THE ECOLOGY AND LIFE HISTORY OF THE VLEI RAT, OTOMYS IRRORATUS (BRANTS, 1827), ON THE VAN RIEBEECK NATURE RESERVE, PRETORIA

by

Richard Marcy Davis

Submitted in partial fulfillment of
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To

my wife Jeri

for her unfailing encouragement and
help in making this work possible

ABSTRACT

THE ECOLOGY AND LIFE HISTORY OF THE VLEI RAT, *OTOMYS IRRORATUS* (BRANTS, 1827), ON THE VAN RIEBEECK NATURE RESERVE, PRETORIA

by

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The ecology and life history of the vlei rat, *Otomys irroratus* (Brants, 1827), were ~~determined~~ studied in a population on the Van Riebeeck Nature Reserve near Pretoria. Two main procedures were used to collect the basic information and material for the project. First, a permanent live-trapping grid was established where 333 animals were captured, marked, released, and recaptured over a period of 26 months. Second, snap-trapping and live-trapping were conducted elsewhere in the study area for supplementary material. Because *Otomys angoniensis* Wroughton, 1906, a sibling species of *O. irroratus*, also occurred in the study area and grid, it was necessary to define the differences in morphology and ecological distribution between the two species.

The ecology and life history of O. irroratus are described and discussed in regard to the following major topics: taxonomy and morphology, distribution, population dynamics, reproduction, postnatal growth and development, activity, behavior, and economic importance.

In addition to the presently used means of distinguishing O. irroratus and O. angoniensis, it was found that the hind foot length of the two species differed, being 29-34 mm in O. irroratus and 25-28 mm in O. angoniensis. The baculum of the two species was also found to be distinct in both shape and size.

In Southern Africa O. irroratus occurs primarily in the grassland subregion of the Southern Savanna biotic zone, while O. angoniensis occurs primarily in the woodland subregion of the same biotic zone.

The preferred habitats of the two species on the study grid were determined. There was little overlap of niches and each species had a high degree of association with a different veld type, O. irroratus being associated with the more mesic habitat.

The population size of O. irroratus reached a peak in May and a low in September. The population also fluctuated considerably from one year to the next, with rainfall possibly being the main contributing cause.

The ratio of juveniles, subadults, and adults fluctuated primarily in respect to the season when the young were born. The sex ratio did not depart significantly from 1:1. Males comprised 49,5 per cent of the total and females 50,5 per cent.

The rate of disappearance after one month from first capture was 41 per cent, indicating that a large number of transients and individuals dispersing from their birth site were involved. The overall rate of disappearance, excluding the high first month rate of disappearance, was 3,1 per cent per month.

The mortality rate appeared to be at its highest between August and September when the food and cover were of very poor quality and quantity. This was also the period when males demonstrated a significant loss in body weight.

The major factors causing mortality appeared to be flooding of the habitat and owl predation. Floods not only reduced the population but significantly interrupted breeding. Otomys irroratus was one of the most prominent prey species of both barn and grass owls.

Recapture data revealed that the mean home range size was 1 443 m^2, while that of males (1 730 m^2) was highly significantly different ($P<0,01$) from that of females (1 252 m^2). Home range size decreased significantly in winter but only slightly in relation to a doubling of the population size. Of 18 individuals recaptured after a flood, 12 (66,7 per cent) had returned to their previously determined home range.

Despite a small mean litter size (2,33) and relatively long gestation period (about 40 days), the long breeding season (nine months) and precocial birth, rapid development, and nipple-clinging behavior of the young together give *O. irroratus* a good reproductive potential.

Several litters of young were reared. They are precocial at birth and development proceeds rapidly. At birth the incisors are erupted, enabling the young to cling firmly to the nipples of the mother, thereby reducing mortality losses. Most adult behavior patterns are developed before weaning at 13 days of age. Sexual maturity is reached at approximately three months of age.

Otomys irroratus is primarily crepuscular, but activity tests conducted in the field and laboratory indicated some activity throughout the day and night.

Individual and social behavior are described and discussed. The vlei rat is shy and retiring in captivity and in nature is not easily captured by the use of snap-traps.

Interactions of adults were tested and they were found to be antisocial, with intrasexual aggression occurring when caged. Complex threat and communication patterns exist, a feature of asocial behavior. Mating failed to occur in captivity, probably as a result of their antisocial nature.

Marking behavior is very distinctive and, combined with urination and possibly defecation, would appear to be useful in delineating territories. It would also appear from their social habits, marking behavior, and considerable overlap of home ranges that their interactions with conspecifics in nature are represented by a dominance hierarchy.

The influence of *O. irroratus* upon the environment was found to be slight. The species serves as a common prey item for a number of predators and was found to harbor several endo- and ectoparasites of public health importance.

SAMEVATTING

THE ECOLOGY AND LIFE HISTORY OF THE VLEI RAT, *OTOMYS IRRORATUS* (BRANTS, 1827), ON THE VAN RIEBEECK NATURE RESERVE, PRETORIA

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Voorgelê aan die

Departement Dierkunde
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Doctor Scientiae

Die ekologie en lewenswyse van die vleirot, *Otomys irroratus* (Brants, 1827), was vasgestel uit 'n bevolking op die Van Riebeeck Natuurreservaat naby Pretoria. Teneinde basiese inligting en materiaal vir die projek te bekom, is hoofsaaklik van twee hoofstudiemetodes gebruik gemaak. Eerstens is 'n permanente studierooster neergelê om vleirotte lewendig mee te vang. Driehonderd drie en dertig diere is gevang, gemerk, vrygelaat en weer gevang oor 'n tydperk van 26 maande. Tweedens is lewende en dooie eksemplare, as aanvullende studiemateriaal, op 'n ander deel van die studiegebied versamel. Omdat *Otomys angoniensis*

Wroughton, 1906, 'n sibling spesie van *O. irroratus*, ook in die studiegebied voorkom en in die ruit gevang is, was dit nodig om die verskille in die morfologie en ekologiese verspreiding tussen hierdie twee spesies te definieer.

Die ekologie en lewenswyse van *O. irroratus* word met betrekking tot die volgende hoofpunte beskryf en bespreek: taksonomie en morfologie, verspreiding, bevolkingsdinamika, voortplanting, nageboortelike groei en ontwikkeling, aktiwiteit, gedrag en ekonomiese belangrikheid.

Bykomstig by die middele wat tans gebruik word om tussen *O. irroratus* en *O. angoniensis* te onderskei is daar gevind dat die lengte van die agtervoet in die twee spesies verskil. In *O. irroratus* is dit 29 - 34 mm en in *O. angoniensis* is dit 25 - 28 mm. Die baculum van die twee spesies verskil ook in sowel vorm en grootte.

In Suidelike Afrika word *O. irroratus* hoofsaaklik in 'n subgebied van die Suidelike Savanna biotiese sone, nl. die grasveld aangetref terwyl *O. angoniensis* hoofsaaklik in die bos-subgebied van dieselfde biotiese sone sy tuiste het.

Die habitatsvoorkeur van die twee spesies is m.b.t. die studieruit vasgestel. Die nisse van die twee spesies het min oorvleuel en elke spesie het 'n hoë graad van assosiasie met 'n verskillende veldtipe getoon. *Otomys irroratus* was veral geassosieer met die natter habitat.

Die bevolkingsgrootte van *O. irroratus* het 'n hoogtepunt in Meimaand en 'n laagtepunt in September bereik. Die bevolking het ook aansienlik van die een jaar tot die volgende gewissel, waarskynlik as gevolg van die effek van reënval.

Die verhouding van kleintjies, onvolwassenes, en volwassenes het hoofsaaklik gewissel ten opsigte van die seisoen waarin die kleintjies gebore is. Die geslagsverhouding het nie betekenisvol afgewyk van 1:1 verhouding nie. Mannetjies het 49,5 persent van die totaal uitgemaak en wyfies 50,5 persent.

'n Maand vanaf die eerste vangste het 41 persent van versamelde individue verdwyn. Dit dui op 'n groot aantal kortstondige besoekers aan die gebied en individue wat vanaf hul geboorteplek versprei het. Die totale verdwyningstempo, afgesien van die hoë verdwyningstempo gedurende die eerste maand, was 3,1 persent per maand.

Dit wil voorkom asof die sterftesyfer gedurende die maande Augustus en September die hoogste was toe die gehalte en hoeveelheid voedsel asook skuiling baie swak was. Tydens die tydperk het die mannetjies 'n betekenisvolle verlies in liggaamsgewig getoon.

Die belangrikste mortaliteitsfaktore was blykbaar oorstromings van hul laagliggende vlei-habitat asook uile. Oorstromings het nie alleen die bevolking verminder nie maar ook voortplanting betekenisvol onderbreek. *Otomys irroratus* was een van die mees prominente prooi-items van sowel nonnetjiesuile as grasuile.

Hervangs-gegewens het getoon dat die gemiddelde grootte van die tuisgebied 1 443 m^2 was, terwyl dié van mannetjies (1 730 m^2) hoogs betekenisvol verskil het ($P<0,01$) van dié van wyfies (1 252 m^2). Die grootte van die tuisgebied het tydens die winter betekenisvol verminder maar dit was slegs 'n geringe hoeveelheid in verhouding tot 'n verdubbeling van die bevolkingsgrootte. Van 18 individue wat na 'n oorstroming versamel is, het 12 (66,7 persent) teruggekeer na hulle voorheen vasgestelde tuisgebiede.

Ten spyte van 'n klein gemiddelde werpselgrootte (2,33), 'n blykbare lang dragtigheidstydperk (ongeveer 40 dae), het 'n lang teelseisoen (nege maande) en prekosiale geboorte, 'n vinnige ontwikkeling, en die gewoonte om aan die tepels vas te kleef, saam daartoe bygedra om vir *O. irroratus* 'n goeie voortplantingspotensiaal te verseker.

Verskeie werpsels van kleintjies is grootgemaak. Hulle was prekosiaal by geboorte en ontwikkeling het vinnig plaasgevind. By geboorte was die incisivi reeds deurgebreek, wat die kleintjies toegelaat het om ferm aan die tepels van die moeder vas te byt. Dit het lewensverlies deur mortaliteit verminder. Die meeste volwasse gedragspatrone was reeds ontwikkel voordat die kleintjies op 'n ouderdom van 13 dae gespeen is. Geslagsvolwassenheid is op 'n ouderdom van ongeveer 3 maande bereik.

Otomys irroratus is hoofsaaklik aktief teen sonop en sononder, maar aktiewiteitstoetse wat in die veld en in die laboratorium uitgevoer is, dui op 'n mate van aktiwiteit dwarsdeur die dag en nag.

Individuele en sosiale gedrag word beskryf en bespreek. Die vleirot is in gevangenisskap skaam en skugter en word in die natuur nie maklik deur gebruikmaking van muisvalle gevang nie.

