **18** : 67), *Mus barbarus* Linnaeus.

The striped grass mice are characterized by the presence of a dark mid-dorsal line and numerous white dorsal and dorso-lateral stripes which may or may not be broken up into spots. The underside is pure white. The tail is hairy and as long as, or longer than the head and body. The fifth finger is shortened.

White dorsal and dorso-lateral stripes continuous	<i>L. barbarus</i>
White dorsal and dorso-lateral stripes broken into spots	<i>L. striatus</i>

Lemniscomys barbarus (Linnaeus)

1766. *Mus barbarus* Linnaeus, *Syst. Nat.* 12th ed., pt. 2, add. not paged. Morocco.

DESCRIPTION. Slightly smaller than *L. striatus* ; continuous stripes along body.

DISTRIBUTION. Paraa, Acholi ; Nabilatuk, Karomoja ; Ajeluk, Malera, Serere, Teso ; Rhino Camp, Wadelai, West Nile. Text-fig. 7.

MEASUREMENTS. H. & b. ♂ 105.7 mm. (7 meas., range 98 to 118 mm.), one ♀ 105 mm. ; tail ♂ 107.3 mm. (7 meas., range 95 to 116 mm.), ♀ 118 mm. ; h. f. 23.3 mm. (7 meas., range 22 to 25 mm.), ♀ 23 mm. ; ear ♂ 12.9 mm. (7 meas., range 12 to 15 mm.), ♀ 12 mm. ; weight ♂ 30.0 g. (6 weighed, range 23 to 36 g.), ♀ 41 g.

BREEDING. Foetuses (1 × 5) Oct., Nabilatuk.

HABITAT. Typically grass and scrub in dryer areas.

BIOLOGY. No information available.

Lemniscomys striatus (Linnaeus)

1758. *Mus striatus* Linnaeus, *Syst. Nat.* 10th ed., pt. 1 : 62. "India" = Sierra Leone (Thomas 1911, *Proc. zool. Soc. Lond.* **1911** : 148).

1910. *Arvicanthis macculus* Thomas & Wroughton, *Trans. zool. Soc. Lond.* **19** : 515. Muhokya, Toro.

1919. *Lemniscomys macculus* Hollister, *Bull. U.S. nat. Mus.* **99** : 138.

DESCRIPTION. Slightly larger of the two species. The white stripes broken into spots which may be joined to each other.

DISTRIBUTION. Awack, Fort Patiko, Pamdero, Acholi ; Congo Road, Maramagambo Forest, north of Maramagambo Forest, between Rwempuno and Kaizi Rivers, Kagambah, Ankole ; Entebbe, Kabanyolo, Kabula, Kajansi, Kampala, Kasai Forest, Kisingo, Lunyo, Mabira Forest, Nabugabo, Buganda ; Lwakaka, Bugisu ; Tororo, Bukedi ; Busingiro, Hoima, Masindi, Bunyoro ; Moroto, Namalu, Karamoja ;

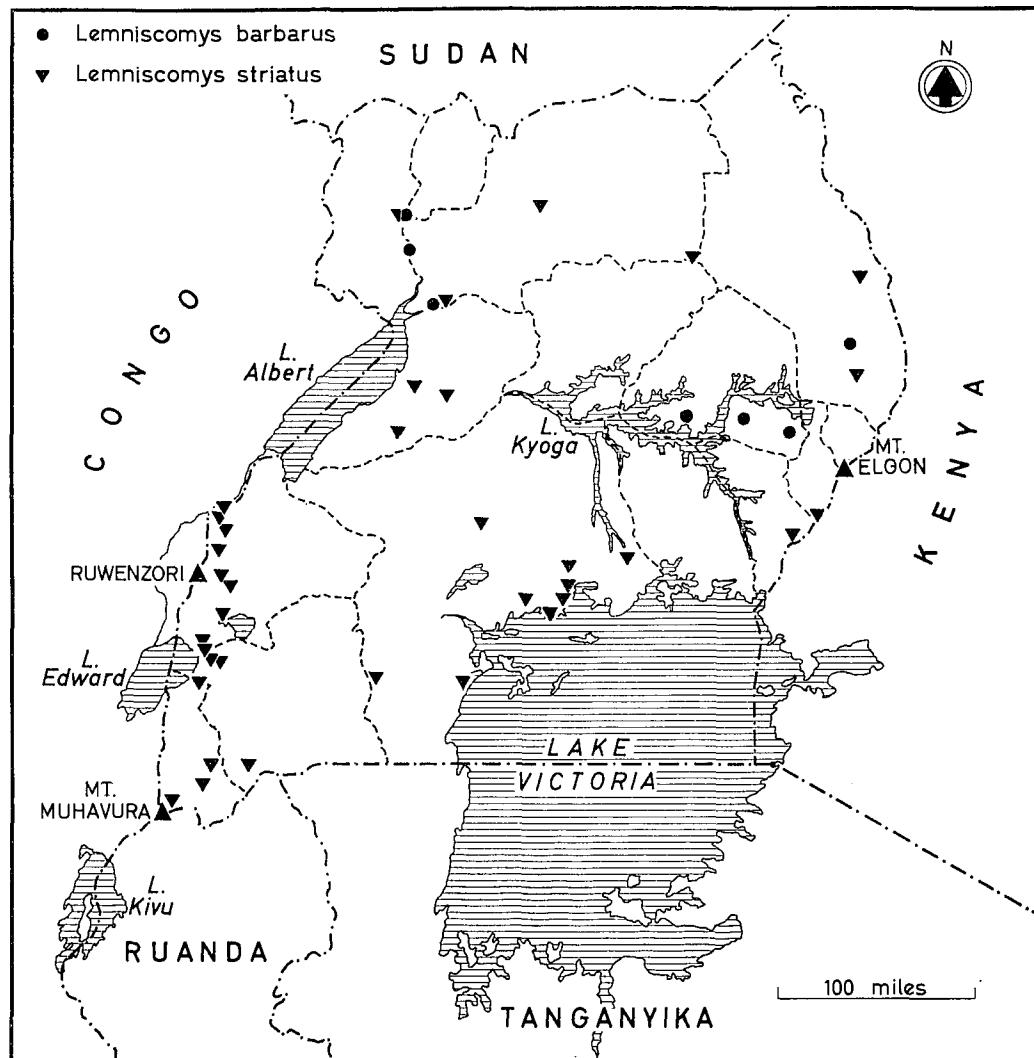


FIG. 7. Distribution of *Lemniscomys* spp.

Bugoye, Bundibugyo, Crater Track, Ilumia, Mihunga, Mpanga Forest, Mubuku Valley, Muhokya, Mweya, south east Ruwenzori, Tokwe, Toro ; Rhino Camp, West Nile. Text-fig. 7.

MEASUREMENTS. H. & b. ♂ 111.7 mm. (27 meas., range 93 to 131 mm.), ♀ 113.9 mm. (24 meas., range 91 to 142 mm.); tail ♂ 119.4 mm. (25 meas., range 92 to 144 mm.), ♀ 124.2 mm. (18 meas., range 103 to 141 mm.); h. f. ♂ 24.2 mm. (28 meas., range 20.5 to 27.5 mm.), 24.4 mm. ♀ (24 meas., range 20.5 to 27 mm.); ear ♂ 15.3 mm. (21 meas., range 14 to 17.5 mm.), ♀ 15.8 mm. (15 meas., range 14 to 17 mm.); weight ♂ 36.7 g. (13 weighed, range 27 to 46 g.), ♀ 38.2 g. (12 weighed, range 18 to 68 g.).

BREEDING. Foetuses (1 × 5) Aug. Maramagambo Forest ; Allen & Loveridge (1942) report (1 × 5) Dec. Kibale Forest, (1 × 5) Dec. Bundibugyo. Juveniles—4 nestlings Nov. Mabira Forest, 2 blind nestlings Jan. Mihunga, 2 young late Jan. Bugoye. Misonne (1963) reports litters of 3 to 6 in Congo.

HABITAT. Inhabits grassland, savanna, dense scrub and cultivated land. It is also apparently found in quite thick forest.

BIOLOGY. Nocturnal and diurnal. Omnivorous, observation of stomach contents showed leaf and stem remains, seeds and insects to be numerous. "Natives state that this species eats young shoots of grass, sweet potatoes, cassava and fallen maize cobs. The nest is often placed at the base of a tussock of tall grass, and is made from grass" (Hopkins MS.).

Genus **RHABDOMYS** Thomas. Four-striped Grass-mice

1916. *Rhabdomys* Thomas, *Ann. Mag. nat. Hist.*, (8) **18** : 69. Genotype, by original designation, *Mus pumilio* Sparrman.

Characterized by having four black stripes along length of body and a pale mid-dorsal line. Yellow to grey-brown ground colour. Tail black above, light brown below.

***Rhabdomys pumilio* (Sparrman)**

1784. *Mus pumilio* Sparrman, *K. svenska VetenskAkad. Handl.* **1784** : 236. Sitzicamma Forest, on Snake River, east of Cape of Good Hope, South Africa [33° 55' S. 23° 47' E.].

DESCRIPTION. As for genus.

DISTRIBUTION. Mudangi, Bugisu. Text-fig. 8.

MEASUREMENTS. H. & b. ♂ 106 mm., ♀ 103 mm. ; tail ♂ 82 mm., ♀ 81 mm. ; h. f. ♂ 22 mm., ♀ 20 mm. ; ear ♂ 12 mm., ♀ 11 mm.

BREEDING. Foetuses (2 × 5, 1 × 3) in Kenya. From South West Africa 6 and 7 foetuses have been reported (Shortridge, 1934). Breed at 3 months.

HABITAT. In East Africa only recorded from high altitudes. In South West Africa frequent in bushy and semi-dry vlei country, mainly in scrub, long grass and forest edges (Shortridge, 1934).

BIOLOGY. Ground-dwelling but also, to a limited extent, arboreal. Makes burrows. Diurnal. Mainly vegetarian but also recorded as eating snails, insects and eggs and nestlings of birds.

Genus **HYBOMYS** Thomas. Back-striped Mice

1910. *Hybomys* Thomas, *Ann. Mag. nat. Hist.*, (8) 5 : 85. Genotype, by original description, *Mus univittatus* Peters.

1911. *Typhomys* Thomas, *Ann. Mag. nat. Hist.*, (8) 7 : 382. Genotype, by original description, *Mus trivirgatus* Temminck. Synonym of *Hybomys* (Ingoldby, *Ann. Mag. nat. Hist.*, (10) 3 : 522).



FIG. 8. Distribution of *Rhabdomys pumilio* and *Hybomys univittatus*.

Medium sized rats characterized by having a rather indistinct mid-dorsal black line running from between the ears to the base of the tail. Upperside light brown, usually with a strong reddish tinge which is particularly well marked on the rump. Underside light buffy-grey contrasting sharply with the flanks. Scales of tail not at all obscured by the short hairs. Tail slightly shorter than head-and-body length. Hindfeet with long toes. Incisors not grooved.

***Hybomys univittatus* (Peters)**

1876. *Mus univittatus* Peters, *Monatsb. K. preuss. Akad. Wiss. Berl.* **1876** : 479. Donghila, Gaboon [$0^{\circ} 12'$ N. $9^{\circ} 44'$ E.].

DESCRIPTION. As for genus.

DISTRIBUTION. Kalinzu Forest, Maramagambo Forest, Ankole; Malabigambo Forest, Mpanga Forest, Buganda; Impenetrable Forest, Kigezi; Mpanga Forest, Mubuku Valley, north Ruwenzori, Toro. Text-fig. 8.

MEASUREMENTS. H. & b. ♂ 118.5 mm. (8 meas., range 103 to 128 mm.), ♀ 117.9 mm. (11 meas., range 108 to 127 mm.); tail ♂ 105.5 mm. (8 meas., range 85 to 116 mm.), ♀ 103.9 mm. (11 meas., range 86 to 115 mm.); h. f. ♂ 27.2 mm. (8 meas., range 26 to 29 mm.), ♀ 26.4 mm. (11 meas., range 24 to 28 mm.); ear ♂ 15.6 mm. (8 meas., range 15 to 17 mm.), ♀ 15.5 mm. (11 meas., range 14 to 17.5 mm.); weight ♂ 50.7 g. (6 weighed, range 46 to 61 g.), ♀ 49.4 g. (7 weighed, range 38 to 56 g.).

BREEDING. Foetuses (2×3) (1 lactating) Oct. Impenetrable Forest, (1 \times 2) lactating Jul. Mpanga Forest (Buganda). Two ♀ lactating Sep. Maramagambo Forest. Misonne (1963) reports two embryos in Congo animals.

HABITAT. Apparently confined to forest being found in rain forest, transition forest and mountain forest but not bamboo forest. It has not been found in gallery forest. It is more abundant in secondary vegetation than in primary forest; apparently prefers the wetter parts of forest.

BIOLOGY. Reported by the Congo expedition to eat "the red fruit of a lily-like plant of which chimpanzees are so fond" (Hatt, 1940). Two stomachs examined by Delany (1964b) contained only vegetable matter. Apparently a good swimmer.

Genus ***AETHOMYS*** Thomas. Bush Rats

1915. *Aethomys* Thomas, *Ann. Mag. nat. Hist.*, (8) **16** : 477. As a subgenus of *Epimys* Trouessart = *Rattus* Fisher; genotype, by original designation, *Epimys hindei* (Thomas).

Medium sized rats with tail usually a little shorter than head-and-body length. Incisor teeth ungrooved. Fur soft, smooth and tidy, but not silky and with a metallic lustre. Hairs of underside with pure white tips, with long slate grey bases, mottled when hairs displaced. The backs of the hands and feet are white.

Tail sparsely haired, nearly as long as, or occasionally slightly longer than head and body; dorsal pelage light brown in colour ***A. kaiseri***
 Tail more hairy, barely longer than body without head; dorsal pelage rich warm brown ***A. nyikae***

Aethomys kaiseri (Noack)

1887. *Epimys kaiseri* Noack, Zool. Jb. Syst. 2 : 228. Qua Mpala (Marungu), southern Congo [6° 46' S. 29° 32' E.].

DESCRIPTION. Tail sparsely haired; upper side dark brownish grey or brown; underside mainly white, grey bases of hairs show if the fur is ruffled.

DISTRIBUTION. Chua, Fort Patigo, Paraa, Acholi; Entebbe, Kabanyolo, Kabulamuleri, Kakumiro, Kampala, Kikonda, Kisingo, Lialo, Nabugabo, Nkyanuna, Zika Forest, Buganda; Tororo, Bukedi; Hoima, Bunyoro; Moroto, Nabilatuk, Namalu, Karamoja; Ajeluk, Serere, Teso; Kimara, Wanka R., Wassa R., Toro; Nebbi, Ngal, Offude, Pakwach, Rhino Camp, West Nile. Text-fig. 9.

MEASUREMENTS. H. & b. ♂ 160·4 mm. (18 meas., range 140 to 184 mm.), ♀ 149·5 mm. (10 meas., range 135 to 169 mm.); tail ♂ 156·8 mm. (18 meas., range 140 to 186 mm.), ♀ 145·8 mm. (10 meas., range 121 to 180 mm.); h. f. ♂ 29·2 mm. (17 meas., range 26 to 32 mm.), ♀ 29·0 mm. (10 meas., range 26 to 32 mm.); ear ♂ 19·0 mm. (13 meas., range 17 to 21 mm.), ♀ 19·0 mm. (8 meas., range 16 to 23 mm.); weight ♂ 109·0 g. (10 weighed, range 62 to 150 g.), ♀ 82·4 g. (7 weighed, range 58 to 100 g.).

BREEDING. Foetuses (1 × 3) Sep. Kabanyolo, (3 × 3) Kampala (Hopkins MS.). Three large young observed attached to nipples of ♀ in Tanzania (Allen & Loveridge, 1942).

HABITAT. Open country, thick grassland. Southern & Hook (1963a) report finding this rat in the ground layer of seasonal forest, the swamp edge of lakeside forest and in deserted shambas at the edge of forest.

BIOLOGY. Occasionally enters houses (Hopkins MS.).

Aethomys nyikae (Thomas)

1897. *Mus nyikae* Thomas, Proc. zool. Soc. Lond. 1897 : 431. Nyika Plateau, northern Nyasaland [approximately 10° 30' S. 33° 52' E.].

1907. *Mus walambae* Wroughton, Mem. Manchr. lit. phil. Soc. 51 : 21. Msufu River, Rhodesia [close to 13° 30' S. 29° E.].

DESCRIPTION. Tail more hairy and the underside a darker grey than in *A. kaiseri*. Dorsal pelage a rich warm brown. Tail shorter in proportion to head-and-body length than *A. kaiseri*.

DISTRIBUTION. Kagambah, Mbarara, near Lake Nakivali, Ankole; Koki Co., Buganda; "Kigezi". Text-fig. 9.

MEASUREMENTS. Two ♂ h. & b. 159 mm., 162 mm.; tail 124 mm., 150 mm.; h. f. 28 mm., 28·5 mm.; ear 21 mm., 22 mm.; none weighed. ♀ h. & b. 167·9 mm. (7 meas., range 148 to 196 mm.); tail 138·4 mm. (7 meas., range 131 to 151 mm.); h. f. 30·3 mm. (7 meas., range 28 to 33 mm.); ear 22·3 mm. (7 meas., range 20 to 24 mm.); none weighed.

BREEDING. Foetuses, in Zambia, (1 × 2), (1 × 4), (1 × 5) (Ansell, 1960).

HABITAT. In Zambia, usually in ant hills in woodland (Ansell, 1960).

BIOLOGY. No information available.

Genus **RATTUS** Fischer. House Rats

1803. *Rattus* [sic] Fischer, *Natmus. Naturg. Paris* 2: 128. Genotype, by subsequent designation (Hollister, 1916, *Proc. biol. Soc. Wash.* 29: 126), *Mus decumanus* Pallas = *Mus norvegicus* Berkenhout.

1881. *Epimys* Trouessart, *Bull. Soc. Sci. Angers* 10: 117. As a subgenus of *Mus* Linnaeus; genotype *Mus ratus* Linnaeus.



FIG. 9. Distribution of *Aethomys* spp.

Medium sized rats with incisor teeth ungrooved. Dorsal pelage not striped, rather long and slightly harsh; varying shades of grey and brown. Underside varies in colour from creamy to dark slate, never pure white. No clear demarcation between flanks and belly. Tail usually longer than head and body, and uniformly dark coloured along length.

***Rattus rattus* (Linnaeus)**

1758. *Mus rattus* Linnaeus, *Syst. Nat.*, 10th ed., 1: 61. Uppsala, Sweden [59° 55' N. 18° 08' E.].

DESCRIPTION. As for genus.

DISTRIBUTION. Patiko, Acholi; Gayoza, Kichwamba, Ankole; Entebbe, Kampala, Mabira Forest, Masaka, Buganda; Biso, Budongo Forest, Butiaba, Masindi Port, Bunyoro; Iriri, Moroto, Namalu, Karamoja; Nyakabande, Kigezi; Kapiri, Serere, Teso; Bundibugyo, Fort Portal, Isungo, Katwe, Mihunga, Muhokya, south east Ruwenzori, Toro; Rhino Camp, West Nile. Probably occurs in all towns throughout Uganda. Text-fig. 10.

MEASUREMENTS. H. & b. ♂ 142.2 mm. (9 meas., range 109 to 193 mm.), 3 ♀ measured, 126 mm., 150 mm., 170 mm.; tail ♂ 172.6 mm. (9 meas., range 148 to 198 mm.), ♀ 124 mm., 189 mm., 192 mm.; h. f. ♂ 31.7 mm. (9 meas., range 31 to 33 mm.), ♀ 29 mm., ?, 33 mm.; ear ♂ 21.3 mm. (9 meas., range 19 to 24 mm.), ♀ 21 mm., ?, 22.5 mm.; weight ♂ 62.5 g. (5 weighed, range 47 to 92 g.), ♀ 58 g., 100 g., ?.

BREEDING. Breeding data from Kenya and Congo (Misonne, 1963) indicate that *Rattus* breeds throughout the year, with a peak during the long rains in the early part of the year and with a second smaller peak during the later rains. Breeding at a minimum during the dry seasons. The average number of foetuses in 54 pregnant females collected in Kampala was 6 (Hopkins MS.). Watson (1950) reports that the average number in a litter is 6 or 7 in Uganda. The young when born are blind with the external ears sealed down. The eyes open on the fourteenth day, weaning takes place about a month after birth. The gestation period is 21 days.

HABITAT. Essentially a dweller in huts and houses; when found in open usually in close proximity to buildings. Generally found in thatch of huts, but occasionally may be found in the walls and floor.

BIOLOGY. Exclusively nocturnal. Omnivorous, food includes all kinds of grain, groundnuts, cotton seed, meat, potatoes etc. Competes with *Mastomys*, the other commensal rat, which it has now excluded from most towns. It is a vector of the flea *Xenopsylla* and there is no doubt that it is also the principle vector of plague in Uganda (Hopkins MS.). Allen & Loveridge (1942) report that predators include the owl (*Bubo africanus*), brown house snake (*Boaedon lineatus*), gaboon viper (*Bitis gabonica*), nose-horned viper (*Bitis nasicornis*) and the black-necked cobra (*Naja nigricollis*).

Genus *PRAOMYS* Thomas. Soft-furred Rats

1915. *Praomys* Thomas, Ann. Mag. nat. Hist., (8) 15 : 477. As a subgenus of *Epimys* Trouessart = *Rattus* Fischer; genotype, by original designation, *Epimys tullbergi* (Thomas).

Similar to *Mastomys* with fur of silky texture; tail appreciably longer and only three pairs of mammae present. Tail almost naked. Fur brown to black dorsally, greyish white ventrally.

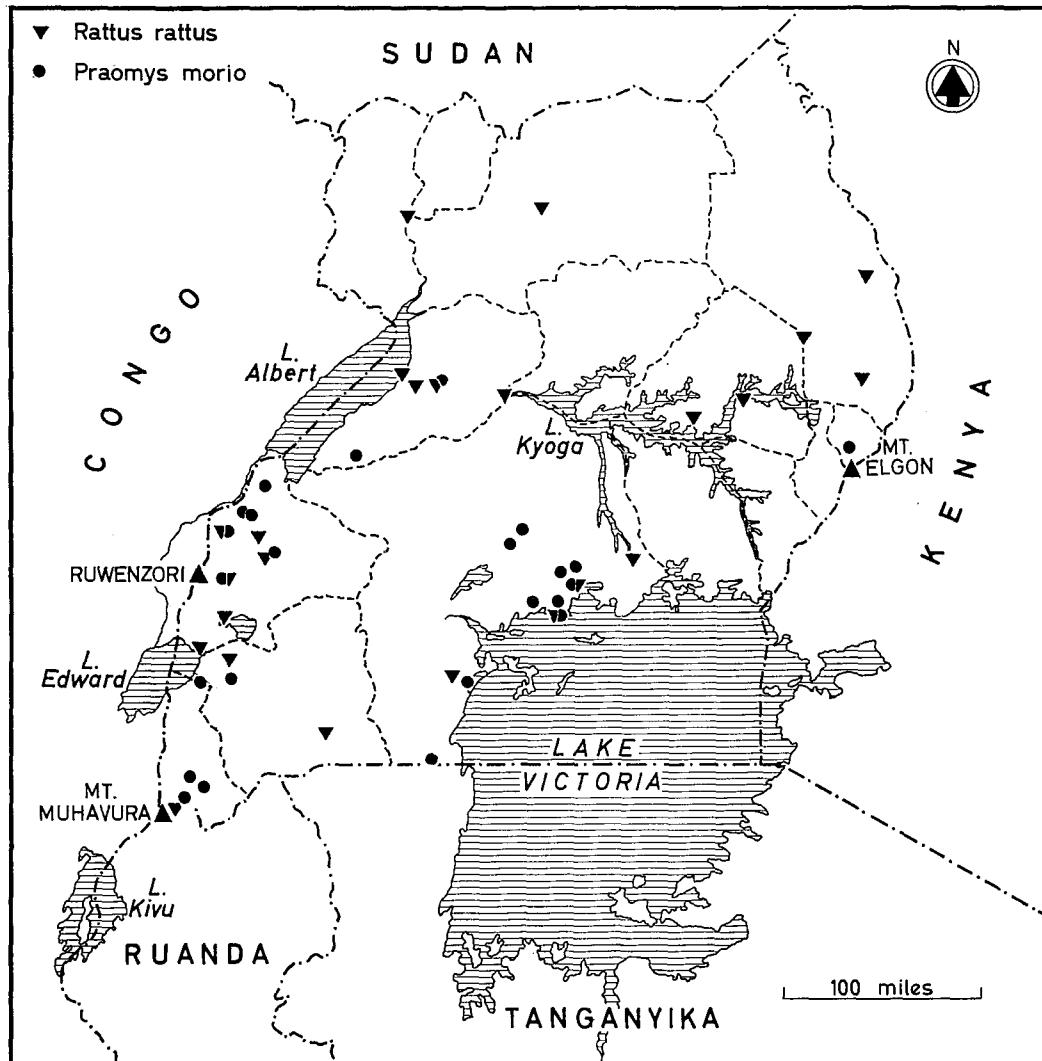


FIG. 10. Distribution of *Rattus rattus* and *Praomys morio*.

Praomys morio (Trouessart)

1881. *Mus morio* Trouessart, *Bull. Soc. Sci. Angers* **10** : 121. Cameroon Mountains [$4^{\circ} 13' N.$
 $9^{\circ} 10' E.$].
1897. *Mus jacksoni* de Winton, *Ann. Mag. nat. Hist.*, (6) **20** : 318. Entebbe.

DESCRIPTION. As for genus.

DISTRIBUTION. Maramagambo, Kalinzu Forests, Ankole; Entebbe, Kabanyolo, Kabulamuliro, Kampala, Kikandwa, Kisimbiri, Lunyo Forest, Malabigambo Forest, Mpanga Forest, Nabugabo, Zika Forest, Buganda; Budongo, Bugoma Forests, Bunyoro; Echuya, Impenetrable Forests, Kumba, Kigezi; Benet, Sebei; Bundibugyo, Bwamba, Kimara, Makoga, Mihunga, Mongiro, Mpanga Forest, Mubuku Valley, Wasa River, Toro. Text-fig. 10.

MEASUREMENTS. H. & b. ♂ 119.9 mm. (50 meas., range 97 to 140 mm.), ♀ 115.3 mm. (45 meas., range 95 to 135 mm.); tail ♂ 138.4 mm. (49 meas., range 121 to 160 mm.), ♀ 136.1 mm. (45 meas., range 94 to 160 mm.); h. f. ♂ 25.0 mm. (43 meas., range 22 to 27 mm.), ♀ 24.2 mm. (41 meas., range 21 to 27 mm.); ear ♂ 17.5 mm. (43 meas., range 15 to 20 mm.), ♀ 17.4 mm. (39 meas., range 15 to 19 mm.); weight ♂ 44.1 g. (40 weighed, range 21 to 57 g.), ♀ 37.0 g. (40 weighed, range 21 to 55 g.).

BREEDING. Foetuses (1×5 lactating) Oct. Echuya; (1×3) Sep. Chambura; (1×5), (1×4 lactating) Sep. Maramagambo. Three lactating, Mpanga (Buganda), May. Litters 2 to 6, normally 3 or 4 (Hopkins MS.). Foetuses (1×5) in Zambia.

HABITAT. Typically medium and high altitude forest.

BIOLOGY. Nocturnal. Omnivorous; plant and insect remains found in stomachs.

Genus **HYLOMYSCUS** Thomas. Climbing Wood-mice

1926. *Hylomyscus* Thomas, *Ann. Mag. nat. Hist.*, (9) **17** : 178. Genotype, by original designation, *Epimys aeta* Thomas.

The climbing mice are small with the tail always longer than the head-and-body length; they are very like *Praomys*. They differ from the latter in their smaller size and in the hind foot rarely attaining a length of 22 mm. whereas in *Praomys* it is always at least 22 mm.

Underside whitish grey with buff, flanks grey to dull brown	.	.	.	<i>H. denniae</i>
Underside white or silvery grey, flanks rich buff	.	.	.	<i>H. stella</i>

Hylomyscus denniae (Thomas)

1906. *Mus denniae* Thomas, *Ann. Mag. nat. Hist.*, (7) **18** : 144. Mubuku Valley, Toro.

DESCRIPTION. Dorsal surface grey to buff, the fur soft and rather woolly. Underside whitish grey touched with buff, well demarcated from the flanks. Tail longer than head and body.

DISTRIBUTION. Mpanga Forest, Buganda; Impenetrable Forest, Kigezi; Mubuku Valley, Toro. Kokanjiro. Text-fig. 11.

MEASUREMENTS. H. & b. ♂ 89.8 mm. (21 meas., range 71 to 103 mm.), ♀ 87.2 mm. (14 meas., range 76 to 99 mm.); tail ♂ 125.6 mm. (21 meas., range 84 to 154 mm.), ♀ 121.2 mm. (14 meas., range 97 to 145 mm.); h. f. ♂ 20.1 mm. (21 meas., range 18 to 22 mm.), ♀ 19.7 mm. (14 meas., range 18 to 21.5 mm.); ear ♂ 16.9 mm. (21 meas., range 13 to 21 mm.), ♀ 15.4 mm. (14 meas., range 13 to 20 mm.); weight ♂ 17.3 g. (12 weighed, range 8 to 24 g.), ♀ 20.0 g. (11 weighed, range 12 to 42 g.).