Die wisselwerkinge tussen volwassenes is getoets en daar is gevind dat hulle antisosiaal is en intraseksuele aggressie in gevangenisskap openbaar. Komplekse dreig en kommunikasie-gedragspatrone bestaan, wat 'n kenmerk van asosiale gedragspatrone is. Geen paring het in gevangenisskap plaasgevind nie, waarskynlik ook as gevolg van hul antisosiale geaardheid.

Merkgedrag is baie kenmerkend en, tesame met urinering en moontlik ontlasting, is dit skynbaar nuttig in die afbakening van territoria. Uit hulle sosiale gewoontes, merkgedrag, die aansienlike oorveueling van hul tuisgebiede, en die wisselwerkinge tussen lede van dieselfde spesies in die natuur wil dit voorkom dat daar 'n dominansie-hierargie bestaan.

Die invloed van _O. irroratus_ op die omgewing het gering geblyk te wees. Hulle dien as prooi vir 'n verskeidenheid van roofdiere en huisves verskeie endo- en ektoparasiete wat van belang is vir die openbare gesondheid.

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INTRODUCTION

Africa, in regard to the study of mammals, is a continent awaiting intensive ecological study (Delany, 1972). What little contribution there has been to date on mammalian ecology in Africa has been primarily concentrated on big game, which is becoming scarce in most parts of Africa. What little is known of the small mammals of Africa, especially the rodents, is limited to their taxonomy, distribution, and parasites because of their importance as vectors of disease and as agricultural pests. Several other authors have urged that more research effort be concentrated on ecological studies of African mammals, especially the small mammals (see Meester, 1954; Ansell, 1958; Dorst, 1965; Du Toit, 1965; Davis, 1966).

The vlei rat, *Otomys irroratus* (Brants, 1827), belongs to the small African subfamily Otomyinae which contains two genera (*Otomys* and *Parotomys*) and 12 nominal species. At present there are 10 recognized species of *Otomys* which occur throughout most of Africa from Cameroun and Ethiopia southward to the Cape (Misonne, 1968). Five of the six species which occur in Southern Africa are endemic to that region and include *O. irroratus*.

The taxonomic status of most African rodents, including the Otomyinae, is frequently confusing, species having been split and lumped numerous times. The taxonomic situation has recently improved, but in certain respects still remains unclear. At the turn of the present century the differences between some of the sympatrically occurring species of *Otomys*, particularly the two sibling species *O. irroratus* and *Otomys angoniensis* Wroughton, 1906, were unknown. Even though there was a distinction drawn later between these two species, the difference was still not always clear since numerous subsequent authors continued to confuse the two. Recently some authors have considered *Otomys tropicalis*

Thomas, 1902, a synonym of *O. irroratus* (see Delany and Neal, 1966; Dieterlen, 1968). Pending adequate revision *O. tropicalis* and *O. irroratus* are here regarded as distinct. The main point of the above discussion is that in utilizing ecological information from the literature it is only too easy to allocate this information to the wrong taxon.

The vlei rat, *O. irroratus*, frequently attracted the attention of early collectors and authors, but only scattered bits and pieces of ecological information were recorded. Also, what little was recorded was often contradictory. More recently, ecological knowledge concerning *O. irroratus* has been slightly advanced because it has been linked with the transmission of plague, because it inflicts considerable damage to young trees in pine plantations, and because it is a common prey of owls, the regurgitated pellets of owls often being an object of interest in determining the distribution and population ecology of prey species. Nevertheless, the only comprehensive ecological investigation to date specifically carried out on any of the species of *Otomys* was by Dieterlen (1968) on *O. tropicalis* (which he mistakenly referred to as *O. irroratus*). The findings of Dieterlen, therefore, are used extensively in this study for contrast and comparison with those on *O. irroratus*.

The purpose of this study was to determine the ecology and life history of the vlei rat, *O. irroratus*, in a population on the Van Riebeeck Nature Reserve near Pretoria. The information desired on the ecology and life history of *O. irroratus* in this study came under the following major headings: ecological distribution, population dynamics, postnatal growth and development, activity periods, behavior, and public health importance. In an effort to collect information for each of these categories data were accumulated by two main procedures. The first of these consisted of a permanent live-trapping grid where animals were captured, marked, released, and recaptured. The other involved the snap-trapping and live-trapping elsewhere in the study area of specimens for examination and experimentation in the laboratory.

Preliminary trapping was begun on the Reserve in December 1969 in an effort to locate an area satisfactory for the study grid. The grid was established in March 1970 and trapping was conducted at regular intervals for a year and then for varying intervals until May 1972, during which time 333 *O. irroratus* were marked.

Supplementary snap-trapping and live-trapping was generally conducted at the same time as live-trapping on the grid. Approximately 150 specimens were studied or examined in the laboratory.

Otomys angoniensis was also captured on the study grid and at other localities in the Reserve. Some information was further collected on this species in an effort to determine the differences between the two species in respect of morphology and ecological distribution.

DESCRIPTION OF STUDY AREA

The study area is located in the Van Riebeeck Nature Reserve (Rietvlei Dam), 20 km SSE of Pretoria ($25^{o}53'$S, $28^{o}17'$E). The Reserve comprises a totally protected and reasonably natural area of 3 355 ha. The elevation varies little in the Reserve and is approximately 1 500 m throughout. The Reserve occurs in the highveld grassland region of the Southern Savanna biotic zone and the vegetation is composed of primarily sour, wiry grassveld. The low-lying areas are covered primarily by sedges, rushes, and moisture-loving grasses.

The climate is warm and temperate with a mean annual precipitation of 723 mm. The annual rainfall is derived mainly from showers and thunderstorms occurring in the summer months from October through March, during which 84 per cent of the annual precipitation occurs. The mean monthly rainfall and the amount of precipitation each month from 1969 to mid-1972 can be seen in Table 1. During 1969 and 1971 the rainfall was considerably above normal, 19,9 and 18,4 per cent respectively. Rainfall, in fact, was so excessive and of such a nature in October 1969 and January 1972 that floods occurred in the area of the study grid. During both 1970 and the first half of 1972 (despite the excessive rainfall in January) the rainfall was 12,4 per cent below normal. The monthly rainfall during the study period fluctuated considerably above and below the mean.

The summers are relatively hot with mean daily maximum and minimum temperatures, recorded at nearby Irene, during January of $27,7^{o}$C and $14,2^{o}$C respectively, and a maximum recorded temperature of $37,2^{o}$C. During the winter the days are mild but the nights cold with mean daily maximum and minimum temperatures during July of $18,6^{o}$C and $-1,2^{o}$C respectively, and a minimum recorded temperature of $-8,7^{o}$C (Weather Bureau, 1954). The mean monthly temperatures at Irene and Pretoria and the mean temperatures each month from 1969 to mid-1972 can be seen in Table 2. The mean annual temperature in Pretoria during 1969 and 1970 was above normal, 2,3 and 4,0 per cent respectively. During 1971 and the first half of 1972 the mean annual temperature was slightly below normal, 1,7 and 1,0 per cent respectively. The temperature in Pretoria during the study period, as compared with the fluctuation of rainfall, varied only slightly from the mean.

The permanent study grid was located in the southeastern portion of the Reserve in a moist, low-lying area. This low-lying area was basically treeless and much of it was periodically covered with standing water, thus it can be classified as a typical vlei or marsh.

The vegetation of the study grid was mainly moisture-loving and not typical of the greater part of the highveld region, with the exception of other moist, low-lying areas. The plants that occurred in the study grid or were common in typical _O. irroratus_ habitat elsewhere in the study area are listed below in phylogenetic order:

Family Poaceae (=Gramineae)

- _Hemarthria altissima_ (Poir.) Stapf and C.E. Hubb.
- _Elyonurus argenteus_ Nees
- _Imperata cylindrica_ (L.) Beauv.
- _Andropogon appendiculatus_ Nees
- _Hyparrhenia dregeana_ (Nees) Stapf ex Stent
- _Paspalum dilatatum_ Poir.
- _Pennisetum thunbergii_ Kunth
- _Phalaris arundinaceae_ L.
- _Arundinella nepalensis_ Trin.
- _Helictotrichon turgidulum_ (Stapf) Schweick.
- _Phragmites australis_ (Cav.) Trin. ex Steud.
- _Agrostis lachnantha_ Nees
- _Eragrostis planiculmis_ Nees
- _Cynodon dactylon_ (L.) Pers.
- _Bromus willdenowii_ Kunth

Family Cyperaceae

- _Pycreus lanceus_ (Thunb.) Turrill
- _Pycreus unioloides_ (R. Br.) Urban
- _Mariscus congestus_ C.B. Cl.

  - *Mariscus capensis* Schrad.
  - *Fuirena gracilis* Kunth
  - *Eleocharis dregeana* Steud.
  - *Carex schlechteri* Nelmes
- Family Juncaceae
  - *Juncus arabicus* Adam.
  - *Juncus exsertus* Buch.
  - *Juncus punctorius* L.
- Family Liliaceae
  - *Kniphofia porphyrantha* Bak.
  - *Asparagus laricinus* Burch.
- Family Polygonaceae
  - *Rumex crispus* L.
- Family Ranunculaceae
  - *Ranunculus multifidus* Forsk.
- Family Rosaceae
  - *Agrimonia odorata* Mill.
- Family Leguminosae
  - *Melilotus alba* Desr.
  - *Trifolium africanum* Ser. var. *lydenbergensis* Gillett
- Family Thymelaeaceae
  - *Gnidia gymnostachya* (C.A. Mey.) Gilg
- Family Onagraceae
  - *Oenothera rosea* Ait.
- Family Apiaceae (=Umbelliferae)
  - *Berula erecta* (Huds.) Cov.
- Family Gentianaceae
  - *Chironia palustris* Burch. subsp. *transvaalensis* (Gilg) Verdoorn
- Family Convolvulaceae
  - *Convolvulus ulosepalus* Hall.f.
- Family Verbenaceae
  - *Verbena bonariensis* L.
- Family Labiatae
  - *Mentha aquatica* L.
- Family Scrophulariaceae
  - *Veronica anagallis-aquatica* L.
- Family Plantaginaceae
  - *Plantago lanceolata* L.

Family Asteraceae (=Compositae)

Erigeron floribundus (H.B.K.) Sch. Bip.
Conyza podocephala DC.
Helichrysum leptolepis DC.
Helichrysum rugulosum Less.
Tagetes minuta L.
Senecio erubescens Ait.
Berkheya radula (Harv.) de Wild.
Cirsium vulgare (Savi) Airy-Shaw
Sonchus dregeanus DC.

The study grid was more or less bordered on one side, at a distance of 40 to 80 m, by a perennial stream, and on another side, from 35 to 200 m away, by a dirt road (Fig. 1). There existed a definite moisture gradient in the grid, the wettest part being nearest the stream with conditions becoming drier as one moved away from the stream. Standing water occurred throughout the year in the small dips and depressions in the wet part, but for only a short period after heavy rainfall in the drier part. The moisture gradient in the grid was reflected in the occurrence of two recognizable veld types, one on the wetter and the other on the drier part. These two veld types were divided by a narrow ecotone composed primarily of plant species common to disturbed areas. (See the section on Ecological Distribution for further details of the vegetation.)