BREEDING. No data available. Large numbers of males with small testes suggesting large juvenile population in October in Kigezi.

BIOLOGY. No information available.



FIG. II. Distribution of *Hylomyscus denniae*, *H. stella* and *Myomys fumatus*.

Hylomyscus stella (Thomas)

1911. *Rattus stella* Thomas, *Ann. Mag. nat. Hist.*, (8) 7 : 590. Between Mawambi and Avakubi, Ituri, E. Congo [between 1° 00' N. 28° 55' E. and 1° 18' N. 27° 32' E.].

DESCRIPTION. Slightly larger in size than *H. denniae*; upperside and flanks a bright ochraceous colour; underside a whitish or silvery grey colour well demarcated from the flanks. Tail longer than head and body.

DISTRIBUTION. Kalinzu Forest, Maramagambo Forest, Ankole; Mabira Forest, Malabigambo Forest, Mpanga Forest, Zika Forest, Buganda; Bwamba, Toro. Text-fig. II.

MEASUREMENTS. H. & b. ♂ 98.3 mm. (6 meas., range 89 to 104 mm.), ♀ 90.3 mm. (7 meas., range 85 to 101 mm.); tail ♂ 125.3 mm. (6 meas., range 121 to 133 mm.), ♀ 131.9 mm. (7 meas., range 111 to 140 mm.); h. f. ♂ 17.8 mm. (5 meas., range 17 to 19 mm.), ♀ 18.0 mm. (7 meas., range 17 to 20 mm.); ear ♂ 15.0 mm. (5 meas., range 14 to 16 mm.), ♀ 15.1 mm. (7 meas., range 14 to 16 mm.); weight ♂ 18.6 g. (6 weighed, range 16 to 23.5 g.), ♀ 17.4 g. (7 weighed, range 15 to 22 g.).

BREEDING. Hatt (1940) reports a female from the Congo containing three embryos.

HABITAT. Typically found in rain forest, especially around the bases of trees.

BIOLOGY. No information available.

Genus **MYOMYS** Thomas. African Meadow Rats

1915. *Myomys* Thomas, *Ann. Mag. nat. Hist.*, (8) 16 : 447. As a subgenus of *Epimys* Trouessart = *Rattus* Fischer; type, by original designation, *Epimys colonus* (Smith) = *Mus colonus* Brants.

The meadow rats have a similar dorsal coloration to *Mastomys* but are smaller in size; the tail is longer than the head and body; the underside is pure white.

Myomys fumatus (Peters)

1878. *Mus fumatus* Peters, *Mber. preuss. Akad. Wiss. Berl.* 1878 : 200. Ukamba, Kenya [1°-2° S. 37°-38° E.].

DESCRIPTION. As for genus.

DISTRIBUTION. Fort Patiko, Acholi; Kotido, Nakiloro, Karamoja. Text-fig. II.

MEASUREMENTS. H. & b. ♂ 98.0 mm. (5 meas., range 88 to 105 mm.), two ♀ 75 mm., 103 mm.; tail ♂ 126.4 mm. (5 meas., range 110 to 150 mm.), ♀ 97 mm., 130 mm.; h. f. ♂ 21.8 mm. (5 meas., range 21 to 24 mm.), ♀ 20 mm., 21 mm.; ear ♂ 16.2 mm. (5 meas., range 14 to 18 mm.), ♀ 13 mm., 14 mm.; weights ♂ 30.4 g. (5 weighed, range 24 to 35 g.), ♀ 12 g., 31 g.

BREEDING. No information available.

HABITAT. Dry savanna.

BIOLOGY. No information available.

Genus **MASTOMYS** Thomas. Multimammate Rats

1915. *Mastomys* Thomas, *Ann. Mag. nat. Hist.*, (8) **16** : 477. As a subgenus of *Epimys* Trouessart = *Rattus* Fischer; type by original designation, *Epimys coucha* Smith = *Mus marik-quensis* Smith, a race of *Mus natalensis* Smith.

The multimammate rats have no distinctive markings being very like *Praomys* in general appearance. The colour of the dorsal pelage is very variable, usually a grey-brown, but melanic specimens, entirely coal-black are common, especially in Kigezi. The underside is also of very variable colour ranging from a silvery grey to a pale grey touched with buff. The fur is distinctly soft and silky. Tail generally shorter than head and body. Female with teats in a continuous row, numbering up to 12 pairs, not divided into pectoral and inguinal sets.

Mastomys natalensis Smith

1834. *Mus natalensis* Smith, *S. Afr. quart. J.* **2** : 156. "About Port Natal" = Durban, Natal [29° 53' S. 31° 00' E.]. The nomenclature of this species is very confusing; Swynnerton & Hayman (1950) argue cogently in favour of the use of the specific name *coucha* Smith.
 1836. *Mus coucha* Smith, *Rept. Exp. C. Afr.* : 43. 'The country between the Orange River and the Tropic' of Capricorn.
 1897. *Mus ugandae* De Winton, *Ann. Mag. nat. Hist.*, (6) **20** : 377. Entebbe, Buganda.
 1923. *Rattus somereni* Kershaw, *Ann. Mag. nat. Hist.*, (9) **11** : 594. Kaborini, Bukedi.

DESCRIPTION. As for genus.

DISTRIBUTION. Fort Fatiko, Gulu, Kitgum, Pamdero, Para, Acholi; Burumba, Kichwamba, north of Maramagambo Forest, Ankole; Chagwe, Entebbe, Kabanyolo, Kabulamuliro, Kampala, Kikandwa, Kikonda, Kisimbiri, Kisingo, Lialo, Mabira Forest, Mengo, Mubende, Buganda; Kabaroni Camp, Mbale, Bugisu; Busia, Tororo, Bukedi; Fadja, Hoima, Masindi, Bunyoro; Isegero, Kama Island, Busoga; Amudat, Iriri, Kamchuru, Kotido, Moroto, Nabilatuk, Nakiloro, Namalu, Karamoja; Kumba, Kigezi; Kacheba, Kibusi, Ngai, Lango; Ajeluk, Serere, Teso; Bundibugyo, Crater Track, Kamulikwezi, Kimara, Makoga, Mubuku Valley, Mweya, Wasa River, Toro; Login, Rhino Camp, Vurra, Yumbe, West Nile. Usaga. Text-fig. 12.

MEASUREMENTS. H. & b. ♂ 122.8 mm. (57 meas., range 90 to 154 mm.), ♀ 125.1 mm. (53 meas., range 95 to 148 mm.); tail ♂ 112.3 mm. (57 meas., range 88 to 150 mm.), ♀ 114.0 mm. (52 meas., range 95 to 135 mm.); h. f. ♂ 23.7 mm. (59 meas., range 18 to 30 mm.), ♀ 23.3 mm. (49 meas., range 20 to 27 mm.); ear ♂ 16.6 mm. (58 meas., range 14 to 24 mm.), ♀ 16.8 mm. (50 meas., range 11 to 21 mm.); weight ♂ 48.0 g. (32 weighed, range 23 to 70 g.), ♀ 44.6 g. (34 weighed, range 20 to 60 g.).

BREEDING. Female with 2 or 3 embryos Jul., Murchison Falls National Park. Two females lactating Jun. and Jul. from Mweya and Tororo respectively. Hopkins (MS.) states that number of embryos varies between 3 and 12, but 16 has been recorded. First litters are usually small, young females frequently containing 2 to 4 foetuses. In Tanzania, Chapman, Chapman & Robertson (1959) note that the popu-

lation drops to a minimum at the end of the dry season and that breeding is at its maximum towards the end of the rains. Large catches from Uganda in the dry season and not in breeding condition confirm this.

HABITAT. Practically in all types of habitat including buildings, swamps and cultivation. It was formerly the prevalent hut-rat throughout Uganda until driven out by the invading *Rattus rattus*.

BIOLOGY. Nocturnal. Omnivorous, plant remains were the commonest material observed in the stomachs; seeds and insects have been observed. The species is a

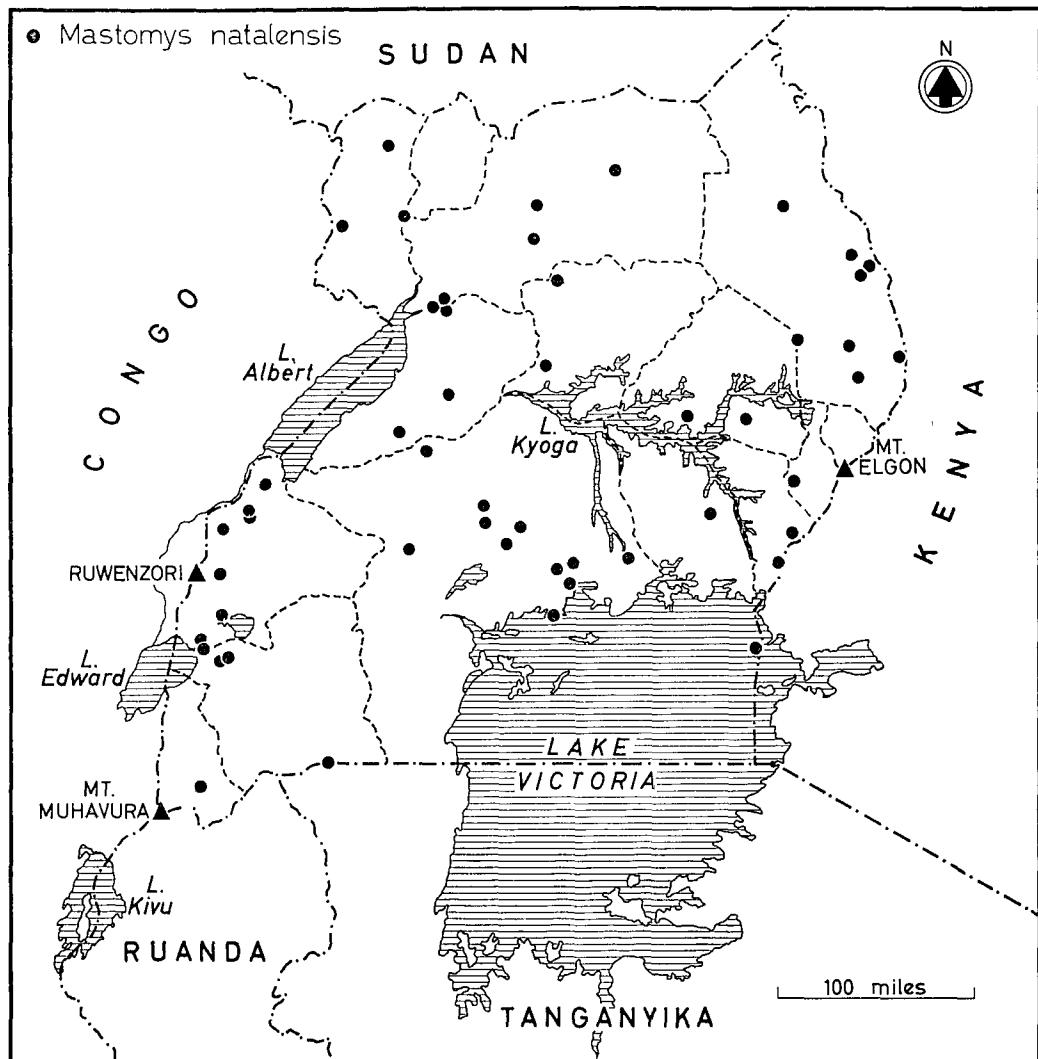


FIG. 12. Distribution of *Mastomys natalensis*.

good burrower and climber although less active than *R. rattus*. Nests in burrows. This species is a vector of the flea *Xenopsylla* and in the past has been an efficient vector of plague. The gaboon viper (*Bitis gabonica*) has been observed to prey on it (Allen & Loveridge, 1942).

Genus **MALACOMYS** Milne-Edwards. Swamp Rats

1877. *Malacomys* Milne-Edwards, *Bull. Soc. philom. Paris* 12: 10. Genotype, by original designation, *Malacomys longipes* Milne-Edwards.

The swamp rats are characterized by the great elongation of the hind feet. The metatarsals are loosely held together so as to splay out on soft ground. The tail is longer than the head and body ; the underside of the body is greyish.

***Malacomys longipes* Milne-Edwards**

1877. *Malacomys longipes* Milne-Edwards, *Bull. Soc. philom. Paris* 13: 9. Gaboon River, West Africa [approximately 0° 10' N. 10° 00' E.].

DESCRIPTION. As for genus.

DISTRIBUTION. Kalinzu Forest, Ankole ; Kabanyolo, Mpanga Forest, Zika Forest, Buganda ; Mpanga Forest, Toro. Text-fig. 13.

MEASUREMENTS. H. & b. ♂ 154.2 mm. (11 meas., range 120 to 172 mm.), ♀ 155.6 mm. (14 meas., range 127 to 183 mm.) ; tail ♂ 172.6 mm. (12 meas., range 158 to 190 mm.), ♀ 165.9 mm. (14 meas., range 151 to 186 mm.) ; h. f. ♂ 38.2 mm. (11 meas., range 35.5 to 40 mm.), ♀ 37.6 mm. (14 meas., range 35 to 40 mm.) ; ear ♂ 24.2 mm. (11 meas., range 21 to 29 mm.), ♀ 23.2 mm. (14 meas., range 19 to 28 mm.) ; weight ♂ 94.4 g. (9 weighed, range 65 to 120 g.), ♀ 93.3 g. (13 weighed, range 50 to 130 g.).

BREEDING. Foetuses (1 × 3) reported from Congo (Hopkins MS.) ; Ansell (1960) reports (1 × 3) from Zambia.

HABITAT. Wetter parts of forests.

BIOLOGY. Believed to be nocturnal. Omnivorous ; food includes vegetable matter, insects, slugs and toads (Hopkins MS.). Makes a grass nest on the ground, also a climber (Misonne, 1963).

Genus **ZELOTOMYS** Osgood. Broad-headed Mice

1910. *Zelotomys* Osgood, *Publ. Field Mus. Nat. Hist., Zool.*, ser. 10, no. 2: 7. Genotype *Mus hildegardeae* Thomas.

Medium sized with distinctly pro-odont upper incisors. Dorsal pelage grey-brown, individual hairs with grey bases and brown tips. Backs of hands and feet brown. Tail covered in scales ; hairs very sparse ; appreciably shorter than length of head and body.

Zelotomys hildegardae (Thomas)

1902. *Mus hildegardae* Thomas, *Ann. Mag. nat. Hist.*, (7) 9: 219. Machakos, Kenya [$1^{\circ} 31'$ S. $37^{\circ} 15'$ E.].

DESCRIPTION. As for genus.

DISTRIBUTION. Between Rwempuno and Kaizi Rivers, Ankole; Crater Track, Toro. Text-fig. 13.

MEASUREMENTS. Two ♂ h. & b. 124 mm., 120 mm., two ♀ 129 mm., 136 mm.; tail ♂ 89 mm., 86 mm., ♀ 92 mm., 90 mm.; h. f. ♂ 22 mm., 25 mm., ♀ 21 mm., 22 mm.; ear ♂ 15 mm., 13 mm., ♀ 15 mm., 13 mm.; weights ♂ 64 g., 57 g., ♀ 56 g., 64 g.



FIG. 13. Distribution of *Malacomys longipes* and *Zelotomys hildegardae*.

BREEDING. Foetuses (1 × 5) Jul., Crater Track.

HABITAT. *Imperata* grassland and scrub.

BIOLOGY. Examination of stomachs of four animals indicates an insectivorous diet.

Genus **MUS** Linnaeus

1758. *Mus* Linnaeus, *Syst. Nat.*, 10th ed. 1: Genotype *Mus musculus* Linnaeus.

1837. *Leggada* Gray, *Charlesworth's Mag. nat. Hist.*, 1: 586. Genotype *Leggada booduga* Gray.

The forms of this genus are all small mice (head-and-body length usually under 90 mm.), with the tail almost always shorter than the head and body. The fur is fairly soft but also quite crisp, falling back stiffly into place after being ruffled. We have included *grata* and *tenellus* with the species *minutoides*.

1	Underside grey or tinged with buff	²
	Underside pure white or nearly so; very small size	
2	Underside grey	
	Underside grey tinged with buff	

***Mus bufo* (Thomas)**

1906. *Leggada bufo* Thomas, *Ann. Mag. nat. Hist.*, (7) 81: 145. Mubuku Valley, Toro.

DESCRIPTION. Large dark species with underside well washed with ochraceous-buff. Bases of belly hairs slate grey. General colour above dark coppery brown. Tail shorter than head and body.

DISTRIBUTION. Echuya Swamp, Echuya Forest, Impenetrable Forest, Kumba, Kigezi; Mihunga, Mubuku Valley, Toro. Text-fig. 14.

MEASUREMENTS. H. & b. ♂ 72.3 mm. (11 meas., range 68 to 79 mm.), ♀ 68.9 mm. (9 meas., range 61 to 73 mm.); tail ♂ 62.1 mm. (11 meas., range 53 to 69 mm.), ♀ 63.2 mm. (9 meas., range 56 to 68 mm.); h. f. ♂ 16.3 mm. (11 meas., range 15 to 18 mm.), ♀ 15.6 mm. (9 meas., range 13.5 to 16.5 mm.); ear ♂ 10.8 mm. (11 meas., range 9 to 12 mm.), ♀ 11.9 mm. (9 meas., range 10 to 13 mm.); weight ♂ 9.1 g. (8 weighed, range 7 to 12 g.), ♀ 9.3 g. (3 weighed, range 7 to 12 g.).

BREEDING. No data available.

HABITAT. Caught in bamboo, moist montane forest and at edge of sedge swamp.

BIOLOGY. No information available.

***Mus minutoides* Smith**

1834. *Mus minutoides* Smith, *S. Afr. quart. J.* 2: 157. Cape Town [33° 56' S. 18° 28' E.].

1910. *Leggada grata* Thomas & Wroughton, *Trans. zool. Soc. Lond.* 19: 507. Mubuku Valley, Toro.

1911. *Mus tenellus* Heller, *Smithson. misc. Coll.* 56: 6. Rhino Camp, West Nile.

1911. *Mus bellus* Heller, *Smithson. misc. Coll.* 56: 8. Rhino Camp, West Nile.

1911. *Mus musculoides* Heller, *Smithson. misc. Coll.* 56: 28. Kabulamuliro, Buganda.

DESCRIPTION. Small species with pure white underside.

DISTRIBUTION. Para, Acholi; Congo Road, Kalinzu Forest, Lutoto, Maramagambo Forest, north of Maramagambo Forest, Ankole; Kabanyolo, Kabulamuliro, Kampala, Kikandwa, Kikonda, Kisimbiri, Kisingo, Lunyo, Mpanga Forest, Nabugabo, Nkyanuna, Buganda; Butiaba, Hoima, Kajuia, Masindi, Bunyoro; Lotome, Moroto, Nabilatuk, Karamoja; Echuya Swamp, Kigezi; Crater Track, Mweya, Mihunga, Mubuku Valley, Toro; Rhino Camp, Wadelai, West Nile. Text-fig. 14.

MEASUREMENTS. H. & b. ♂ 60.6 mm. (13 meas., range 45 to 76 mm.), ♀ 60.8 mm. (11 meas., range 49 to 77 mm.); tail ♂ 43.8 mm. (12 meas., range 35 to 54 mm.), ♀ 45.5 mm. (11 meas., range 35 to 63 mm.); h. f. ♂ 13.1 mm. (10 meas., range 12 to

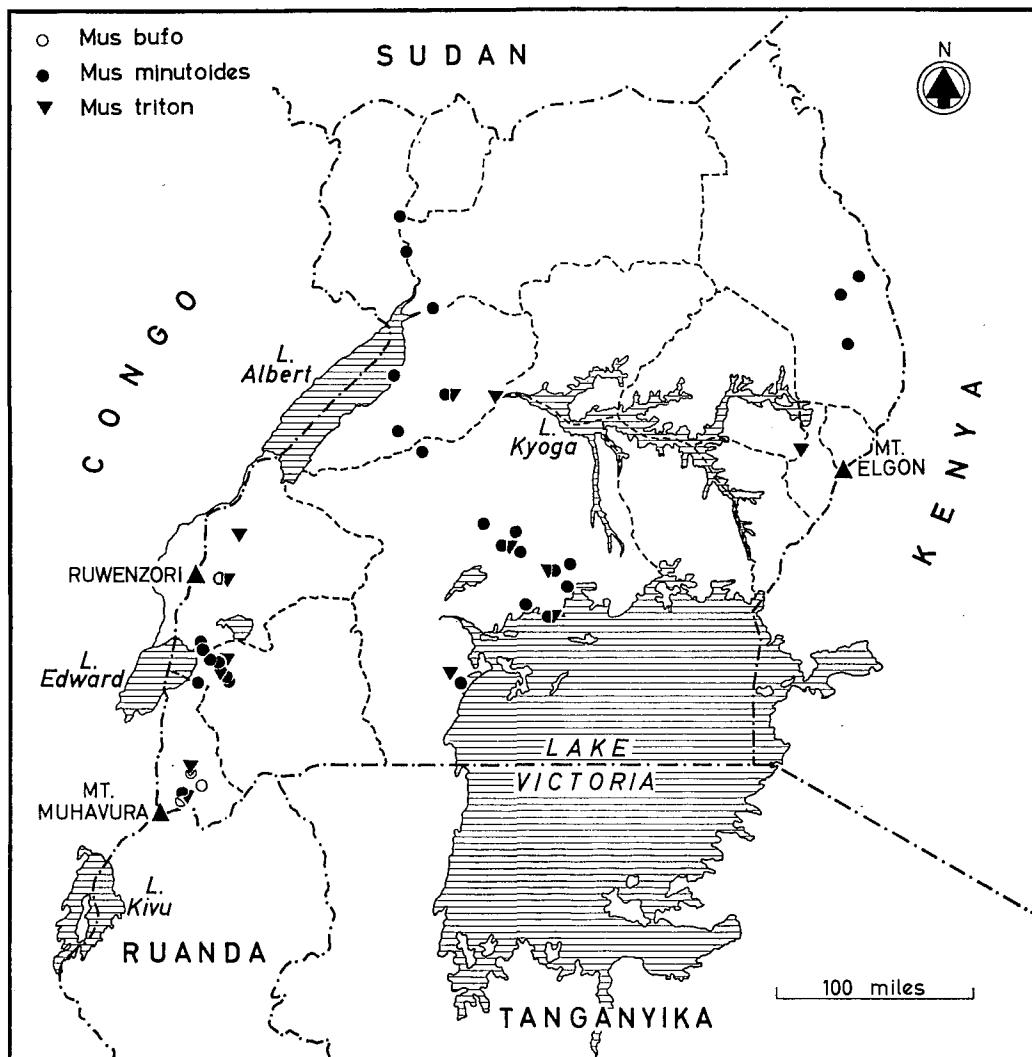


FIG. 14. Distribution of *Mus* spp.

14.5 mm.), ♀ 13.1 mm. (8 meas., range 12 to 14 mm.); ear ♂ 9.7 mm. (9 meas., range 8 to 11 mm.), ♀ 8.7 mm. (8 meas., range 7 to 10 mm.); weight ♂ 6.4 g. (7 weighed, range 4 to 10 g.), ♀ 5.9 g. (9 weighed, range 2.5 to 10 g.).

BREEDING. Foetuses (1 × 5) Jul. Mpanga, (1 × 4) Aug. Maramagambo Forest, (1 × 4) Nov. Moroto. Allen & Loveridge (1942) report (1 × 7) foetuses and groups of 3, 6, 7 and 8 blind nestlings in Tanzania. Ansell (1960) reports (1 × 3) well developed foetuses and groups of 4 and 5 juveniles from Zambia.

HABITAT. Very varied ranging from dry sandy ground to forest.

BIOLOGY. Nocturnal. Makes shallow burrows with a bed of grass in the bottom. Predators include the brown house snake (*Boaedon lineatus*), the burrowing viper (*Astractaspis bibroni*), mamba (*Dendraspis* sp.) and viper (*Atheris niscalis*). Omnivorous, the stomachs containing leaves, seeds and insect remains.

Mus triton (Thomas)

1909. *Leggada triton* Thomas *Ann. Mag. nat. Hist.*, (8) 4 : 548. Kirui, southern foothills of Mt. Elgon, Kenya [approximately 0° 45' N. 34° 40' E.].

DESCRIPTION. Differs from *Mus bufo* in the belly fur not being tinged with buff and the tail being appreciably shorter.

DISTRIBUTION. Kichwamba, Lutoto, north of Maramagambo Forest, Ankole; Entebbe, Kikandwa, Kisimbiri, Masaka, Buganda; Siroko Valley, Bugisu; Masindi Port, Bunyoro; Echuya Swamp, Ingezi, Kigezi; north Ruwenzori, Toro. Text-fig. 14.

MEASUREMENTS. H. & b. ♂ 78.3 mm. (11 meas., range 57 to 93 mm.), ♀ 73.8 mm. (10 meas., range 66 to 85 mm.); tail ♂ 48.5 mm. (10 meas., range 42 to 53 mm.), ♀ 46.8 mm. (9 meas., range 44 to 48 mm.); h. f. ♂ 15.4 mm. (11 meas., range 14 to 19 mm.), ♀ 14.9 mm. (9 meas., range 14 to 16 mm.); ear ♂ 10.6 mm. (9 meas., range 9 to 12 mm.), ♀ 10.7 mm. (9 meas., range 9 to 11 mm.); weight ♂ 11.4 g. (9 weighed, range 10 to 13 g.), ♀ 9.4 g. (9 weighed, range 7 to 13 g.).

BREEDING. No data available.

HABITAT. Found in grassland, heath and scrub principally in wetter areas.

BIOLOGY. Nocturnal. Makes nests of both fine and coarse rootlets and leaves of grass. Loveridge (1953) reports that the brown house snake (*Boaedon lineatus*) is a predator.

Genus *LOPHUROMYS* Peters. Harsh-furred Mice

1866. *Lasiomys* Peters, *Mber. preuss. Akad. Wiss. Berl.* 1866 : 409. Genotype = *Mus sikapusi* Temminck. Not *Lasiomys* 1854, in Mammalia (Octodontidae).

1874. *Lophuromys* Peters, *Mber. preuss. Akad. Wiss. Berl.* 1874 : 234. *Lasiomys afer* Peters = *Mus sikapusi* Temminck. To replace *Lasiomys* Peters, preoccupied.

The texture of the fur is very characteristic. It is smooth, sleek, stiff and brush-like. This is particularly obvious when the fur is stroked against the lie of the hairs.

Dorsally the fur is red to brown whilst the underside is rather paler in colour. Ellerman, Morrison-Scott & Hayman (1953) list two species of short-tailed *Lophuromys* both of which occur in Uganda. In addition, two species of long-tailed *Lophuromys* have been described from mountainous regions of western Uganda but as they are obviously very similar they are included here under *L. woosnami* which is the prior name.

1	Tail short, usually less than 80 mm.	2
	Tail long, usually more than 100 mm.	<i>L. woosnami</i>
2	Fur finely speckled	<i>L. flavopunctatus</i>
	Fur not speckled	<i>L. sikapusi</i>

Lophuromys flavopunctatus Thomas

1888. *Lophuromys flavo-punctatus* Thomas, Proc. zool. Soc. Lond. 1888: 14. Shoa, Ethiopia (probably obtained at Ankober [9° 32' N. 39° 43' E.], Thomas, 1903, Proc. zool. Soc. Lond., 1902: 314).

1892. *Mus aquilus* True, Proc. U.S. nat. Mus., 15: 460. Kilimanjaro, Tanzania [3° 00' S. 37° 25' E.].

DESCRIPTION. Dorsal fur dark brown-red speckled with yellow or buff. Belly buff washed with red, overall effect buffy-pink.

DISTRIBUTION. Burumba, Lutoto, Kalinzu and Maramagambo Forests, between Rwempuno and Kaizi Rivers, Ankole; Entebbe, Kabanyolo, Kabulamuliro, Kampala, Kikonda, Kisingo, Lialo, Mabira Forest, Nabugabo, Nalwendo, Zika Forest, Buganda; Hoima, Bunyoro; Echuya Forest, Echuya Swamp, Impenetrable Forest, Nyakabande, Kigezi; Bundibugyo, Mihunga, Mpanga Forest, Mubuku Valley, Toro; Rhino Camp, West Nile. Text-fig. 15.

MEASUREMENTS. H. & b. ♂ 125.3 mm. (18 meas., range 117 to 141 mm.), ♀ 125.0 mm. (20 meas., range 112 to 144 mm.); tail ♂ 62.8 mm. (17 meas., range 46 to 69 mm.), ♀ 62.6 mm. (19 meas., range 55 to 94 mm.); h. f. ♂ 20.3 mm. (17 meas., range 19 to 21 mm.), ♀ 20.1 mm. (18 meas., range 18 to 21 mm.); ear ♂ 15.2 mm. (15 meas., 13 to 17 mm.), ♀ 15.5 mm. (18 meas., range 14 to 18 mm.); weight ♂ 52.0 g. (18 weighed, range 40 to 62 g.), ♀ 46.1 g. (18 weighed, range 36 to 56 g.).