MATERIALS AND METHODS

Preliminary live-trapping was conducted at various localities within the Reserve from December 1969 to February 1970 in an attempt to locate a suitable site for a permanent live-trapping grid. A square grid, comprised of 10 rows of 10 stations per row (100 trap stations in all), was laid out in March 1970. Numbered trap markers were placed every 15 m in rows 15 m apart. The grid covered an area of 2,25 ha, which includes the equivalent of one half the distance to a hypothetical next trap row.

Trapping was begun in March 1970 and continued monthly (excluding July) for one year. Trapping was then conducted on four different occasions at varying intervals during the succeeding 15 months, the last session being in May 1972.

Two different types of live-traps were used. One was a National Live Trap made of open wire mesh measuring 14 by 14 by 30 cm. Use of these traps was discontinued after six months of trapping because they proved ineffective in catching animals smaller than 50 g, such as _Crocidura_, _Leggada_, _Myosorex_, _Praomys_, _Rhabdomys_, and juvenile _Otomys_. There also appeared to be a gradual decline in their trapping success for the much larger _Otomys_ (see Table 8), and during rains or cold winter nights captured animals were too exposed in such an open trap. The other type of live-trap used was a homemade variety built primarily of tempered hardboard (Masonite). For specific details of its construction and dimensions see Fig. 2. This trap proved to be far more effective than the other trap and also provided the necessary protection against rain and cold. Traps were painted white on top to offer some protection to the trapped animals against the intense summer sun and also as an aid in locating the traps in the thick vegetation.

Originally two live-traps, one of each type, were placed at each station. After the first trapping session in March 1970 it was realized that there existed a high population density on the wettest part of the grid. It was then decided to place an additional hardboard trap at each station in the five rows nearest the stream, thereby increasing the number of traps used from 200 to 250. All of the National wire traps were replaced with hardboard traps after the September 1970 trapping session for the reasons stated above.

In setting the traps in the study grid an attempt was made to locate them in the most likely-looking places within an approximate radius of 1,5 m of the trap station marker. The traps were put out upside down and prebaited with a dry mixture of rolled oats and currants or raisins. After three days of prebaiting the traps were placed upright, rebaited with the same bait, and then set. The traps were then examined in the early morning and late afternoon for the following three or four days. During four days of trapping 95 per cent of the Otomys were captured during the first three days. From this it was decided to reduce the trapping period to only three days, which would decrease the risk of animals dying in the traps from too many captures in one session. Each time a trap was examined, whether morning or afternoon, was regarded as a trap "night". During the study period 22 750 live-trap "nights" were completed and 333 O. irroratus were captured a total of 2 613 times.

Animals live-trapped on the grid were transferred from the trap into a strong plastic bag and weighed (in g) with a tension spring scale, after which they were measured and sexed; and their physical and reproductive condition was noted. The measurements recorded (in mm) were head-body length (from tip of nose to anus), tail length (from anus to tip of tail), and hind foot length (from heel to tip of longest toe, including the claw). Each animal was weighed and measured only once during each trapping session. The reproductive status of females was classified as either perforate or nonperforate (vaginal orifice either open or closed). The condition of the mammae was noted and palpation was employed to determine if they were lactating and also whether they were gravid. The position of the testes in males was noted as either scrotal or abdominal. Handling of the animals did not appear to affect the position of the testes nor the status of the vaginal orifice. For identification each individual was toe-clipped at first capture, the 1-2-4-7 formula being applied. The animals were then released near the point of capture and the traps reset. All information was later transferred to a permanent record card maintained for each individual.

Snap-trapping and additional live-trapping in various other localities of similar habitat were conducted at the same time for supplementary material for dissection and experimentation in the laboratory. Animals that died in traps on the study grid were also dissected.

Dead specimens were placed in individual plastic bags and kept frozen in a deep freeze for later examination. When examined later the following were recorded: body measurements, status and weight of reproductive organs, number and position of embryos, weight of adrenal glands, gut weight, and stomach contents. The study skin, skull, and phallus and baculum were prepared for later examination. The external and internal parasites were preserved for later identification.

The four standard field measurements were recorded for each study specimen prepared. These measurements (in mm) were as follows: total or overall length, tail length (from the base of the spine to the tip of the tail), hind foot length (including the claw), and ear length (from the notch). The total weight of these specimens was taken with a spring balance and recorded in grams.

The skulls were cleaned by dermestid beetles and the following measurements taken (in mm): greatest length of skull, condylobasal length, basilar length, zygomatic breadth, interorbital breadth, braincase breadth, rostral breadth, nasal length, bulla length, incisive foramen length, and maxillary toothrow length. The number of lamellae on M^3 was recorded as well as the shape of the posterior petrotympanic foramen. The approximate age of each specimen was determined from a toothwear formula developed by D.H.S. Davis (pers. comm.) and also by comparison with the skulls of known-age animals reared in the laboratory.

External and internal parasites were preserved in a solution of 70 per cent alcohol-5 per cent glycerol. The parasites from individual specimens were kept separate and given a catalogue number corresponding with that of the specimen from which they were recovered.

The phalli of the males were examined in order to determine whether there exist significant differences in phallic morphology and baculum shape and size between O. irroratus and O. angoniensis. The phalli were prepared following the procedures of Lidicker (1968). The unpreserved phalli were first cleared in a two per cent solution of KOH for approximately three days. They were then placed in a 0,003 per cent solution of alizarin red S for two days, which stained the bone. Finally, the specimens were placed successively in 25, 50, 75 and 100 per cent solutions of glycerol, each step taking one day. The phallus was drawn with the aid of a drawing tube attached to a binocular dissecting microscope. The bacula were measured to the nearest 0,1 mm with a calibrated eyepiece in a binocular dissecting microscope. The cleared tissue of the phallus was found to distort the true measurements of the baculum and had to be removed.

The ovaries, testes, embryos, and adrenal glands were weighed on an electrical analytic balance accurate to 0,1 mg. The gut (from the lower esophagus to the rectum) was removed and weighed to the nearest 0,2 g. Gross weight of animals less the weight of the gut, and of the uterus and embryos whenever this exceeded 5 g, gives the clean weight. The weights of the ovaries, testes, and adrenals were then expressed as a percentage of the clean weight.

The presence of sperm in the cauda epididymis was confirmed microscopically, but it was found, as also by Coetzee (1965), that when abundant sperm were present the coiled tubules of the epididymis were clearly visible and microscopic examination was unnecessary.

Some of the animals captured alive away from the study grid were used for behavior and breeding experiments in the laboratory. Animals were maintained in a variety of cages, aquaria of various sizes being utilized for observations on maintenance behavior, maternal care, and development of the young. Animals were fed primarily on fresh green lettuce supplemented with fresh carrots, carrot tops, cabbage, and standard mouse cubes. Water was not taken when offered, therefore it was generally not provided.

Since these animals are active during the day most behavioral observations were done during daylight hours. Descriptions of postures and movement sequences were recorded in notebooks and with the aid of a tape recorder. An attempt was made to photograph various postures and behavior patterns. The animals were marked for easy identification during observation by either clipping or painting the ears.

Behavioral interactions and activity studies in the laboratory were conducted in an observation chamber similar to that described by Brown (1964). The main chamber was 60 cm square with 60 cm long and 10 cm wide runways leading away from all four sides. A nest box 30 cm square was attached to the end of each runway. The chamber was constructed primarily of wood and hardboard (Masonite) with clear plastic (Perspex) covering all upper surfaces for observation. This enclosure was kept in an environmental control room with a constant temperature of 20°C and relative humidity of 50 per cent. Lighting was regulated on a 12-hour on-off cycle.

For study of adult behavioral interactions two males and two females were placed in the observation chamber, each in a separate nest box. After varying periods of familiarization dividing partitions were removed and interactions observed.

Activity periods in the laboratory were recorded in the same enclosure by means of a photoelectric cell placed midway in each runway and connected to a multichannel Esterline Angus event recorder. In order to avoid the effect of social contact upon normal activity, animals were tested either individually or with dividing partitions placed in the central chamber, thus isolating them. This latter procedure proved the most efficient as four animals could be tested simultaneously.

Activity periods in the field were determined by examining the traps in the study grid every two hours over a 24-hour period.

Animals paired for breeding were maintained in various types and sizes of cages, none exceeding 50 by 75 cm, for periods of up to two months. Breeding in the laboratory proved unsuccessful so all gravid females live-trapped away from the grid were brought into the laboratory in order to study parent-offspring relationships and postnatal growth and development.

The following abbreviations have been used throughout:
km = kilometer, m = meter, cm = centimeter, mm = millimeter, g = gram, mg = milligram, mg/g = milligram per gram, ha = hectare, °C = degree celsius, m^2 = square meter, and cm^3 = cubic centimeter.

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TAXONOMY AND MORPHOLOGY

Taxonomic Status

Otomys irroratus is one of the 10 presently recognized species belonging to the genus *Otomys* of the small subfamily Otomyinae. The Otomyinae have been included in the Muridae, but Davis (1965) and Dieterlen (1969) both suggested that they belong to the cricetids. Hooper and Musser (1964) stated that on the basis of the morphology of the phallus and baculum the murids and cricetids all belong to one major group of great variation. Misonne (1969) stated that because of their lamellate molars and the trend toward enlargement of M^3 the Otomyinae have nothing in common with the Muridae and should be included in the Cricetidae.

Otomys irroratus was originally described by Brants in 1827 as *Euryotis irrorata*. No type locality was designated so Roberts (1929) ~~nominated~~ elected Uitenhage, Cape Province, South Africa, as the type locality. Roberts at the same time described a new subspecies of *O. irroratus*, *O. i. randensis*, from Fontainebleau, Johannesburg, and later (1951) gave the distribution of the latter as the highveld, from Pretoria to Johannesburg. Roberts (1929) also described *O. tugelenis pretoriae* from Fountains Valley, Pretoria, and later (1951) gave the distribution as the western Transvaal below the highveld, but penetrating up the valleys to just below the highveld, and overlapping the range of *O. i. randensis*. Ellerman *et al.* (1953) synonymized *O. tugelensis*, including *O. t. pretoriae*, with *O. irroratus*. Meester *et al.* (1964) stated that *O. tugelensis* should be considered a synonym of *O. angoniensis* and that the latter is definitely distinct from *O. irroratus*. Davis (1962) also stated that *O. irroratus* and *O. angoniensis* are morphologically distinct. Meester *et al.* (1964) included *auratus*, *cupreoides*, *cupreus*, *natalensis*, *orientalis*, and *randensis*, of earlier authors, as synonyms of the subspecies *O. i. irroratus*;

and *mashona*, *pretoriae*, *sabiensis*, and *tugelensis*, of earlier authors, as synonyms of the subspecies *O. angoniensis rowleyi*.