BREEDING. Foetuses (2 × 3) Jun. Entebbe; (4 × 2) Sep. Echuya. Embryos near full term weigh 4–5 g. Ansell (1960) reports 3 embryos from Zambia. Litter size 1 to 4 (average 2.4) of 43 gravid females examined in Malawi (Hanney, 1964). Allen & Loveridge (1942) report foetuses (1 × 4) from Tanzania and (1 × 3) from Congo.

HABITAT. Moist situations in scrub and forest; recorded at altitudes up to 12,000 ft.

BIOLOGY. Diurnal and nocturnal. Omnivorous, mainly arthropods; slugs, snails, seeds, worms, frogs or toads and birds also recorded. Nests at base of grass tussocks (Hanney, 1964). Numerous scars on back of Mabira specimens.

Lophuromys sikapusi Temminck

1853. *Mus sikapusi* Temminck, *Esq. Zool. Cote de Guine*: 160. Dabacrom, Ghana [$7^{\circ} 40' N.$
 $2^{\circ} 58' W.$].

1911. *Lophuromys pyrrhus* Heller, *Smithson. misc. Coll.* 56: 10. Rhino Camp, West Nile.

DESCRIPTION. Dorsal fur a rich red-brown without any form of speckling. Underside usually a richer red than *L. flavopunctatus*. Tail short.

DISTRIBUTION. Kagambah, Kichwamba, between Rwempuno and Kaizi Rivers, Rutanda, Ankole; Entebbe, Kampala, Mpanga Forest, Buganda; Bubungi,



FIG. 15. Distribution of *Lophuromys* spp.

Lwakaka, Bugisu ; Butiaba, Bunyoro ; Jinja, Busoga ; Nyalasanje, Kigezi ; Moyo, Madi ; Serere, Teso ; Bwamba, Crater Track, Kamulikwezi Swamp, Fort Portal, Ruwenzori, Wasa River, Toro ; Rhino Camp, West Nile. Text-fig. 15.

MEASUREMENTS. H. & b. ♂ 133.1 mm. (27 meas., range 100 to 153 mm.), ♀ 136.6 mm. (16 meas., range 105 to 159 mm.) ; tail ♂ 71.6 mm. (26 meas., range 49 to 91 mm.), ♀ 72.7 mm. (16 meas., range 56 to 82 mm.) ; h. f. ♂ 23.0 mm. (27 meas., range 20 to 25 mm.), ♀ 22.8 mm. (16 meas., range 21 to 24 mm.) ; ear ♂ 14.8 mm. (23 meas., range 12 to 17.5 mm.), ♀ 14.1 mm. (13 meas., range 12 to 16 mm.) ; weight ♂ 76.8 g. (20 weighed, range 50 to 104 g.), ♀ 79.0 g. (14 weighed, range 43 to 100 g.).

BREEDING. Foetuses (1 × 2) Aug. Kichwamba. Two ♀ lactating Jul. Q. E. P. Usually 2 to a litter (Watson, 1950).

HABITAT. Heavily grassed bush country.

BIOLOGY. Diurnal and nocturnal. Examination of contents of 37 stomachs suggests that ants form major food. Insectivorous.

Lophuromys woosnami Thomas

1906. *Lophuromys woosnami* Thomas, *Ann. Mag. nat. Hist.*, (7) **18** : 146. Mubuku Valley, Toro.

1911. *Lophuromys prittieei* Thomas, *Ann. Mag. nat. Hist.*, (8) **8** : 377. Mufumbiro region, Kigezi.

DESCRIPTION. Easily separated from the other two species by its relatively long tail. The dorsal fur is not as richly coloured as in the other species tending to be rather more grey-brown. The speckling is sparse or absent. Underside without trace of pink or red and much more grey to brown.

DISTRIBUTION. Echuya Swamp, Impenetrable Forest, Muhavura, Kigezi ; Mihunga, Mubuku Valley, north Ruwenzori, Toro. Text-fig. 15.

MEASUREMENTS. H. & b. ♂ 118.0 mm. (5 meas., range 114 to 126 mm.), ♀ 107.2 mm. (11 meas., range 84 to 123 mm.) ; tail ♂ 113.0 mm. (5 meas., range 110 to 117 mm.), ♀ 107.1 mm. (11 meas., range 97 to 118 mm.) ; h. f. ♂ 23.6 mm. (5 meas., range 22 to 25 mm.), ♀ 23.1 mm. (11 meas., range 22.5 to 26 mm.) ; ear ♂ 19.0 mm. (5 meas., range 19 to 23 mm.), ♀ 19.1 mm. (11 meas., range 17 to 22 mm.) ; weight ♂ 45 g. (1 weighed), ♀ 36.5 g. (7 weighed, range 23 to 48 g.).

BREEDING. Foetuses (1 × 2) Sep. Echuya ; (2 × 2) Oct., Impenetrable.

HABITAT. Obtained in moist situations in scrub and forest at altitudes of 6,000 to 8,200 feet.

Genus *ACOMYS* Geoffroy. Spiny Mice

1838. *Acomys* Geoffroy, *Ann. Sci. nat. Zool.* **10** : 126. Genotype, by monotypy, *Mus cahirinus* Desmarest.

The spiny mice are small mice characterized by having the hair of the dorsal surface converted into coarse spines. They inhabit arid semi-desert country. Two species

have been collected in Karamoja from apparently similar types of habitat. Tail hard and scaly. Incisors ungrooved.

Dorsal pelage uniform grey-brown not speckled	<i>A. percivali</i>
Dorsal pelage speckled light and dark brown	<i>A. wilsoni</i>

***Acomys percivali* Dollman**

1911. *Acomys percivali* Dollman, *Ann. Mag. nat. Hist.*, (8) **8** : 126. Chanler Falls, N. Guaso Nyiro, Kenya [$0^{\circ} 47' N.$ $38^{\circ} 03' E.$].

DESCRIPTION. Dorsal pelage uniform grey-brown, tail relatively long, hind foot large.

DISTRIBUTION. Kotido, Namalu, Karamoja. Text-fig. 16.

MEASUREMENTS. Two ♂ h. & b. 82 mm., 94 mm.; tail 67 mm., 84 mm.; h. f. 15 mm., 15 mm.; ear 11 mm., ?; weights 19 g., 5 g. Two ♀ h. & b. 93 mm., 74 mm.; tail 79 mm., 48 mm.; h. f. 14 mm., 14 mm.; ear 12 mm., 11 mm.; weights 33 g., 11 g.

BREEDING. Foetuses (1×1) Nov. Kotido.

HABITAT. Dry savanna, semi-desert.

BIOLOGY. No information available.

***Acomys wilsoni* Thomas**

1892. *Acomys Wilsoni* Thomas, *Ann. Mag. nat. Hist.*, (6) **10** : 22. Mombasa, Kenya [$4^{\circ} 3' S.$ $39^{\circ} 40' E.$].

DESCRIPTION. Dorsal pelage annulated light and dark brown; annulations may tend to disappear posteriorly. Tail short; hind foot small.

DISTRIBUTION. Amudat, Kachere, Lorengikipi, Lotome, Manimani, Moroto Forest, Nabilatuk, Karamoja. Text-fig. 16.

MEASUREMENTS. Two ♂ h. & b. 87 mm., 83 mm.; tail 43 mm., 45 mm.; h. f. 12 mm., 13 mm.; ear 10 mm., 10 mm.; weights, 22 g., 21 g. Three ♀ 96 mm., 86 mm., 84 mm.; tail 48 mm., 47 mm., 41 mm.; h. f. 13 mm., 14 mm., 13 mm.; ear 12 mm., 10 mm., 10 mm.; weights 25 g., 27 g., 19 g.

BREEDING. Foetuses (1×2) Oct. Nabilatuk, (1×1) Nov. Moroto, (1×3) Nov. Amudat.

HABITAT. Dry savanna semi-desert. Watson (1950) only found it in less arid parts or alongside rivers.

BIOLOGY. No information available.

Genus *URANOMYS* Dollman

1909. *Uranomys* Dollman, *Ann. Mag. nat. Hist.*, (8) 4: 155. Genotype *Uranomys ruddi* Dollman.

Texture of fur brush-like; hairs harsh and long measuring about 17 mm. Back grey-brown paling to buff on sides and on upper surfaces of limbs. Nasal region and head darker than back. Similar to *Lophuromys* but distinguished from it by the pure white backs to the hands and feet (in *Lophuromys* they are at least tinged with black or brown). In *Uranomys* the belly fur is white and in *Lophuromys* brown, orange, red or grey. Upper incisors are orthodont in *Lophuromys* and slightly proodont in *Uranomys*.



FIG. 16. Distribution of *Acomys percivali*, *A. wilsoni* and *Uranomys ruddi*.

***Uranomys ruddi* Dollman**

1909. *Uranomys ruddi* Dollman, *Ann. Mag. nat. Hist.*, (8) **4** : 552. Kirui, southern foothills of Mt. Elgon, Kenya [approximately $0^{\circ} 45' N.$ $34^{\circ} 40' E.$].
 1911. *Uranomys ugandae* Heller, *Smithson. misc. Coll.* **56** : 12. Kikonda, Buganda.

DESCRIPTION. As for genus.

DISTRIBUTION. Kikonda, Buganda; Lwakaka, Bugisu; Budama, Bukedi. Text-fig. 16.

MEASUREMENTS. Two ♀ h. & b. 104 mm., 95 mm.; tail 50 mm., 66 mm.; h. f. 17 mm., 16 mm.; ear 15 mm., 13 mm.

BREEDING. No information available.

HABITAT. No information available.

BIOLOGY. No information available.

Genus ***SACCASTOMUS* Peters. Pouched Mice**

1846. *Saccostomus* Peters, *Ber. Verh. preuss. Akad. Wiss. Berl.* **1846** : 258. Genotype, by monotypy, *Saccostomus campestris* Peters.

Medium sized with long, soft, silky fur and a relatively short tail. Cheek pouches present. Grey dorsally with brown tinge in some specimens; paler on flanks; belly hairs with white tips and slate bases. Ears small and hairy; tail dark above, paler below. Backs of hands and feet white. Ellerman, Morrison-Scott & Hayman (1953) believe there is only one species in this genus.

***Saccostomus campestris* Peters**

1846. *Saccostomus campestris* Peters, *Ber. Verh. preuss. Akad. Wiss. Berl.* **1846** : 258. Tete, Portuguese East Africa [$16^{\circ} 10' S.$ $33^{\circ} 35' E.$].

1936. *Saccostomus cricetus* Allen & Lawrence, *Bull. Mus. comp. Zool. Harv.* **79** : 100. South bank of Greek River, Sebei.

DESCRIPTION. As for genus.

DISTRIBUTION. Amudat, Lotome, Moroto, Nabilatuk, Karamoja; Greek River, Sebei. Text-fig. 17.

MEASUREMENTS. H. & b. ♂ 116.0 mm. (4 meas., range 94 to 130 mm.), ♀ 144.9 mm. (7 meas., 127 to 157 mm.); tail ♂ 45.3 mm. (4 meas., range 34 to 55 mm.), ♀ 53.9 mm. (7 meas., range 50 to 58 mm.); h. f. ♂ 21.0 mm. (4 meas., range 19 to 25 mm.), ♀ 21.9 mm. (7 meas., range 21 to 22 mm.); ear ♂ 18.3 mm. (4 meas., range 14 to 25 mm.!), 18.3 mm. (7 meas., range 16 to 20 mm.); weight ♂, 2 weighed, 24 g., 34 g., ♀ 65.2 g. (6 weighed, range 41 to 84 g.).

BREEDING. Foetuses (1×7) Nov. Amudat. Ansell (1960) reports (1×7 , 1×6) from Zambia and Shortridge (1934) (1×8) from South West Africa.

HABITAT. Dry savanna. Attracted to cultivated areas.

BIOLOGY. Nocturnal, very slow moving. From contents of cheek pouches food apparently largely of seeds, grain, fruits and also occasionally, insects. Lives in burrows.

Genus **CRICETOMYS** Waterhouse. Giant Rats

1840. *Cricetomys* Waterhouse, *Proc. zool. Soc. Lond.* **1840** : 2. As a subgenus of *Mus* Linnaeus; genotype, by original designation, *Cricetomys gambianus* Waterhouse.

Very large rat with head-and-body length usually exceeding 300 mm. The tail is longer than the head and body; it has a dark proximal portion and a white distal portion. Cheek pouches are present.



FIG. 17. Distribution of *Saccostomus campestris* and *Cricetomys gambianus*.

Cricetomys gambianus Waterhouse

1840. *Cricetomys gambianus* Waterhouse, *Proc. zool. Soc. Lond.* **1840** : 2. River Gambia, West Africa [$13^{\circ} 30' N.$ $13^{\circ} 30' - 16^{\circ} 40' W.$].

DESCRIPTION. As for genus.

DISTRIBUTION. Aiago River, Fort Patigo, Acholi; Kampala, Mabira Forest, Malabigambo Forest, Buganda; "Bunyoro"; Jinja, Busoga; Moroto, Namalu, Karamoja; Mt. Sabinio, Kigezi; Mt. Elgon, Sebei; Ngora Rest House, Ongino, Serere, near Soroti, Teso; Bundibugyo, Mihunga, Mongiro, Mubuku Valley, Toro. Text-fig. 17.

MEASUREMENTS. Two ♂ h. & b. 350 mm., 350 mm.; tail 380 mm., 418 mm.; h. f. 70 mm., 72 mm.; ear 37 mm., 42 mm. Two ♀ h. & b. 335 mm., 330 mm.; tail 370 mm., 390 mm.; h. f. 66 mm., 66 mm.; ear ? mm., 42 mm.; weight 910 g., ?.

BREEDING. Foetuses (1 × 1) Mt. Sabinio (Hopkins MS.); (1 × 1) Congo (Misonne, 1963); (1 × 4) Zambia (Ansell, 1960).

HABITAT. Ubiquitous, being found in rain forest, mountain forest, gallery forest and very dry savanna.

BIOLOGY. Strictly nocturnal. Herbivorous, feeding mainly on seeds of trees. They live in deep burrows in the ground and do serious damage to agriculture. It is reported that they often climb trees and shrubs in search of fruit. Infected with an ectoparasitic Dermapteran (*Hemimerus talpoides* Walker) peculiar to itself.

Subfamily DENDROMURINAE Allen

1939. Dendromurinae Allen, *Bull. Mus. comp. Zool. Harv.* **83** : 349.

Genus **DENDROMUS** Smith. African Tree Mice

1829. *Dendromus* Smith, *Zool. J.* **4** : 438. Genotype, by original designation, *Dendromus typus* Smith = *Mus mesomelas* Brants.

1830. *Dendromys* Fischer, *Synop. Anim. Add.* : 658. Substitute for *Dendromus* Smith.

1916. *Poemys* Thomas, *Ann. Mag. nat. Hist.*, (8) **18** : 238. As a subgenus of *Dendromus* Smith; type, by original designation, *Dendromus melanotis* Smith.

Small mice. The fore feet have three well-developed digits only; hind feet narrow with very short hallux and fifth digit nearly as long as second. There is often a single dark, dorsal stripe along the length of the body. The upper incisors are grooved. Bohmann's (1942) revision of the genus has been adopted together with Ellerman, Morrison-Scott & Hayman's (1953) use of the specific name *mystacalis* in place of *pumilio*.

1	No dorsal stripe	<i>D. mystacalis</i>
	Dark dorsal stripe running the length of the body	2
2	Small size; dorsal stripe broken to form spot on the head; tail shorter than h. & b.; hind foot less than 18 mm.	<i>D. melanotis</i>
	Larger size; dorsal stripe not broken to form a spot on the head; tail longer than h. & b.; hind foot more than 19 mm.	<i>D. mesomelas</i>

***Dendromus melanotis* Smith**

1834. *Dendromus melanotis* Smith, *S. Afr. quart. J.* **2** : 158. Near "Port Natal" = Durban, Natal [29° 53' S. 31° 00' E.].
 1911. *Dendromus spectabilis* Heller, *Smithson. misc. Coll.* **56** : 3. Rhino Camp, West Nile.

DESCRIPTION. Colour of upper parts light brown, gradually turning a grey-brown on the sides to a pale grey on the under parts. A wide black median dorsal stripe runs from the shoulders to the base of the tail, widest anteriorly and narrowing gradually posteriorly. A median black spot occurs on the forehead between the ears and eyes. At the anterior base of the ears are a few white hairs and a larger white patch just below the ear. Hind foot less than 18 mm.

DISTRIBUTION. Hoima, Bunyoro; Mweya, Toro; Rhino Camp, West Nile. Text-fig. 18.

MEASUREMENTS. Three ♂ h. & b. 67 mm., 73 mm., 61 mm.; tail 65 mm., 68 mm., ?; h. f. 16 mm., 17 mm., 16 mm.; ear 13 mm., 12 mm., 11 mm.; weight 5 g., 7 g., 6 g. Two ♀ h. & b. 91 mm., 56 mm.; tail 67 mm., 64 mm.; h. f. 16 mm., 16 mm.; ear 10 mm., ?; weight 8 g., 7 g.

BREEDING. Foetuses (1 × 3) Jul. Mweya. Ansell (1960) reports (4 × 3, 4 × 4, 1 × 5, 4 × 6) from Zambia.

HABITAT. Found in short herbs where *D. mystacalis* is uncommon. Typically in dry savanna.

BIOLOGY. Nocturnal. Herbivorous, although Ansell (1960) reports that they also eat insects. Apparently nest in burrows in the ground in Zambia but in the Congo, Misonne (1963) reports that they build nests in herbs at heights ranging from 10 cm. to 1 m. above the ground. (Further information under *D. mystacalis*.)

***Dendromus mesomelas* (Brants)**

1827. *Mus mesomelas* Brants, *Het Geslacht der Miuzen* : 122. "Near Zondags River" (Sundays River, just east of Port Elizabeth, Eastern Cape Province) [approximately 33° 45' S. 25° 45' E.].

DESCRIPTION. Colour of upper parts light brown, the sides not grey-brown as in *D. melanotis*. Dorsal stripe distinctly narrower than in *D. melanotis*. No white patch as base of ears. Tail longer than head and body. Hind foot longer than 19 mm.

DISTRIBUTION. Echuya Swamp, Kumba, Kigezi; Mubuku Valley, Toro. Text-fig. 18.

MEASUREMENTS. H. & b. ♂ 80.8 mm. (4 meas., range 76 to 87 mm.), ♀ 81.3 mm. (3 meas., range 78 to 87 mm.); tail ♂ 89.8 mm. (4 meas., range 86 to 93 mm.), ♀ 97.0 mm. (3 meas., range 93 to 102 mm.); h. f. ♂ 21.0 mm. (4 meas., range 20 to 22 mm.), ♀ 21.0 mm. (3 meas., all 21 mm.); ear ♂ 12.5 mm. (4 meas., range 11 to 15 mm.), ♀ 13.0 mm. (3 meas., range 12 to 14 mm.); weight ♂ 13.7 g. (3 weighed, range 11 to 15 mm.), ♀ two weighed, 13 g., 15 g.

BREEDING. Allen & Loveridge (1942) record litters of 3 and 4 young.

HABITAT. Found in swamp and associated vegetation in Kigezi.

BIOLOGY. Ansell (1960) reports that they feed largely on grass seeds but are to some extent insectivorous. Live in tall grass in which they are arboreal; also semi-terrestrial. Misonne (1963) claims that they are often caught around villages in the Congo. Apparently less communal than *D. mystacalis* and *D. melanotis*.

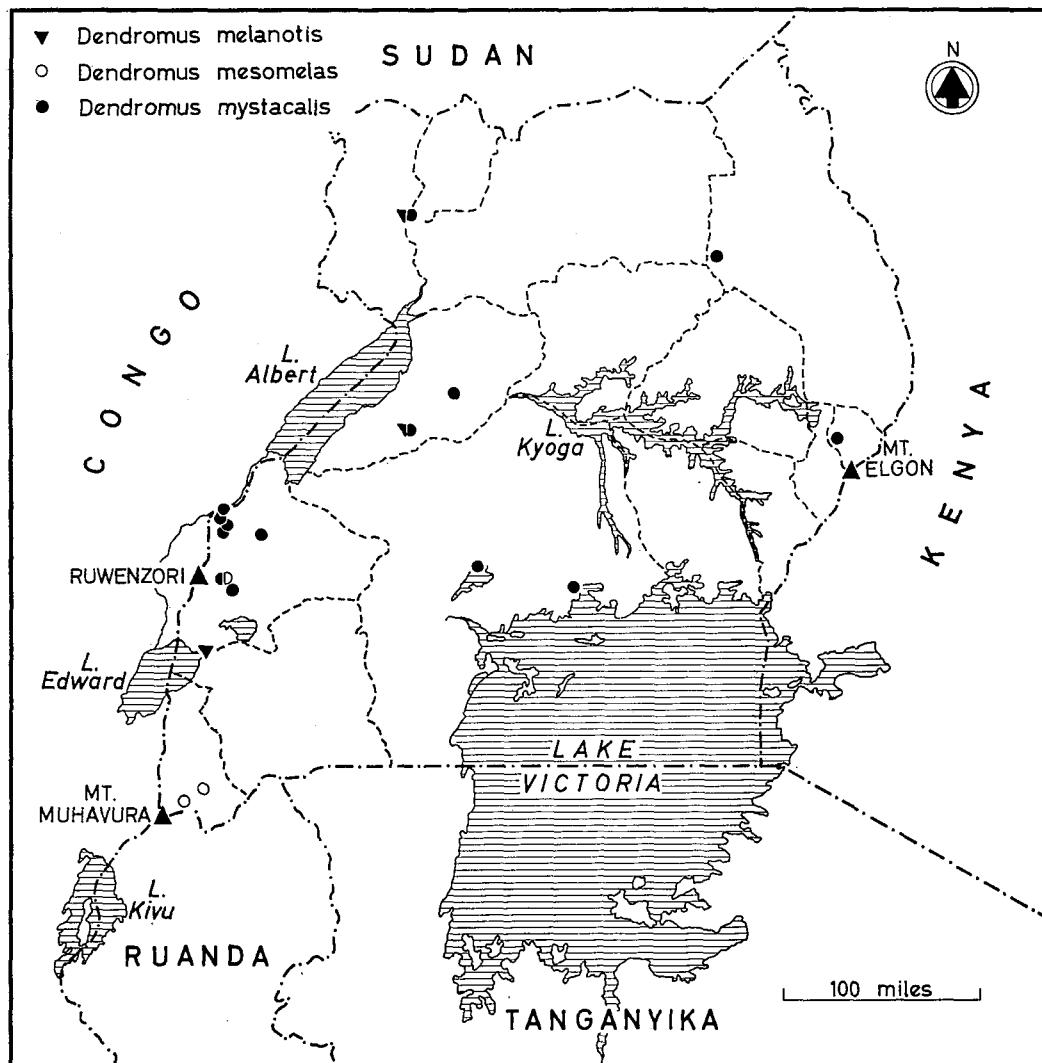


FIG. 18. Distribution of *Dendromus* spp.

Dendromus mystacalis Heuglin

1863. *Dendromus mystacalis* Heuglin, *Nova Acta Leop. Carol.* **30**, art. 2, suppl. : 5. Ifag, east of Lake Tana, Ethiopia [12° 15' N. 37° 45' E.]
 1911. *Dendromus lineatus* Heller, *Smithson. misc. Coll.* **56** : 4. Rhino Camp, West Nile.

DESCRIPTION. No dorsal stripe running the length of the body. Tail about one and a third times length of the head and body.

DISTRIBUTION. Buligi, Kampala, Kawenge, Buganda ; Budadin Camp, Bugisu ; Hoima, Kajuia, Masindi, Bunyoro ; Kamchuru, Karamoja ; Sebei Camp, Sebei ; Bubukwanga, Bugoye, Bumatta, Bummaddu, Bundibugyo, Bundimali, Fort Portal, Humya, Kyabombo, Mihunga, Tokwe, Toro ; Rhino Camp, West Nile. Text-fig. 18.

MEASUREMENTS. H. & b. ♂ 69.2 mm. (20 meas., range 59 to 68 mm.), ♀ 61.7 mm. (6 meas., range 50 to 73 mm.) ; tail ♂ 90.4 mm. (20 meas., range 81 to 101 mm.), ♀ 86.0 mm. (6 meas., range 75 to 95 mm.) ; h. f. ♂ 16.6 mm. (21 meas., range 14 to 19 mm.), ♀ 16.2 mm. (6 meas., range 16 to 17 mm.) ; ear ♂ 12.8 mm. (21 meas., range 10 to 14 mm.), ♀ 12.3 mm. (6 meas., range 10 to 13 mm.) ; weight ♂ 8.7 g. (15 weighed, range 7.5 to 10.5 g.), ♀ 7.6 g. (4 weighed, range 6.5 to 9 g.).

BREEDING. Normally 3 in a litter, occasionally 4 (Hopkins MS.). Foetuses (1 × 5) in Zambia (Ansell, 1960). Three naked, blind nestlings, Jan. Mihunga ; 4 juveniles Jan. Bugoye. Seven naked nestlings and 4 furred with eyes open in Tanzania (Allen & Loveridge, 1942). Juveniles in Zambia : (5 × 4, 1 × 6) (Ansell, 1960).

HABITAT. Common in banana shambas where the nests are usually among the leaf-bases (Hopkins MS.). Also in grass and amongst herbage.

BIOLOGY. Nocturnal and herbivorous. Quarrelsome and aggressive animals. *D. mystacalis* and *D. melanotis* fight constantly when placed together ; in the course of the fighting the subordinate animal puts itself on its back and defends itself ; *D. mesomelas* is the less aggressive. *Dendromus* walks with the first and fifth digits at right angles. *Dendromus* dominates *Mus minutoides* and *M. triton* when they are together. They climb easily, the tail is prehensile and their light weight allows them to scale the lighter herbage, where they may construct nests.

Genus **STEATOMYS** Peters. Fat Mice

1846. *Steatomys* Peters, *Ber. Verh. preuss. Akad. Wiss. Berl.* **1846** : 258. Genotype, by monotypy, *Steatomys pratensis* Peters.

The fat mice are small with relatively short tails. Their plump appearance is due to a layer of fat beneath the skin. Upper incisors grooved. Fur of the back light brown-fawn ; sharp line of demarcation between flanks and belly ; hairs of the latter pure white. Hairs of back grey with brown tips. Backs of hands and feet white. Tail brown above, white below, moderately haired.

Steatomys parvus Rhoads

1896. *Steatomys parvus* Rhoads, *Proc. Acad. nat. Sci. Philad.* **1896** : 529. Reshiat, Lake Rudolf, Ethiopia [approximately 4° 33' N. 36° 00' E.].

DESCRIPTION. As for genus.

DISTRIBUTION. Lotome, Nabilatuk, Napyananya, Karamoja. Text-fig. 19.

MEASUREMENTS. Two ♂ h. & b. 59 mm., 60 mm.; tail 37 mm., 35 mm.; h. f. 13 mm., 15 mm.; ear 10 mm., 13 mm.; weight 5 g., ?.

BREEDING. No information available.

HABITAT. Dry savanna, semi-desert.

BIOLOGY. No information available.

Genus *DEOMYS* Thomas

1888. *Deomys* Thomas, *Proc. zool. Soc. Lond.* **1888** : 130. Genotype *Deomys ferrugineus* Thomas.

Similar to *Grammomys* with rufous upperside, white underside and pencilled tail 1.5 times head-and-body length. Differences include the presence of stiff fur along the back (soft in *Grammomys*), two faint grooves on the upper incisors (none in *Grammomys*), long and narrow snout of the skull (short and broad in *Grammomys*) and elongate feet (*Grammomys* short).

Deomys ferrugineus Thomas

1888. *Deomys ferrugineus* Thomas, *Proc. zool. Soc. Lond.* **1888** : 130. Lower Congo.

DESCRIPTION. As for genus.

DISTRIBUTION. Bwamba Forest, Toro. Text-fig. 19.

MEASUREMENTS. One ♀ h. & b. 122 mm.; tail 191 mm.; h. f. 33 mm.; ear 24 mm.

BREEDING. Foetuses (2 × 2) in Congo (Hatt, 1940).

HABITAT. In the Congo typical of primary forest; does not penetrate *Cynometra* or transitional forest; rare (Misonne, 1963).

BIOLOGY. Eight stomachs examined of animals caught in the Congo contained grasshoppers, ants, termites and flesh resembling that of a rat (Hatt, 1940).

Genus *DELANYMYS* Hayman. Delany's Swamp-mice

1962. *Delanymys* Hayman, *Rev. Zool. Bot. afr.* **65** : 129. Genotype, by original designation, *Delanymys brooksi* Hayman.