Bohmann (1953) included the central and east African ~~form~~ taxon, *O. tropicalis*, as a subspecies of *O. irroratus*. Delany and Neal (1966) and Dieterlen (1968) both referred to that ~~form~~ taxon as *O. irroratus*. Davis (1962) and Misonne (1968) stated that the two species may be conspecific. Because there exist character differences and a considerable geographical separation between *O. irroratus* and *O. tropicalis* they will for the present be considered as distinct, at least until a proper taxonomic study is done. There already exists too much confusion within the genus *Otomys* as to what species is exactly what without accepting another change upon circumstantial evidence. It also seems preferable for the time being and for the same reasons that attempts to distinguish subspecies of *O. irroratus* be abandoned in the present report. Meester (1954) stated that the taxonomy of Southern African rodents was in a state of chaos, and much later several authors pointed out a particular need for a revision of either part or all of the genus *Otomys* (Ansell, 1964 and 1965; Delany, 1966; Delany and Neal, 1966; and Vesey-FitzGerald, 1966).

Morphology

Briefly, *O. irroratus* can be said to be moderate to large in size, with a short, stout-looking body, blunt face, and large, rounded, well-haired ears. The short tail (approximately 60 per cent of the head-body length) is fairly well haired, darker above than below, and not pencilled at the tip. The pelage is long and soft giving the animal a shaggy appearance. The general dorsal color is a dark slate-gray heavily suffused with buff, brown, and black. The sides are lighter, lacking the suffusion of black, and the underparts slightly paler and more gray. They are also characterized, as are ~~all~~ most of the *Otomys*, by large, yellow, deeply grooved incisors.

Some of the main diagnostic features of *O. irroratus* are as follows: one deep outer and one shallow inner groove on the lower incisors; a molar lamina formula of 3-2-6/4-2-2; the posterior petrotympanic foramen a relatively large round hole; the transition from the broad to the narrow region of the nasals marked by a distinct, spoon-shaped angle; and the maxillary toothrow exceeding 8,8 mm in length.

Two useful morphological characters, occasionally used in classification, are the phallus and the baculum. Hooper and Musser (1964) examined these structures from an *Otomys* (*O. tropicalis*; Hooper, pers. comm.) and classified ~~it as~~ them of the complex type, typical of most other murids and cricetids studied. In their complex type the baculum generally consists of four parts--a basal bone and three digits; the spongy layer is comparatively thin and functionally apparently partly replaced by pairs of sac-like sinuses that are situated alongside the baculum below the floor of the terminal crater; and usually an array of processes and embellishments are present which are not seen in the simple phallus. Apparently some of the types classified by Hooper and Musser (1964) as complex did not demonstrate all of the above characteristics. This was the case in the specimens of *O. irroratus* examined, as the baculum is made up of only a single bone as in the simple type, but the spongy layer is comparatively thin and almost nonexistent and there exists an array of processes. Both of the latter features are as in the complex type. Further details of the phallus and baculum can be seen in Figs. 4 and 5. It will be noted that the spongy layer or sinuses are not shown as they were not obvious enough to define. It can be concluded that because these layers or sinuses were not obvious they would be characteristic of the complex and not the simple type, in which they are large and clearly obvious.

A brief description of the morphology of the digestive tract of six adult *O. irroratus* from the study area is included as it is suspected that this species has a very efficient means of digesting herbaceous vegetation. The digestive tract of *O. irroratus* compares very closely with that described for *O. tropicalis* (Dieterlen, 1968) and for the herbivorous meadow vole, *Microtus pennsylvanicus* (Golley, 1960). The stomach of the vlei rat is U-shaped and can be divided into the following three areas as in *Microtus*: an esophageal sac, fundic gland region, and pyloric stomach. The esophageal sac of the vlei rat stomach is capable of tremendous expansion. Dieterlen (1968) recorded the volume of the stomach of *O. tropicalis* varying from 2 to 16 cm^3.

The small intestine of the six *O. irroratus* averaged 35,7 cm in length and varied from 5 to 8 mm in diameter, and could be divided into a duodenum (15,2 cm in length) and an ileum (20,5 cm).

Dieterlen (1968) found, in 15 adult *O. tropicalis*, a mean small intestine length of 32 cm.

The caecum of the vlei rat is large and the dominant structure of the digestive tract, nearly filling the posterior half of the body cavity and concealing the other organs. The mean length was 14,9 cm and the diameter exceedingly variable. Dieterlen (1968) found a mean length of 16,5 cm in *O. tropicalis*. The caecum has many convolutions which may serve to increase the surface area. It apparently serves as a storage place for food where further microbial action may occur.

The large intestine of the six vlei rats averaged 27,4 cm in length and varied from 2 to 5 mm in diameter; it could be divided into a colon (9,2 cm in length and 5 mm in diameter) and a rectum (18,2 cm in length and 2 to 3 mm in diameter). Dieterlen found a mean length of 29,3 cm in *O. tropicalis*.

A comparison of the total length of portions of the digestive tract in *O. irroratus*, *O. tropicalis* (Dieterlen, 1968), *Microtus pennsylvanicus* (Golley, 1960), and *Neotoma*, an herbivorous wood-rat (Golley, 1960, after Howell, 1926), is shown below:

Per Cent of Total Length of Digestive Tract

	O. irroratus	*O. tropicalis*	*Microtus*	*Neotoma*
Small Intestine	46	41	58	46
Caecum	19	21	18	7
Large Intestine	35	38	24	47

Golley (1960) stated that the caecum is unusually long and the large intestine unusually short in *Microtus*, as compared with *Neotoma*. The above data suggest that the caecum of *Otomys* is likewise unusually long. The large intestine of *Otomys*, however, falls about midway between those of *Microtus* and *Neotoma*. Golley suggested that the large caecum of *Microtus* may be a contributing factor to its high digestive efficiency. If this is the case then *Otomys* may also be considered to have high digestive efficiency.

Distinction Between O. irroratus and O. angoniensis

The distinction between *O. irroratus* and *O. angoniensis* has always proved difficult, especially in the field, where their ranges overlap. Davis (1959 and 1962) and Misonne (1968) stated that they are probably sibling species. Both species occurred in the study area, thus necessitating a means of distinguishing between them, both alive and as study specimens. Externally members of these two species may be distinguished by color and size (O. irroratus is darker and larger) and by length of the hind foot (shorter and narrower in O. angoniensis). Of 143 O. irroratus and 15 O. angoniensis specimens from the study area the hind foot length of the two demonstrated a distinct difference with no overlap. Hind foot length of O. angoniensis (including the claw) has a range of 25-28 mm and that of O. irroratus 29-34 mm.

Another previously unrecorded character useful in differentiating between the two species was pointed out by P.J. Geldenhuys (pers. comm.) and was found to hold true. This character, consisting of a ring of orange hair approximately 2 mm in width around the eyes of O. angoniensis, is absent in O. irroratus. A brief check of specimens of both species from various localities presently in the Transvaal Museum collection showed this character to be consistent throughout Southern Africa. However, it should be checked to see if it is consistent throughout the ranges of both species. For additional differences in body size between the two species see Fig. 8.

The following cranial characters can often be used in differentiating between O. irroratus and O. angoniensis: the relative size of the posterior petrotympanic foramen on the bulla; the degree of angular transition between the broad and narrow portions of the nasals; the number of laminae on M^3; and the difference in greatest width of the upper molars.

Davis (1959, 1962, and 1965) made reference to the use of the posterior petrotympanic foramen on the bulla and also included (1965) a good photograph showing its position and how it differs between the two species. In O. irroratus the foramen is clearly round and large, while in O. angoniensis it is much smaller, not clearly round, and the depression on the inner face of the bulla is slightly deeper, forming a "slit". This character was consistent in all of the specimens examined.

The degree of angular transition between the broad and narrow portions of the nasals is mentioned by most authors and appears to be consistent. In O. irroratus this angular transition is very distinct and somewhat spoon-shaped, whereas in O. angoniensis the angular transition is not so sudden (Fig. 3).

The number of laminae on M^3 has been referred to by numerous authors, but some (notably Roberts, 1951) appeared to have experienced confusion regarding this character. Part of the confusion no doubt arose because this character is not always consistent. Generally, O. irroratus has six laminae on M^3 and O. angoniensis seven. Among the 143 specimens of O. irroratus from the study area 137 (95,8 per cent) had six laminae, five (3,5 per cent) had seven laminae, and one (0,7 per cent) had six laminae on one side and seven on the other. Among the 15 O. angoniensis examined one (6,7 per cent) had seven laminae on one side and six on the other.

The use of the width of the molars as a distinguishing character was mentioned by Davis (1959) but was not examined in the present study. It would appear that this character varies with age and amount of wear on the molars. Nevertheless, if this is a valid character it would also be extremely useful in analyzing skull remains from owl pellets in areas where the two species occur together.

Dollman (1915), in differentiating between O. angoniensis and O. tropicalis in East Africa, stated that the nasals were exceptionally broad anteriorly (more than 8 mm in width) in O. angoniensis, but not exceptionally broad (less than 8 mm) in width) in O. tropicalis. This character also was not analyzed but may have application in differentiating between O. angoniensis and O. irroratus. For additional differences between O. irroratus and O. angoniensis in sizes and proportions of the skull see Fig. 8.

The baculum has been used as a character in differentiating between species and sometimes sibling species (Hoffmeister and Lee, 1963). The phalli of 39 O. irroratus and three O. angoniensis were cleared and the baculum stained so that the shape and size of the bacula could be compared. The morphology of the phallus (Fig. 4) appeared identical, but the baculum was significantly different in both shape and size (Figs. 5 and 6). The proximal portion of the baculum in both species is composed of bone and the distal portion of cartilage. The bases of the two bacula differ in shape, the general shape being obovate in O. irroratus and spatulate in *O. angoniensis* (Fig. 5), very similar to what Hoffmeister and Lee (1963) found in *Peromyscus eremicus* and *P. merriami* respectively. In ventral view there is a central raised portion down the middle of the base in *O. angoniensis*, whereas in *O. irroratus* the base is U-shaped with a groove over part of its length, as in the dorsal aspects of both (Fig.5). The base of the baculum of *O. irroratus* changes significantly with age, as the oldest bacula develop processes on the sides (Fig. 5). There was only one baculum of an old *O. angoniensis* among the three studied and it did not differ from the one illustrated in Fig. 5. Although there were only three bacula of *O. angoniensis*, and not enough to do a statistical analysis, it appears that given enough specimens the two species would be significantly different in size (Fig. 6). The mean and extreme values for the two measurements (in mm) taken of the proximal portion of the bacula of each species are as follows: total length, *O. irroratus* 5,44 (4,3-6,5), *O. angoniensis* 4,40 (3,9-4,9); greatest width of base, *O. irroratus* 1,71 (0,9-2,3), *O. angoniensis* 0,97 (0,7-1,2). The size of the baculum gradually increases with age (Fig. 7). The rather high value for age class I in respect of greatest width of the base could be the result of small sample size. There were no specimens of age class 0 for comparison.

Cytogenetics is another tool used to distinguish between taxa. Matthey (1964) described the chromosome pattern of *O. irroratus* and compared it to his findings of *O. angoniensis*. He found the following differences: *O. irroratus*, 2N=28, fundamental number of 50; *O. angoniensis*, 2N=56, fundamental number of 56. He stated that the fundamental numbers are nearly identical and that they differ essentially in their central fusions. He concluded that their differences could not be the result of polyploidy.

External and Cranial Measurements

Five external and 11 cranial measurements were taken on all study specimens prepared. The following are the means and extremes of the external and cranial measurements (in mm) of 79 adult *O. irroratus* (age classes III-V). Despite the existence of significant differences between age classes III-IV-V for most of the following measurements (Table 3), the measurements are pooled to represent the generalized adult size. *External measurements*--total length 259,0 (229-303);

tail length 98,0 (82-117); hind foot length 31,5 (29-34); ear length 20,9 (19-23); total body weight (less large embryos) 143,7 (102-206); *cranial measurements*— greatest length 40,6 (38,3-44,8); condylobasal length 39,5 (36,8-43,5); basilar length 33,1 (30,8-36,9); zygomatic breadth 21,1 (19,7-23,2); interorbital breadth 4,4 (3,9-4,8); braincase breadth 16,8 (15,6-18,7); rostral breadth 7,5 (7,0-8,3); nasal length 18,5 (16,7-20,8); bulla length 7,3 (6,7-8,4); incisive foramen length 7,2 (6,5-8,2); and maxillary toothrow length 10,1 (9,5-11,0).

The following are the means and extremes of the measurements of 12 adult *O. angoniensis* (age classes III-V): *external measurements*— total length 232,8 (212-251); tail length 84,4 (77-92); hind foot length 26,7 (25,5-28,0); ear length 19,6 (17,0-20,5); total body weight 103,3 (87-121); *cranial measurements*—greatest length 37,5 (35,5-38,5); condylobasal length 36,4 (33,9-37,8); basilar length 30,1 (28,0-31,2); zygomatic breadth 19,4 (18,3-20,2); interorbital breadth 4,3 (4,0-4,7); braincase breadth 15,1 (14,2-16,4); rostral breadth 7,2 (6,9-7,6); nasal length 16,3 (14,9-17,6); bulla length 6,9 (6,5-7,4); incisive foramen length 6,6 (5,9-7,2); and maxillary toothrow length 9,0 (8,6-9,4).

Age and Seasonal Variation

Individuals may vary in morphology and size with age, season, and sex. One of the best means of determining the relative age of rodents is by means of arbitrarily extablished categories of molar toothwear. The following molar toothwear categories were established by D.H.S. Davis (pers. comm.) and were based on a classification of toothwear seen in *O. irroratus* from the western Cape:

0. The top of the laminae narrower than width of tooth; base of laminae within socket below alveolar level; age, birth to five weeks.

I. Bases of laminae in M^{1-3} still below alveolar margin (M^1 occasionally level with or slightly above alveolar margin); top of laminae about as wide as tooth and showing signs of wear; age, five to 12 weeks.

II. Bases of laminae in M^1 above alveolar level, those of M^{2-3} at or below alveolar level (M^2 occasionally level with or slightly above alveolar margin); age, 12 weeks to five months.

IV. Laminae of M^{1-3} nearly worn to their bases; gaps between inner roots of M^{2-3} just at or a little above alveolar level; age, 10 to 13 months.

V. Laminae worn down almost to their bases; root gaps in M^{1-3} all above alveolar level; age, 13 months and older.

VI. Laminar pattern worn away. (Never seen by D.H.S. Davis or myself).

These categories were compared, by me, with known age animals reared in captivity and taken from the study area. The age range of each group agrees favorably with the categories used. Once these toothwear categories were determined as satisfactory all the individuals from each age group were placed together and a statistical analysis completed for each external and cranial measurement within each group (Fig. 8). In order to determine significance of differences between age groups for each of the measurements compared the Student's *t*-test was used. The results of this analysis can be seen in Table 3. Between age groups total weight is the external measurement with the most highly significant differences. Of all cranial measurements the differences between age groups are significant or highly significant with the exception of interorbital breadth, braincase breadth, and rostral breadth.

Seasonal variation was not as clearly discernible as age variation. Because *Otomys* is strictly vegetarian it would appear that seasonal variation in quality and abundance of vegetation would have a telling effect on growth, and especially on increase in body weight. During the winter, animals on the study grid gained little weight and some lost weight. An analysis of the body weights of male *O. irroratus* demonstrated a sharp decline in weight during August and September (Fig. 9). Pregnancy interfered with consecutive weighings of females. While climatic conditions are severest during June and July this sharp decrease in weight during August and September coincides closely with the period when the veld is at its poorest. The vegetation suffers greatly during the winter and the rain, which greatly stimulates vegetational growth, does not normally begin until October (Table 1). Rainfall during September of both 1970 and 1971 was above normal (Table 1), which is probably part of the reason for the sharp increase in weight of males during October. Also, the increased temperature during August and September (Table2) was apparently enough to initiate some growth of the vegetation. The males reached their peak weight in November and December when the veld was at its best. The decrease in mean weight from January to May was the result of an abundance of newly matured adults within the population just entering that category. There was only a very gradual increase in weight of the males from May to July which coincides with what was found to be the case with younger animals. It was noted that individuals beginning the winter as juveniles or subadults grew very slowly during the winter and did not mature beyond subadults until after the winter was past. Pinter (1970) also found seasonal variation in growth and maturation rates in grasshopper mice, *Onychomys*, and stated that it was also well known for voles.

The omnivorous multimammate mouse, *Praomys natalensis*, in the Transvaal highveld showed a decrease in body weight, especially of males, during June and July (Coetzee, 1965). Coetzee tended to dismiss the lack or poor quality of food as a possible contributing cause of the decrease because there appeared to be abundant food and the animals were fat. *Otomys* also had considerable amounts of fatty tissue in the abdominal cavity during the winter months, which, however, disappeared by August and September. As illustrated in Fig. 9 and as discussed in the preceding paragraph, males lost weight only during August and September following the disappearance of the fat supply, but prior to the improvement of the quality and abundance of food. It would, therefore, appear that the fatty tissue helped to sustain *Otomys* through the winter when they underwent a great amount of stress due to the low temperatures and poor quality and abundance of food.

Heavy mortality during winter was suggested as a cause of the decrease in maximum body weight of *Praomys* (Coetzee, 1965). It is assumed that he meant that if there was a high mortality rate it would have a greater effect upon the older individuals (which would generally be the heaviest as well), the result being a decrease in the mean body weight. Although *Otomys* is longer-lived than *Praomys* this could be part of the answer to the decrease in the mean weight of *O. irroratus* during August and September when the food is at its poorest. The data in Table 6 indicate that there was a mean decrease in the population size on the grid between August and September of 11,0 per cent. This rate of 11,0 per cent is more than three times greater than the normal overall monthly rate of decrease of 3,1 per cent (see Mortality). During 1970 the population size was at its lowest during September (Fig. 14). It is thus suggested that there are three contributing causes to the decrease in mean weight of *O. irroratus* during August and September. One is the scarcity and poor quality of vegetation, another is that the fatty tissue stores in the body cavity have been used up, and the third is the high mortality rate of older animals, again possibly the result of scarcity and poor quality of food.

DISTRIBUTION

Geographic

The geographic distribution of O. irroratus is limited to Southern Africa and is markedly discontinuous. In South Africa O. irroratus occurs from the Cape Province through Natal and the Orange Free State to the Transvaal. It also occurs in Lesotho and is isolated on the eastern escarpment of Rhodesia and just across the border in Mozambique (Vumba Mountain) (Fig. 10).

Otomys tropicalis, a possible conspecific of O. irroratus, occurs primarily in western Kenya, Uganda, Rwanda, Burundi, and eastern Zaïre.

Otomys angoniensis is distributed from South Africa to Angola in the west and Kenya in the north. In South Africa O. angoniensis is limited primarily to Natal and the Transvaal (Fig. 10). The Transvaal highveld between Pretoria and Johannesburg is where most of the overlap in distribution occurs between O. angoniensis and O. irroratus.

Southern Africa has been geographically subdivided into four biotic zones, differing from each other climatically, vegetationally, and in respect of the animal species occurring in them (Davis, 1962; Meester, 1965). Both suggested that two of these biotic zones (Southern Savanna and South-West Arid) may each have two distinct subregions. The four biotic zones and their possible subregions are as follows (also Fig. 11):

Southern Savanna--The moister eastern part of Southern Africa, with rainfall exceeding 500 mm annually, extending south nearly as far as the eastern limits of the South-West Cape zone. The grassland area of the southern Transvaal, Orange Free State, western Natal, Lesotho, and parts of the eastern Cape Province may form a distinct subregion, with the woodland area of the northern Transvaal, Swaziland, eastern Natal, parts of the eastern Cape Province, and the remainder of the Southern Savanna to the north the other subregion.

South-West Cape--A climatically and biotically distinct zone, corresponding to the Cape macchia vegetational zone.

Forest--Isolated patches of montane and subtropical evergreen forest distributed in the Savanna and South-West Cape zones.

South-West Arid--The arid western part of Southern Africa, with a mean annual rainfall less than 500 mm. The Namib Desert of the western coastal strip may form a distinct subregion.

Otomys irroratus occurs mainly in the highveld and the coastal, montane, and submontane grasslands of the Southern Savanna biotic zone, but with a fairly substantial distribution in the South-West Cape zone (Davis, 1962). Considering the grassland subregion of Davis (1962) and Meester (1965) it would appear that *O. irroratus* is nearly endemic to that subregion. There also exist three known relict or isolated populations of *O. irroratus* within the South-West Arid zone (Kamiesberg, Upper Karoo, Kuruman) and another in the Forest patches of eastern Rhodesia-western Mozambique. Davis stated that the populations in the South-West Arid zone are examples of persistence in "oases".

Most African mammal species today show a patchy distribution with isolated populations scattered about their original range (Dorst, 1965). Because the distribution of *O. irroratus* is somewhat patchy and isolated populations exist their past distribution undoubtedly was more extensive. The present distribution pattern has likely come about primarily due to past climatic changes.

The geographical distibution of *O. angoniensis* could be said to be almost entirely confined to the woodland subregion of the Southern Savanna biotic zone.

Altitudinally *O. irroratus* occurs from sea level to 2 400 m near Mokhotlong, Lesotho. *Otomys tropicalis* regularly occurs at high altitudes (800-4 000 m; Dieterlen, 1968) and is one of the most consistently occurring high-altitude rodents in Africa (see Delany, 1972).