A very small mouse with a relatively long tail. Front feet very small, hind feet long and narrow. Tail thinly covered with short stiff hairs. Fur very dense and soft with stout guard hairs on dorsal surface. Basal two-thirds of dorsal and ventral hairs slate grey; dorsally, tips of hairs russet or hazel; ventrally, warm buff. Black patch between each eye and nostril.

Delanymys brooksi Hayman

1962. *Delanymys brooksi* Hayman, Rev. Zool. Bot. afr. 65: 132. Echuya Swamp, Kigezi.

DESCRIPTION. As for genus.

DISTRIBUTION. Echuya Swamp, Kigezi. Text-fig. 19.

MEASUREMENTS. One ♂ h. & b. 57 mm.; tail 100 mm.; h. f. 17 mm.; ear 10 mm.; weight 5 g.

BREEDING. No information available.



FIG. 19. Distribution of *Stearomys parvus*, *Deomys ferrugineus* and *Delanymys brooksi*.

HABITAT. Sedge swamp in bamboo and montane forest. Occurs in similar habitat in the Congo (Hayman, 1962).

BIOLOGY. No information available.

Subfamily OTOMYINAE Thomas

1897. Otomyinae Thomas, *Proc. zool. Soc. Lond.* **1892** : 1017.

Genus OTOMYS Cuvier. Swamp Rats

1823. *Otomys* Cuvier, *Dents. Mamm.* : 168. Genotype, by subsequent designation (Sclater, 1899, *Ann. S. Afr. Mus.* **1** : 195), *Otomys irroratus* (Brants).
 1918. *Anchotomys* Thomas, *Ann. Mag. nat. Hist.*, (9) **2** : 204. As a subgenus of *Otomys* Cuvier; type, by monotypy and original designation, *Euryotis anchietae* Bocage.

The genus *Otomys* is easy to identify as both upper and lower incisors are deeply grooved. The fur is long, thick and soft. A well haired tail appreciably shorter than head-and-body length. The ears are small and the face blunt. The colour is very variable. Swamp rat is probably a misnomer as they can occur in dry situations some distance from water. Many species of this genus have been described although according to Bohmann (1952) there are probably only three occurring in Uganda. In making specific identifications reference has to be made to the number of transverse laminae on the third upper molars. The systematics of this genus are in need of further investigation.

1	Lower incisors with two deep grooves	<i>O. typus</i>
	Lower incisors with a deep outer groove and a shallow inner groove	²
2	Five or six lamellae on third upper molar	<i>O. denti</i>
	Seven lamellae on third upper molar	<i>O. irroratus</i>

Otomys denti Thomas

1906. *Otomys denti* Thomas, *Ann. Mag. nat. Hist.*, (7) **18** : 142. Ruwenzori East, Toro.
 1915. *Otomys kempi* Dollman, *Ann. Mag. nat. Hist.* (8) **15** : 152. Burunga, Mt. Mikeno, Congo [1° 28' S. 29° 25' E.].

DESCRIPTION. Dark coloured; dorsal surface brown-black speckled with copper buff. Backs of hands and feet blackish brown. Ventral surface slaty-black slightly speckled with buff. Tail black above and below. Lower incisor with a shallow inner groove, five or six transverse lamellae on third upper molar.

DISTRIBUTION. Mabira Forest, Buganda; Echuya Swamp and Forest, Kigezi; Kibale Forest, Mubuku Valley, Toro. Text-fig. 20.

MEASUREMENTS. Two ♂ h. & b. 170 mm., 150 mm.; tail 96 mm., 95 mm.; h. f. 26 mm., 27 mm.; ear 23 mm., 21 mm.; weight 125 g., ?. Three ♀ h. & b. 167 mm., 167 mm., 157 mm.; tail 94 mm., 94 mm., 89 mm.; h. f. 26 mm., 27 mm., 27 mm.; ear 23 mm., 25 mm., 21 mm.; weight 120 g., ?, ?.

BREEDING. Litters of two (Misonne, 1963).

HABITAT. Difficult to define in view of the limited number of records but apparently occurs in mixed vegetation and forest at various elevations.

BIOLOGY. Preyed on by harrier (*Circus macrourus*), grass owl (*Tyto capensis*) and leopard in Malawi (Loveridge, 1953).

***Otomys irroratus* (Brants)**

1827. *Euryotis irroratus* Brants, *Het Geslacht der Muizen* : 94. Uitenhage, Cape of Good Hope [33° 41' S. 25° 25' E.]

1915. *Otomys tropicalis* Dollman, *Ann. Mag. nat. Hist.*, (8) 15 : 157. Mt. Kenya, Kenya [0° 08' S. 37° 15' E.]

1915. *Otomys rubeculus* Dollman, *Ann. Mag. nat. Hist.*, (8) 15 : 161. Kagambah, Ankole.

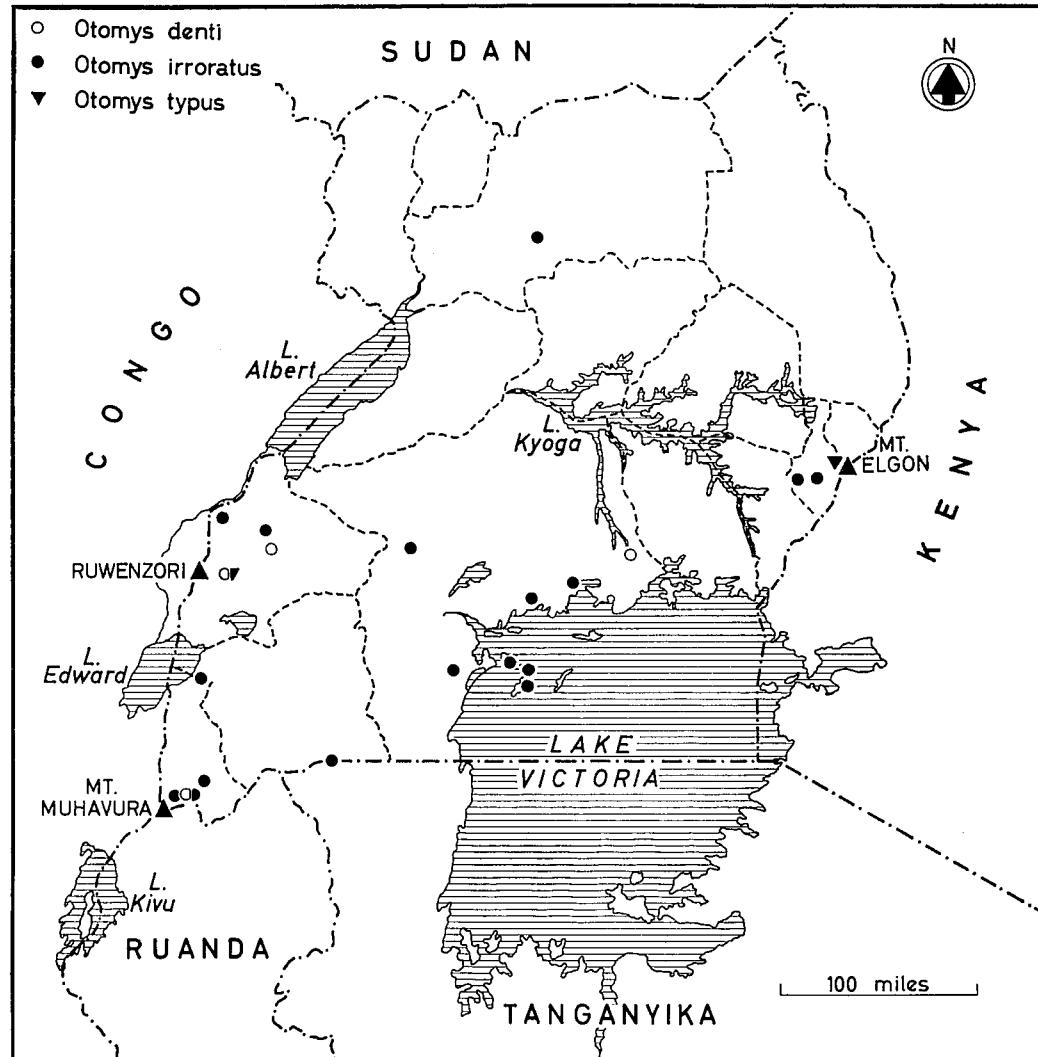


FIG. 20. Distribution of *Otomys* spp.

DESCRIPTION. Colour variable but not usually as dark as *O. denti*. Distinguished from the other species on tooth characters.

DISTRIBUTION. Gulu, Acholi; Burumba, between Rwempuno and Kaizi Rivers, Ankole; Bugala Island, Kampala, Masaka, Mbanga Forest, Mubende, Buganda; Beelrungi, Bubungi, Likima, Mbale, Bugisu; "Bunyoro"; Echuya Swamp, Kiduha, Kumba, Kigezi; Fort Portal, Humya, Toro, Kasiba. Text-fig. 20.

MEASUREMENTS. H. & b. ♂ 168.1 mm. (18 meas., range 124 to 201 mm.), ♀ 164.7 mm. (14 meas., range 139 to 183 mm.); tail ♂ 93.0 mm. (18 meas., range 83 to 112 mm.), ♀ 84.4 mm. (14 meas., range 69 to 96 mm.); h. f. ♂ 29.5 mm. (18 meas., range 27 to 34 mm.), ♀ 28.3 mm. (14 meas., range 26 to 30 mm.); ear ♂ 22.0 mm. (18 meas., range 20 to 25 mm.), ♀ 22.0 mm. (13 meas., range 20 to 25 mm.); weight ♂ 95 g., 110 g. (only 2 weighed), ♀ 101.3 g. (6 weighed, range 60 to 120 g.).

BREEDING. Foetuses (1 × 2) Jul. Mbanga Forest; (1 × 2) between Kaizi and Rwempuno Rivers, Aug.; (1 × 1) Oct. Echuya Swamp. One ♀ from Echuya lactating in Sep. Two embryos obtained in August weighed 25 g. Apparently no fixed breeding season in Zambia (Ansell, 1960); litter size 2 to 3. Hair and incisors erupted at birth. Litter size 2 to 4 (never more) in South West Africa where the young have been found in rough grass nests in dense reed-growth (Shortridge, 1934).

HABITAT. Grassland, scrub where herbage is fairly dense. Has been obtained at relatively large distances from water.

BIOLOGY. Herbivorous; stomachs of nine animals contained leaves and stems.

Otomys typus (Heuglin)

1877. *Oreomys typus* Heuglin, *Reise in Nordost. Afrika* 2: 77. Highlands of Simyen, Ethiopia [13°-14° N. 38°-39° E.].
 1891. *Otomys jacksoni* Thomas, *Ann. Mag. nat. Hist.*, (6) 7: 304. [Crater of] Mt. Elgon.
 1906. *Otomys dartmouthi* Thomas, *Ann. Mag. nat. Hist.*, (7) 18: 141. Mubuku Valley, Toro.

DESCRIPTION. Similar to *O. irroratus* but separated on tooth characters.

DISTRIBUTION. Mudangi, Bugisu; Arugot (Mt. Elgon), Sebei; Mubuku Valley, Toro. Text-fig. 20.

MEASUREMENTS. H. & b. ♂ 142.3 mm. (4 meas., range 132 to 150 mm.), ♀ 140.0 mm. (4 meas., range 135 to 143 mm.); tail ♂ 91.0 mm. (4 meas., range 82 to 101 mm.), ♀ 80.5 mm. (4 meas., range 64 to 93 mm.); h. f. ♂ 26.3 mm. (4 meas., range 25 to 27 mm.), ♀ 24.6 mm. (4 meas., range 21 to 26.5 mm.); ear ♂ 24.3 mm. (4 meas., range 22.5 to 25 mm.), ♀ 23.7 mm. (3 meas., range 21 to 25 mm.). None weighed.

BREEDING. No information available.

HABITAT. Typically an animal of high altitudes occurring at over 11,000 feet on Mt. Elgon and over 12,000 feet on Ruwenzori. Occurs in *Senecio-Lobelia* zone (Misonne, 1963).

BIOLOGY. Apparently active in the early morning and evening. Does not dig burrows but lives in long tunnels under moss and *Sphagnum* (Misonne, 1963).

GAZETTEER

As much information as was obtained is given for places not located.

Adropi, West Nile	2° 48' N.	31° 15' E.
Aigo River, Acholi	2° 21' N.	31° 55' E.
Ajeluk, Teso	1° 30' N.	33° 50' E.
Amudat, Karamoja	1° 58' N.	34° 57' E.
Amuria, Teso	2° 01' N.	33° 38' E.
Anamuget, Karamoja	2° 25' N.	34° 30' E.
Arua, West Nile	3° 01' N.	30° 55' E.
Arugot, north-east Mt. Elgon, Sebei	not located	
Asuya, Acholi	2° 57' N.	32° 36' E.
Awack, Acholi	2° 39' N.	33° 27' E.
Beelrunqi, south Bugisu	not located	
Benet, Sebei	1° 20' N.	34° 33' E.
Biso, Bunyoro	1° 45' N.	31° 25' E.
Bokora, Karamoja	2° 25' N.	34° 25' E.
Bubukwanga, Toro	0° 45' N.	30° 05' E.
Bubungi, Bugisu	1° 05' N.	34° 20' E.
Budadin Camp, Bugisu	not located	
Budama, Bukedi	0° 40' N.	34° 03' E.
Budongo Forest, Bunyoro	1° 45' N.	31° 36' E.
Bugala Island, Buganda	0° 24' S.	32° 10' E.
Bugiongolo	not located	
Bugoma Forest, Bunyoro	1° 15' N.	31° 00' E.
Bugoye, Toro	0° 17' N.	30° 07' E.
Buligi, Buganda	0° 27' N.	31° 53' E.
Bulisa, Bunyoro	2° 07' N.	31° 25' E.
Bumatta, Bwamba Co., Toro	not located	
Bummaddu = Bumadu, Toro	0° 43' N.	30° 05' E.
Bundibugyo, Toro	0° 42' N.	30° 04' E.
Bundimali, Toro	0° 55' N.	30° 03' E.
Buruli Co., Buganda	1° 25' N.	32° 25' E.
Burumba, Ankole	1° 00' S.	30° 50' E.
Busia, Bukedi	0° 28' N.	34° 05' E.
Busingiro, Bunyoro	1° 44' N.	31° 28' E.
Butiaba, Bunyoro	1° 49' N.	31° 19' E.
Butiti, Toro	0° 39' N.	30° 32' E.
Buyobo, Bugisu	1° 10' N.	34° 17' E.
Bwamba Co., Toro	0° 55' N.	30° 03' E.
Bwamba Forest, Toro	0° 48' N.	30° 06' E.
Chagwe = Kyagwe Co., Buganda	0° 24' N.	32° 45' E.
Chua Co., Acholi	3° 20' N.	33° 05' E.
Congo Road (Q.E.P.) Ankole	0° 14' S.	29° 59' E.
Crater Track (Q.E.P.), Toro	0° 07' S.	29° 54' E.
Echuya Forest, Kigezi	1° 14' S.	29° 46' E.
Echuya Swamp, Kigezi	1° 14' S.	29° 46' E.
Elgon, Mt., Sebei	1° 08' N.	34° 33' E.
Entebbe, Buganda	0° 03' N.	32° 28' E.

Fadjao, Bunyoro	2° 15' N.	31° 40' E.
Fort Patiko = Baker's Fatiko, Acholi	3° 02' N.	32° 21' E.
Fort Portal, Toro	0° 40' N.	30° 18' E.
Gayaza, Ankole	0° 45' S.	30° 47' E.
Greek River, south bank, Sebei	1° 36' N.	34° 20' E.
Gulu, Acholi	2° 47' N.	32° 18' E.
Hakitengya, Toro	0° 45' N.	30° 05' E.
Hoima, Bunyoro	1° 25' N.	31° 21' E.
Humya = Humiya, Toro	0° 46' N.	30° 02' E.
Ilumia, Toro	0° 53' N.	30° 03' E.
Impenetrable Forest, Kigezi	1° 05' S.	29° 49' E.
Ingezi, Kigezi	1° 00' S.	29° 50' E.
Iriri, Teso	2° 06' N.	34° 12' E.
Isegero, Busoga	0° 50' N.	33° 35' E.
Isungo, Toro	0° 30' N.	30° 21' E.
Jinja, Busoga	0° 27' N.	33° 12' E.
Kabanyolo, Buganda	0° 27' N.	32° 36' E.
Kabaroni Camp, north Bugisu	not located	
Kabula, Buganda	0° 22' S.	31° 10' E.
Kabulamuliro, Buganda	0° 42' N.	32° 13' E.
Kacheba, Lango	not located	
Kacheri, Karamoja	3° 10' N.	33° 56' E.
Kagambah, Ankole	1° 00' S.	30° 15' E.
Kaizi River (Q.E.P.), Ankole	0° 25' S.	29° 51' E.
Kajansi, Buganda	0° 12' N.	32° 32' E.
Kajuia, Bunyoro	not located	
Kakumiro, Buganda	0° 48' N.	31° 20' E.
Kalinzu Forest, Ankole	0° 22' S.	30° 07' E.
Kalule, Buganda	0° 38' N.	32° 32' E.
Kama Island, Busoga	0° 09' S.	33° 54' E.
Kamchuru, Karamoja	2° 40' N.	33° 35' E.
Kampala, Buganda	0° 19' N.	32° 35' E.
Kamulikwezi, Toro	0° 06' N.	30° 04' E.
Kamulikwezi Swamp, Toro	0° 05' N.	30° 09' E.
Kanaba Gap, Kigezi	1° 14' S.	29° 46' E.
Kapiri, Teso	1° 40' N.	33° 48' E.
Kasai Forest = Kasa Forest, Buganda	0° 13' N.	32° 02' E.
Kasiba	not located	
Katwe, Toro	0° 08' S.	29° 52' E.
Kawenge = Kawempe, Buganda	0° 20' N.	32° 35' E.
Kibale Forest = Mpanga Forest, Toro	0° 33' N.	30° 24' E.
Kibandama, ? Kigezi	not located	
Kibiro, Bunyoro	1° 41' N.	31° 15' E.
Kibusi = Kibuji, Lango	1° 53' N.	32° 23' E.
Kichwamba, Ankole	0° 14' S.	30° 06' E.
Kidoko, Bukedi	0° 52' N.	34° 07' E.
Kiduha, Kigezi	1° 15' S.	29° 41' E.
Kikandwa, Buganda	0° 37' N.	32° 07' E.

Kikonda, Buganda	1° 16' N.	31° 31' E.
Kilembe, Toro	0° 12' N.	30° 01' E.
Kimara, Toro	0° 50' N.	30° 15' E.
Kisimbiri, Buganda	0° 24' N.	32° 29' E.
Kisingo, Buganda	0° 45' N.	31° 57' E.
Kitgum, Acholi	3° 17' N.	32° 53' E.
Kokanjiro, Mt. Elgon	not located	
Koki Co., Buganda	0° 43' S.	31° 20' E.
Kome Island, Buganda	0° 06' S.	32° 45' E.
Kotido, Karamoja	3° 01' N.	34° 06' E.
Kumba, Kigezi	1° 08' S.	29° 54' E.
Kyabombo, Toro	not located	
Kyatwe, Toro	0° 27' N.	30° 13' E.
Lialo, Buganda	0° 53' N.	31° 57' E.
Likima, Bugisu	not located	
Locihotome, Karamoja	not located	
Login, West Nile	not located	
Lorengikipi strm., Karamoja	2° 20' N.	33° 51' E.
Lotome, Karamoja	2° 24' N.	34° 31' E.
Lungo, Bukedi	0° 25' N.	34° 00' E.
Lunyo, Bugando	0° 03' N.	32° 28' E.
Lutoto, Ankole	0° 20' S.	30° 06' E.
Lwakaka = Lwakhakha, Bugisu	0° 48' N.	34° 22' E.
Mabira Forest, Buganda	0° 30' N.	33° 00' E.
Makoga, Toro	1° 01' N.	30° 22' E.
Malabigambo Forest, Buganda	0° 57' S.	31° 33' E.
Malera, Teso	1° 26' N.	34° 08' E.
Manimani, Karamoja	2° 19' N.	34° 39' E.
Maramagambo Forest (Q.E.P.) Ankole	0° 25' S.	29° 52' E.
Maramagambo Forest, north of (Q.E.P.), Ankole	0° 15' S.	30° 03' E.
Masaka, Buganda	0° 20' S.	31° 44' E.
Masindi, Bunyoro	1° 41' N.	31° 43' E.
Masindi Port, Bunyoro	1° 42' N.	32° 05' E.
Mbale, Bugisu	1° 04' N.	34° 11' E.
Mbanga Forest = Mpanga Forest, Buganda	0° 11' N.	32° 16' E.
Mbarara, Ankole	0° 37' S.	30° 39' E.
Mengo District, Buganda	0° 17' N.	32° 35' E.
Mfumbiro = Mufumbiro = Bufumbiro region, Kigezi	1° 22' S.	29° 39' E.
Mihunga, Toro	0° 22' N.	30° 03' E.
M.N.P. = Murchison Falls National Park in south-west Acholi and north west Bunyoro		
Mongiro, Toro	0° 50' N.	30° 10' E.
Moroto, Karamoja	2° 33' N.	34° 39' E.
Moroto Forest, Karamoja	2° 33' N.	34° 44' E.
Moruita, Karamoja	1° 55' N.	34° 45' E.
Moyo, Madi	3° 39' N.	31° 42' E.
Mpanga Forest = Mbanga Forest, Buganda	0° 11' N.	32° 16' E.
Mpanga Forest = Kibale Forest, Toro	0° 33' N.	30° 24' E.
Mubende, Buganda	0° 35' N.	31° 23' E.
Mubuku Valley = Ruwenzori East, Toro	0° 22' N.	30° 01' E.
Mudangi, Bugisu	1° 10' N.	34° 29' E.

Muhavura Mt., Kigezi	1° 23' S.	29° 40' E.
Muhokya, Toro	0° 06' N.	30° 04' E.
Mulanda, Bukedi	0° 42' N.	34° 01' E.
Mweya, Toro	0° 11' S.	29° 54' E.
Nabilatuk, Karamoja	2° 03' N.	34° 35' E.
Nabugabo, Buganda	0° 22' S.	31° 53' E.
Nakiloro, Karamoja	2° 37' N.	34° 44' E.
Nakivali Lake, Ankole	0° 47' S.	30° 53' E.
Nalwendo, Buganda	1° 07' N.	31° 16' E.
Namalu, Karamoja	1° 49' N.	34° 38' E.
Napyananya, Karamoja	1° 52' N.	34° 35' E.
Nebbi, West Nile	2° 30' N.	31° 06' E.
Ngai, Lango	2° 30' N.	32° 29' E.
Ngal, West Nile	2° 26' N.	31° 29' E.
Ngora Rest House, Teso	1° 30' N.	33° 45' E.
Nkyanuna = Kyanuna, Buganda	0° 33' N.	32° 14' E.
Nyakabande, Kigezi	1° 18' S.	29° 43' E.
Nyalusanje, Kigezi	1° 00' S.	29° 58' E.
Offude, West Nile	3° 13' N.	30° 58' E.
Ongino, Teso	1° 33' N.	33° 59' E.
Packwack, West Nile	2° 27' N.	31° 29' E.
Pamdero (M.N.P.), Acholi	2° 22' N.	31° 40' E.
Paraa (M.N.P.), Acholi	2° 15' N.	31° 35' E.
Patiko = Baker's Fatiko, Acholi	3° 02' N.	37° 21' E.
Patong, River Naam	not located	

Q.E.P. = Queen Elizabeth National Park in Kigezi, west Ankole and south Toro.

Rhino Camp, West Nile	2° 58' N.	31° 24' E.
Rukiga Co., Kigezi	1° 05' S.	30° 02' E.
Rutanda (Q.E.P.), Ankole	0° 15' S.	30° 04' E.
Ruwenzori East = Mubuku Valley of British Museum							
Ruwenzori Expedition, 1906	0° 22' N.	30° 01' E.
Ruwenzori North, Toro	.	.	.	about	.	0° 40' N.	30° 10' E.
Ruwenzori South East, probably around Muhokya	0° 06' N.	30° 04' E.
Rwamachuchu = Rwamucucu, Kigezi	1° 10' S.	30° 02' E.
Rwempuno River (Q.E.P.), Ankole	0° 23' S.	29° 53' E.
Sabinio Mt., Kigezi	1° 23' S.	29° 36' E.
Salalira, Bugisu	1° 14' N.	34° 17' E.
Sara, Toro	0° 47' N.	30° 05' E.
Sebei Camp, Teso	1° 31' N.	33° 26' E.
Sipi, Bugisu	1° 20' N.	34° 14' E.
Siroko Valley, Bugisu	1° 21' N.	34° 14' E.
Soroti, Teso	1° 44' N.	33° 36' E.
Tokwe, Toro	0° 48' N.	30° 02' E.
Tororo, Bukedi	0° 41' N.	34° 10' E.
Usaga	not located	

Vurra, West Nile	2° 53' N.	30° 53' E.
Wadelai, West Nile	2° 42' N.	31° 27' E.
Walasi, Bugisu	1° 11' N.	34° 13' E.
Wanka River, Toro	0° 51' N.	30° 16' E.
Wasa River, Toro	0° 47' N.	30° 15' E.
Yumbe, West Nile	3° 28' N.	31° 15' E.
Zika Forest, Buganda	0° 10' N.	32° 28' E.

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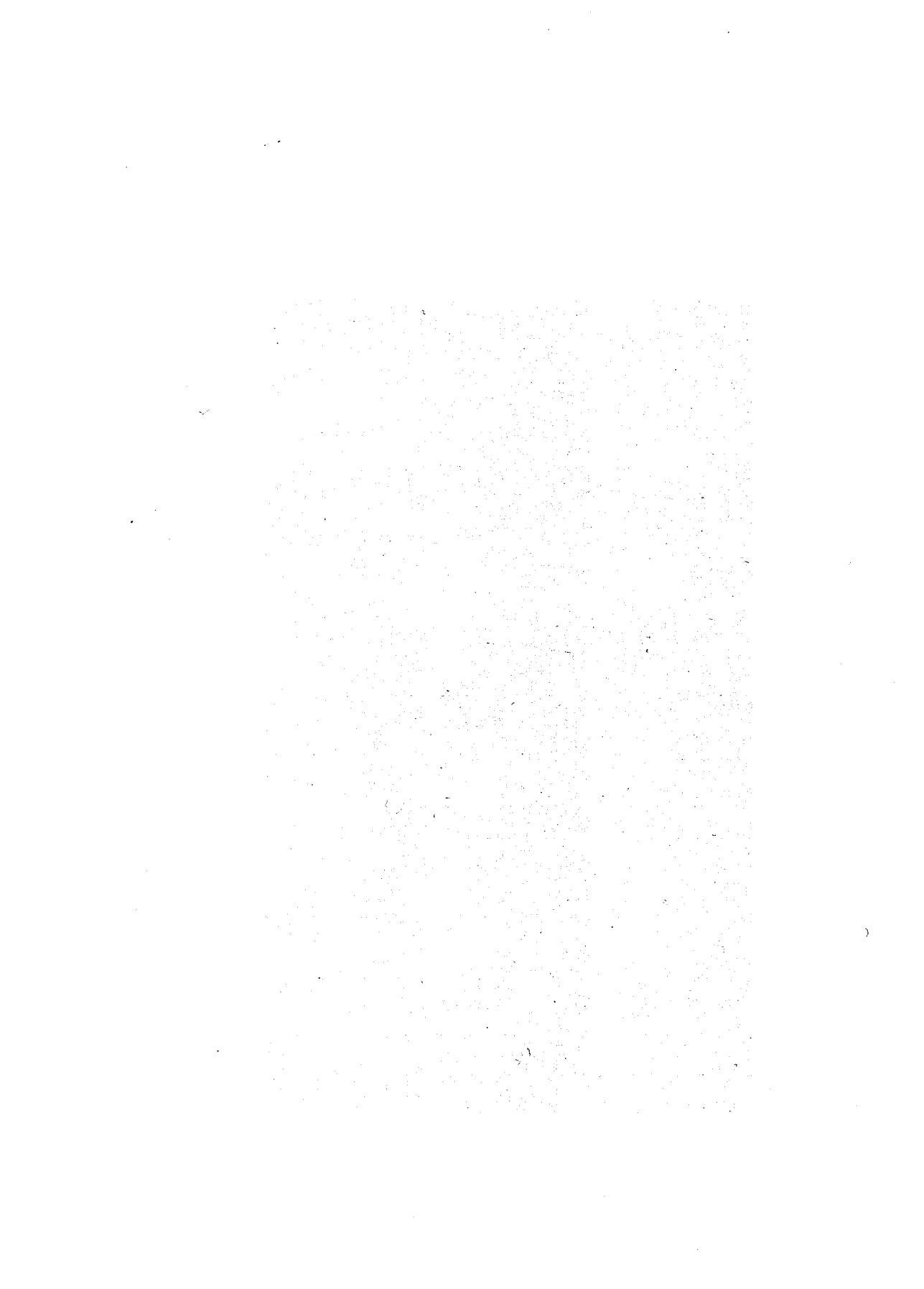
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