Ecological

As the common name implies, the vlei rat, *O. irroratus*, inhabits areas consisting primarily of lush grasses, sedges, and herbaceous vegetation associated with wet soil and sometimes shallow, standing water near rivers and streams and in marshes or vleis. Previous authors have referred to *O. irroratus* as preferring this type of habitat. In montane areas it has also been found living on steep grass-covered hillsides some distance from water (Thomas and Schwann, 1906b; pers. obs.). Being most abundant in low-lying wet areas and occasionally in montane grasslands, populations therefore do not seem to be randomly distributed over a given area, but appear to have a patchy distribution. Ansell (1960) stated that *O. irroratus* (=*O. angoniensis*) in Zambia demonstrates this same patchy distribution.

Most authors have referred to *O. tropicalis* as being found in a similar type of habitat as *O. irroratus*, but occasionally in bush or scrub. *Otomys angoniensis* has also been referred to as living in marshy or vlei areas, but frequently in drier grassland. Roberts (1929) and Davis (1962) stated that in the Transvaal where *O. irroratus* and *O. angoniensis* occur together the latter prefers a drier habitat. Misonne (1968) stated the same and added that this is also true where *O. tropicalis* and *O. angoniensis* occur together.

Because both *O. irroratus* and *O. angoniensis* occurred in the study grid there existed an excellent opportunity to more clearly define their ecological distribution. A description of the study grid has been given above (see Description of Study Area). The grid was situated in a low-lying area occasionally inundated with water and classified as a vlei. There appeared to be a moisture gradient which resulted in what can be referred to as a "wet" part and a "dry" part of the grid. The vegetation was primarily moisture-loving and not typical of the sour, wiry grasses of the highveld. Over the moisture gradient the vegetation can be separated into two basic veld types, one associated with the "wet" and the other with the "dry" part. These two veld types were separated by an ecotonal area characterized by several plant species common to disturbed areas. In the grid the distributions of the two vlei rats appeared to be strongly correlated with the "wet" and "dry" parts, as was stated by Roberts (1929), Davis (1962), and Misonne (1968), with *O. irroratus* occurring mainly in the wet and *O. angoniensis* in the dry part.

The number of times that a different individual was caught at each station in the study grid was plotted for both *O. irroratus* and *O. angoniensis* (Fig. 12). These data were then used to determine the preferred habitat of each species, the highest values indicating the area of greatest preference. The total number of captures per station was not used as this would have led to a skewed picture. Because *O. irroratus* occurred in large numbers it was possible, from the area in which it was captured, to differentiate a preferred from a marginal habitat. Since so few *O. angoniensis* were involved it was difficult to differentiate a preferred and marginal habitat. The marginal habitat tends to be more extensive when the population density in the preferred area is high, as it became in *O. irroratus*. Goertz (1964) found the cotton rat, *Sigmodon hispidus*, occupying marginal habitat only when the population was high. Single-capture stations of *O. irroratus* and of *O. angoniensis* not adjacent to the areas normally occupied were regarded as reflecting abnormal wanderings. Figure 12 shows that the ranges of the two species in the grid are nearly distinct with little area of overlap.

The distribution was plotted of each of the 48 plant species occurring in the study grid. The distribution of each of the 29 most common plants was related to the number of different individuals of each vlei rat species caught per trap station in a test of association. A Chi-square value was calculated for each plant species against each species of vlei rat (Tables 4 and 5). Those plant species demonstrating a highly significant positive association with *O. irroratus* (*Mariscus congestus*, *Eleocharis dregeana*, *Berula erecta*, *Agrostis lachnantha*, *Juncus punctorius*, *Pennisetum thunbergii*, and *Cirsium vulgare*) show a correspondingly significant negative association with *O. angoniensis*. The same is true for those plant species demonstrating a highly significant positive association with *O. angoniensis* (*Helictotrichon turgidulum*, *Cynodon dactylon*, *Melilotus alba*, *Hyparrhenia dregeana*, *Berkheya radula*, *Chironia palustris*, and *Conyza podocephala*), which show a highly significant negative association with *O. irroratus*.

The following six species of plants show an abnormally significant positive association with *O. irroratus*: *Paspalum dilatatum*, *Convolvulus ulosepalis*, *Erigeron floribundus*, *Fuirena gracilis*, *Plantago lanceolata*, and *Juncus exsertus*. The significant Chi-square values obtained for those are the result of their occurrence in the ecotonal area, the marginal habitat area of *O. irroratus*. Therefore, they cannot be considered to be truly associated with the preferred habitat of *O. irroratus*.

The moisture-loving grass *Arundinella nepalensis* was the most abundant and widespread plant in the grid. It was as common on the "wet" as on the "dry" part of the grid and demonstrated no significant association with either O. irroratus or O. angoniensis.

Much emphasis has been placed on the association between the distribution of the two vlei rats and the plant species in the grid to account for their distribution patterns. There may be other factors involved (e.g. competitive exclusiveness), or possibly a combination of vegetation and other factors. Nevertheless, vegetation plays a significant role in their lives. Firstly, both species of vlei rats are strictly vegetarian. Secondly, they are active during the daytime and the vegetation forms a protective canopy over their runway systems. Lastly, the nests of O. irroratus, and possibly O. angoniensis as well, are primarily above ground, therefore they need the protection of good vegetative cover. For further details of burrows, nests, and runways see the discussions at the end of this section.

C.H.B. Grant (in Thomas and Schwann, 1905a) and Davis (1942) suggested that O. irroratus prefers areas with a good vegetative cover, and Schulz (1953) stated that the density and nature of cover is far more important than the plant species involved. Those plants common to the O. irroratus part of the grid provide a more dense basal and canopy cover than do those on the O. angoniensis part. Also, the dorsal color of O. angoniensis is lighter than O. irroratus, which consequently provides it with better protective coloration in its drier habitat. It therefore appears that whatever factor or factors are most important or act as determinants in the ecological distribution of the two vlei rats, the vegetation undoubtedly plays a prominent role. Zimmerman (1965) found a close association in the distributions of two species of Microtus with certain plant species. The distributions of the two were also related to the amount of cover. It would be interesting to compare the plant associations here discussed with those found in other areas where the two species of vlei rats occur, either together or separately.

Otomys tropicalis has been collected in areas dominated by elephant grass, Pennisetum purpureum, (Pirlot, 1958; Dieterlen, 1968). In the study grid O. irroratus showed a highly significant association with another species of elephant grass, Pennisetum thunbergii. Both species of Pennisetum require either a high rainfall or, in low rainfall areas, sufficient moisture as is provided by vleis. Delany (1966) found O. tropicalis associated with certain species of grasses on Mount Moroto, Uganda, but not with P. purpureum. Possibly this was because his collection was made at high altitudes.

The distribution of many mammals in Africa demonstrates a pattern modified by the burning of the grassland, both naturally and by man (Dorst, 1965). The present ecological distribution of *O. irroratus* could be the result of this burning, the wet areas being least likely to burn. This would be an important factor in the case of an animal that generally nests above ground with little refuge from fire. Shortridge (1934) stated that when the local people in the western Caprivi, South West Africa, set fire to the veld during the dry season the vlei rats there, *O. i. maximus* (=*O. angoniensis maximus*), either ran from the fire or took refuge in the damp unburned patches. Vesey-FitzGerald (1966), referring to *O. anchietae* in Zambia and Tanzania, stated that they live in moist habitats which give them immunity from the dry season fires. Neal (1970) could not establish the effects of fire on *O. tropicalis* in Uganda as so few were captured.

Some other habits and microhabitat preferences of vlei rats, such as burrows, nests, and runways, must also be included in a discussion of ecological distribution. *Otomys irroratus* is terrestrial, the soil often being too wet for burrowing. Shortridge (1934) stated that in the eastern Cape Province where reeds are scarce they often live in burrows or crab holes near the edges of rivers. There are other references to them living in burrows but it is doubtful if this is their normal habit. The situation is probably more as reported by FitzSimons (1920), that they live in burrows only in exposed situations. It is probably also true as stated by Roberts (in Shortridge, 1934), that if they do occupy burrows they prefer to occupy those already excavated by crabs, moles, or other burrowing rodents. In the study area only one burrow (in the side of a ridge of dirt running parallel to a stream) out of three found appeared as if it had been excavated by a vlei rat. Because *O. angoniensis* is often found in drier, more exposed, situations it is possible that they would utilize burrows more often than *O. irroratus*. However, no investigation of the nests of *O. angoniensis* was carried out in this study.

The typical nest of *O. irroratus* found in the study area was normally open and shaped like a shallow bowl approximately 15 cm in diameter. Nests consisted of shredded vegetation placed directly on top of the ground and were protected above by a natural canopy of vegetation. It appears that these nests are easily made and may only be temporary. Nests were also found in the study area in a short burrow in the side of a bank and under large rocks, large fallen tree limbs, and p~~o~~iles of litter. The nests in all of these situations were always open, shallow, and bowl-like.

For movements around their habitat vlei rats make intricate, well-defined, runway systems under and through the vegetation. These runways are formed as a result of the normal activity of feeding and they end in new feeding grounds.

POPULATION DYNAMICS

Population Size

The size of a population depends upon three factors or forces operating upon it--reproduction, mortality, and movement. Reproduction has an additive effect on population numbers, mortality a reducing effect, and movement either one or the other. The details of reproduction will be discussed in the following major section.

Several methods were used to arrive at estimates of the population size of *O. irroratus* but none were satisfactory. Three methods, the Lincoln Index, the Schumacher-Eschmeyer Method, and the Schnabel Index, were used as a noncumulative basis of estimates for each time the traps were examined and then a mean estimate calculated for the entire session. The differences, however, between the morning and afternoon estimates were too considerable for these methods to be of valid use. The Lincoln Index was used on a cumulative basis, combining the trapping results from each month before calculation, and appeared to be satisfactory when trapping was conducted on a regular basis with a minimum interval between sessions (Fig. 13). The population estimates during the first year of trapping were reasonably well in line with the total number captured. It was only after the first year, when intervals between trapping sessions became greater, that the standard error of the estimate became greater and that estimates did not appear to be within reason. Hayne (1949) stated that a lengthy interval between the preliminary marking period and the subsequent period when the population is sampled inevitably results in an overestimation of the size of the population. This was obviously the case in using the Lincoln Index on a cumulative basis for *O. irroratus*.

If trapping is conducted in approximately the same way during each trapping period in a long-term study a population estimate is basically a duplication of the actual number captured, the latter merely being a lower number. The most important information is whether the population fluctuated from one period to another and why; complex means of estimating populations in cases such as the present study are unnecessary. Therefore, with the exception of the following paragraph on density, discussions in this report will refer to the actual number of individuals captured on the study grid, as shown in Fig. 14.

The density estimates here used are based upon the actual number of animals captured (Fig. 14) and the area which _O. irroratus_ occupied, excluding single capture stations (Fig. 12). This area was equivalent to 1,575 ha (15 750 m^2). The density estimates, which are undoubtedly low because they are based only upon the trappable population, ranged from a low of 17 per hectare to a high of 72. The mean density of _O. irroratus_ from all the trapping periods was 36 animals per hectare, or one animal per 278 m^2. The density estimates per hectare for each trapping period were as follows: _1970_, March-17, April-27, May-34, June-29, August-28, September-18, October-23, November-24, December-41; _1971_, January-39, February-41, May-72, July-58, November-58; _1972_, May-33. Roberts (1935) stated that Otomyinae are usually plentiful wherever they occur. Ansell (1960) said the same of _O. angoniensis_ in Zambia. Hanney (1965) stated that in specific areas in Malawi _O. angoniensis_ is the most important species in biomass, but this speaks more for its size than it does for numbers. Dieterlen (1968) stated that a true indication of the population size of _O. tropicalis_ cannot be reached because they are difficult to trap. This would be true only in respect of snap-traps, as will be discussed below under Response to traps (see Individual Behavior).

The population size of _O. irroratus_ on the grid fluctuated considerably during the study period (Fig. 14). The smallest number of animals captured was 27 in March 1970 and the greatest number was 113 in May 1971. In 1970 the population reached its peak in May. It appears that the peak during 1971 was also in May, but no trapping was conducted in the months immediately before and after in order to define the exact peak time. Excluding the first trapping period in March the population in 1970 appeared to reach its minimum in September (29). The low probably would have been at approximately the same time in 1971, and it is surmised that the trappable population then would have been between 70 and 80 individuals. The peak in May is the result of this being the end of the period when the young are born and the population has been steadily increasing up to that time. The low in September follows the winter nonbreeding period and precedes the appearance of the first young of the season. September follows the winter and is also the period when the food supply is at its poorest while the mortality rate is likely to be at its highest (see Mortality).

The number of animals captured during May 1971 (113) was more than twice that captured during May 1970 (53) and May 1972 (52). It is difficult to ascertain the direct causes of the increase in the population to its peak in May 1971 as these are usually multiple and complex. Favorable climatic conditions are often considered the basic cause of population increases. The 12-month period beginning in July 1970 and ending in June 1971 can be used as a basis for easy reference in examining temperature and rainfall. The overall mean temperature in nearby Pretoria during that period was less than 0,02 per cent above normal (Table 2). The rainfall at the Reserve was 13,7 per cent above normal (Table1). Considering only these two variables it appears as if the above average rainfall was the most important factor in the population increase. Temperature cannot be excluded as an important factor as it is possible that despite above normal rainfall there is also a need for normal or above normal temperatures at the same time.

All the adult females captured in November 1971 were either gravid or lactating and in the next trapping period (May 1972) the population was expected to be tremendous. Instead, the population in May 1972 was greatly reduced. It is not certain what caused this decline, but in January 1972 the rainfall was 92,4 per cent above normal for the month with most of it occurring on two consecutive days. The result was that the entire study grid was flooded. The area of the grid that suffered most was the lowest or "wet" part. Evidence indicates that the water level on the low part during the flood may have been 1 to 1,5 m. The force of the flood was considerable as two very large and heavy fallen tree limbs found lying in the grid afterwards would have had to be carried from at least 200 to 300 m away. About 1 km upstream, where the stream enters the Reserve, a 250 m section of strong security fence was washed away. One of the most important factors concerning the flood would have been its suddenness. If the water rose gradually the animals may have had time to escape. The data kept at the Rietvlei Waterworks, 3 km downstream from the grid, indicates, however, that the water level rose very suddenly, lessening any chance the animals had to escape. This catastrophic event therefore appears to have been responsible for the tremendous population reduction between November 1971 and May 1972 (Fig. 14). Of the 52 O. irroratus captured during May 1972, 18 (34,6 per cent) were marked prior to the flood. This suggests that some individuals did manage to escape and later return, many even returning to their previous home ranges (see discussion below under Home Range). Because there were no juveniles captured in May 1972 (Fig. 16) it appears as if the flood may have disrupted the social structure and along with it the breeding potential. Also, the rainfall for each month following the flood, up to and including May, was below average. This could also have affected breeding, as discussed above. Adults were most abundant in the May 1972 catch (Fig. 16), indicating that the area was probably repopulated as a result of immigration. Schulz (1953) found that O. irroratus readily moved into an area depopulated by trapping.

Flooding could also have been the reason for the relatively low number of animals, and the absence of juveniles, in March 1970, as a similar flood had occurred in October 1969, during which 178 mm of rain fell. This amounted to 266 per cent above the normal (67 mm) for the month of October (see Table 1). The majority of the rainfall during that month (112 mm, 63 per cent) occurred on one day. On that particular day the area which was to become the study grid was flooded.

The effect of flooding upon populations of rodents has been reported by several authors (Grinnell, 1939; Blair, 1939; Stickel, 1948; McCarley, 1959; Ruffer, 1961). Grinnell (1939) and Blair (1939) concluded that flooding may be one of the most important causative factors of fluctuations in population numbers of terrestrial species in low-lying areas. Blair stated that it may even produce virtual extermination of certain species in some parts of their range. Stickel (1948) and Ruffer (1961) found that floods had little effect on the population size of Peromyscus leucopus. McCarley (1959) stated that short-term flooding produced no detrimental effects on the mice, but that flooding over a three week period produced a 70 per cent decrease in the population. The probable reason that there was less effect on the populations in these last three studies was that the rodents concerned were either arboreal or semiarboreal.

The effects of population size or density upon other aspects of the life history of O. irroratus (e.g. reproduction and mortality) are unknown, apart from the effect of density upon home range, which will be discussed below under Home Range, and the possible effect of density upon adrenal gland weight. It is possible that following November 1971 and prior to the flood in January 1972 the population density increased to such a point that disease or some similar limiting factor reduced the population. There exists nothing to substantiate such a belief, however. The catastrophic effect of the flood appears to be the most logical answer to the population decrease.

The adrenal glands were dissected from 65 O. irroratus (37 males and 28 females) from the study area. Their paired weight during different months of the year is represented in Fig. 15 in milligrams per gram of clean body weight. The mean weight of the paired adrenals was 0,77 mg/g with a range of 0,35 to 1,46. Adrenal weight of females (mean 0,97; range 0,55 to 1,46) averaged considerably larger than that of males (mean 0,63; range 0,35 to 0,98). Goertz (1965) stated that, despite a few exceptions, adrenal weight of females is generally greater than that of males. Adrenal weights appeared to have increased in weight during the winter, nonbreeding season of May through July (Fig. 15). Detailed analysis showed that the adrenal weights of the 44 individuals examined from the winter nonbreeding season were slightly larger (mean 0,80) than the 21 examined from the breeding season (mean 0,71). Although Fig. 15 appears to show differently, the analysis showed that the adrenal weights of females did not fluctuate seasonally (breeding to nonbreeding season) or in respect to their reproductive status (gravid or nongravid). Male adrenal weights, however, did vary slightly in respect to the breeding season. During the breeding season the mean weight was 0,53, while during the nonbreeding season the mean was 0,67. This indicates that although the adrenal weight varies seasonally it only does so in males. It is possible that the adrenal weight of the males increased as a result of increased population density, the density reaching its peak in May (Fig. 14). Christian and Davis (1964) and Valentine and Kirkpatrick (1970) in studying voles (Microtus) attributed an increase in adrenal weight to the stress of high population density and not to reproductive status or to seasonal environmental changes. Sheppard (1968), however, stated that seasonal changes in adrenal weight may be related to seasonal changes in social interaction, but could just as readily be related to other seasonal variables such as reproduction, length of foraging movements, density of cover, and others. It would be interesting to examine this change in adrenal weight of O. irroratus in further detail in larger samples.

Composition

Populations have a definite structure and composition which are constant at any specific time, but which vary with age. A population of rodents at any given moment has a particular composition of males, females, adults, subadults, and juveniles. However, as little as one month later the structure and composition will have changed because of births, deaths, and ageing of individuals.

The age ratio of O. irroratus in the study grid was calculated for each trapping session and was based upon the following categories:

Juvenile--An individual too young to breed and still distinguishable from breeding adults on external characters. These individuals are equivalent to those in age class 0, usually weigh less than 50 g, and range in age from birth to five weeks.

Subadult--An individual which has not bred but which externally resembles an adult. These individuals are equivalent to those in age class I and part of class II, usually weigh between 50 and 90 g, and range in age from five weeks to three months.

Adult--An individual which has bred. These individuals are equivalent to those in the last part of age class II and older, usually weigh in excess of 90 g, and range in age from three or four months to about two years.

The fluctuations in size of each age group from one trapping session to another are represented in Fig. 16. No juveniles were present in March, August, and September 1970, July 1971, and May 1972. The absence of juveniles from July to September is easily explained. This represents the winter period from approximately two months after breeding ceases (May), until spring when breeding has begun (August), but before the first young have been born. The absence of juveniles in March 1970 and May 1972 in both instances represented a similar situation. The situation was preceded by a month of exceptional, above average rainfall (five and four months before, respectively--

Table 1), which resulted in flooding of the grid. This was followed in both cases by a period of below average rainfall (Table 1). It is possible that the flooding disrupted the lives and social structure of the animals sufficiently to cause a halt in breeding for some time afterwards. Therefore, no juveniles had entered the population. The percentage of adult, scrotal males during March and April 1970 was low for that time of the year (Fig. 20), and is a good indication that breeding in males was more seriously disrupted than that of the females. The below average rainfall which followed may also have been the key factor in the interruption of breeding, or the interruption could have been caused by a combination of the two factors. In 1970 there were juveniles present in April and May but the rainfall was below average prior to April and average in April. This would appear to rule out lack of rain as being the sole limiting factor.

It is possible that the absence of juveniles in the first trapping session, March 1970, was the result of the differential trapability of animals of different ages. Wiley (1971) stated that adults of the eastern woodrat, Neotoma floridana, generally dominated the subadults and juveniles. It also stands to reason that subadults would in turn dominate the activity of juveniles. Watts (1970) found the presence of large male red-backed voles, Clethrionomys gapperi, in some way inhibited the first approach to traps by juveniles. Because March was the first time the animals in the grid were ever subjected to traps it is possible that adults and subadults totally dominated juveniles in response to the traps. Dieterlen (1968) stated that the loss of young O. tropicalis must be relatively high because so few were caught. It is possible that what Dieterlen experienced was not a high loss of juveniles, but a similar differential trapability in terms of which juveniles were dominated in their response to traps. The percentage of marked animals recaptured in the following month (April 1970) was low (47,7 per cent) indicating that initial response to traps was poor. The animals captured would, therefore, have been the more dominant ones and possibly any juveniles were excluded from capture. During March there was one less trap at each station on the "wet" part of the grid, which could have limited the chance of capture, especially if this trap dominance of juveniles does occur in O. irroratus.

The highest percentage of juveniles in the population occurred in May, October, and December 1970, and May and November 1971 (Fig. 16). The abundance of juveniles appears to be at its highest near the beginning and at the end of the breeding season, which begins in August and ends in May.

The percentage of subadults in the population ranged from a low in October 1970 (8 per cent) to a high in March 1970 (63 per cent) (Fig. 16). The high percentage of subadults in March is probably the result of unusual or abnormal conditions (see previous discussion concerning flooding and juveniles). Disregarding March, subadults were most numerous in June 1970 (57 per cent) and July 1971 (53 per cent). The high percentage during these two months could be a result of the following: lack of or reduction in the number of juveniles born into the population within the past five weeks; and maturing of an increased number of juveniles born more than five weeks before.

The percentage of adults in the population ranged from a low in June 1970 (36 per cent) to a high in September 1970 (86 per cent) (Fig. 16). The low in June is primarily the result of an increased number of juveniles and subadults within the population. The high in September was the result of the maturation of the previously (March-August) encountered subadults to adults and the absence of any new young animals being born into the population.

In many kinds of mammals there are more males than females at birth, but the females tend to survive better and are more abundant later in life. The sex ratio of the 333 O. irroratus trapped during the study period did not depart significantly from 1:1. Males comprised 49,5 per cent of the total and females 50,5 per cent. Schulz (1953) found the sex ratio of O. irroratus to be about 1:1. Dieterlen (1968) found a sex ratio in 207 O. tropicalis of 56 per cent males and 44 per cent females.

There was considerable variation in the sex ratio of O. irroratus during different months (Fig. 17), but no apparent correlation with season could be determined. Females outnumbered males in 10 of the 15 months trapped, males outnumbered females during four months, and the ratio was equal for one month. A slight preponderance of females was also found in the number of young born in captivity, but the sample size was rather small for dependable results to be obtained. Of 38 young born in captivity 17 (44,7 per cent) were males and 21 (55,3 per cent) were females. Coetzee (1965) found that female Praomys natalensis formed 53,2 per cent of the 4 789 individuals in his sample. Beer et al. (1958) found that one sex was more susceptible to capture in Peromyscus maniculatus, but the sex and ratio varied according to locality. Considering that the overall sex ratio of O. irroratus was approximately equal but females were more commonly caught, it would appear that females were possibly more susceptible to capture. However, there is little evidence to support this view. Dieterlen (1968) caught more male than female O. tropicalis in October, November, and December, and correlated this, not with breeding, but with increased movement of males to investigate new areas not inhabited during the dry season. Myers and Krebs (1971) found, in voles, a deficiency of males as a result of differential mortality. They also found an excess of males to be recruited into the population. The above two possibilities can be tentatively suggested as the reason for the excess of males during four of the months trapped.

Mortality

One of the major forces determining the size of a population is mortality. Part of the difficulty in determining mortality rates is that mortality actually begins prior to birth. The other major difficulty occurs after birth and involves separating loss of animals as a result of emigration from loss attributable to mortality.

Information on the frequency of prenatal mortality in rodents is almost completely lacking, especially for natural populations. Nineteen female O. irroratus were dissected in various stages of pregnancy, but no fetuses were found in the process of resorption.

Most juvenile mammals have been shown to have less chance of survival than adults. Young O. irroratus used in the analysis of weight increase (Fig. 23) decreased from 28 individuals at birth to only six at seven weeks of age. From this it would appear that the mortality rate was quite high, but in actual fact it was not. This apparent "mortality" was more directly related to the effect of captivity stress, and possibly an inadequate diet, on the mother and young (see Social Behavior). The vlei rat does not adapt well to captivity and the effect of stress on the mother or young in some cases caused a complete failure to suckle, while in other cases suckling appeared inadequate. This was the main reason for the sharp decline in numbers during the first week. The decline was more gradual following weaning at the end of the second week. At this stage it was seldom the result of death but occurred because certain individuals failed to continue growing, as a possible result of an inadequate diet. An inadequate diet in captivity could also have caused irregular growth by affecting the quality of the mothers' milk. Considering that the young of _O_. _irroratus_ are precocial at birth and are prominent nipple-clingers (see Postnatal Growth and Development), the mortality rate should be rather low. Precocial young have a better chance of survival because they are soon able to fend for themselves and are not dependent upon the mother for a long period of time. The number of offspring per litter is small (2,45), suggesting again that this species cannot maintain a high juvenile mortality rate.

As stated earlier the major difficulty in determining mortality rates of natural populations is that of separating loss due to emigration from loss due to mortality. It was not possible to distinguish between these two types of loss in the study grid so they are represented as a combined rate of disappearance (Table 6 and Fig. 18). The data in Fig. 18 were extracted from Table 6 and demonstrate more graphically the rate of disappearance during the study period. After one month from the time of first capture 41 per cent of the individuals had disappeared. This high rate of disappearance during the first month indicates that a large number of transients are involved; and that some individuals, upon maturation, were dispersing from their home site in the grid. The overall rate of decrease for the first 20 months (until the last individual disappeared) averaged 5,0 per cent per month. Excluding the first month the average rate of disappearance was 3,1 per cent per month. Only 13 per cent of the animals remained on the grid after one year.

The longest-lived individual was a female that was captured in April 1970. During the trapping session of November 1971 a few known-age animals were sacrificed to assist in establishing ageing criteria. Among them was this particular female. When first captured her age was estimated to be three months and at the time she was sacrificed she had been on the grid for 19 months. In November 1971 she was, therefore, 22 months of age and could probably have lived a while longer. Within age class V, in which she belonged, there were two other females with larger skulls and more wear on the molars, suggesting that some individuals may live longer than 22 months.

It is, therefore, not unreasonable to believe that certain individuals, in nature, may live to an age of two years.

From Table 6 various rates of disappearance were determined between consecutive months, as follows: January to February-6,6 per cent; February to March-2,2; March to April-2,2; April to May-7,6; May to June-7,6; June to July-6,0; July to August-6,3; August to September-11,0; September to October-0,6; October to November-5,8; November to December-0,3; and December to January-5,3. The highest rate of disappearance was 11,0 per cent between August and September following winter and at a time when the veld was at its poorest. This high rate of disappearance at that particular time suggests a high mortality rate, as discussed above under Seasonal Variation in the section on Taxonomy and Morphology. The extremely low rates of disappearance between September and October and between November and December occurred at a time when the population was low (Fig. 14) and more space was available for the large number of juveniles present in the population (Fig. 16). Contrast these rates to the 7,6 per cent found from April-May and from May-June, when there was also a large number of juveniles entering the population, but the population size was much greater after a long build-up through the breeding season. Around May there was far less space available for the young and this may have been the cause of the higher rate of disappearance.

The main factors that generally influence mortality rates are diseases, parasites, predation, intraspecific competition, fires, and climatic mishaps such as floods and extreme cold.

It is generally known that under unusual conditions (e.g. over-population) diseases do great damage to mammalian populations, but in most populations the disease rate is quite low. Powell (1925) and Roberts (1935), referring to members of the Otomyinae, stated that they die off during plague epizootics. Davis (1953 and 1964), De Meillon _et al_. (1961), and Hallett _et al_. (1970) stated that although plague has been isolated from _O. irroratus_ they probably only become secondarily infected, and therefore do not appear important in the perpetuation of plague. It is doubtful that in normal situations plague would have much influence upon mortality. This would probably be also true for tick-bite fever, _Rickettsia conorii_, which has also been isolated from _O. irroratus_ in South Africa (Gear, 1954), and the diseases mentioned below in other species of _Otomys_. In South Africa and Kenya _O. angoniensis_ has been found to be infected with bilharziasis, and in Kenya O. angoniensis and O. tropicalis have been found with various rickettsial and filarial infections (see Relationships With Man under Economic Relationships for futher details of diseases). Parasites are also discussed later under Economic Relationships. Generally, parasites do not kill the host, but they will weaken it, or at least require it to obtain more food to make up for lost nutrition.

Little is known of the effect of intraspecific competition upon mortality. It is known for some rodents that under the stress of high population densities the reproductive rate is suppressed. Because O. irroratus is antisocial (see Social Behavior) a large build-up in density could have an effect on the population, but whether or not this would increase mortality or decrease reproduction is unknown. From past studies of rodents the latter appears the most likely.

The mortality effect of veld fire upon the vlei rat has been discussed above under Ecological Distribution. Cook (1959) reported that a fire totally reduced the populations of small rodents near Berkeley, California, either by killing them directly or by the indirect means of removal of food and cover. One population that was seriously affected by the fire in his study was Microtus californicus, a rodent with nesting and feeding habits similar to O. irroratus. Although O. irroratus lives primarily above ground fires generally would not have a very detrimental effect upon their populations because they prefer moist habitats that are not very likely to burn. It is likely that if a fire would destroy O. irroratus habitat the population would be annihilated.

The probable effect of a climatic mishap--in this case a flood--upon the population of O. irroratus has been discussed above under Population Size. In a period of approximately two and a half years it appears that floods have on two occasions considerably reduced the population on the grid and significantly interrupted breeding. Rain and a rising water level in dips and depressions during excessive rain also have detrimental effects upon O. irroratus confined in traps. When the long, soft, shaggy fur became wet it matted together, leaving large areas of skin exposed. With this loss of insulation they failed to maintain their body temperature and readily died. Falls (1968) made the same observation regarding Peromyscus. This was one of the reasons why the use of open wire mesh traps was discontinued. A few animals also became so wet from their own urine that they died. Of the 49 *O. irroratus* shown in Table 6 as having died on the grid, only 38 died accidentally, the other 11 were known-age animals removed in November 1971 for the ageing study. Nearly all of the 38 accidental deaths were from exposure as a result of becoming wet. Nineteen of the 38 (50 per cent) died in May when nighttime temperatures were quite cold (mean daily minimum for May is 2,7°C). The combination of a low temperature and wet fur frequently proved fatal.

Usually one of the most obvious mortality factors upon rodents is predation. The short life span of small mammals in nature is mostly attributable to this factor (Blair, 1948). Blair also stated that other factors, such as disease, parasitism, starvation, climatic mishaps, and accidents, could possibly aid in shortening life expectancy, but their effects seem to be relatively minor in comparison with the effects of predation. FitzSimons (1920) stated that if it were not for the many predators of *O. irroratus* there would be an extreme overabundance of them. Ranger (1927) stated that owls, hawks, and carnivores were possibly the reason for the disappearance of *O. irroratus* from an area he was studying.

The potential predators of *O. irroratus* living on the Reserve are listed below:

Class Reptilia

Family Colubridae
    Lamprophis aurora--Aurora house snake
    Boaedon fuliginosus--Common house snake
    Pseudaspis cana--Common mole snake
    Psammophylax rhombeatus--Spotted grass snake
    Psammophis crucifer--Cross-marked grass snake
    Psammophis sibilans--Olive grass snake
Family Elapidae
    Naja mossambica--Black-necked spitting cobra
    Hemachatus haemachatus--Rinkals
Family Viperidae
    Bitis arietans--Puff-adder

Class Aves

Family Sagittariidae

Sagittarius serpentarius--Secretary bird

Family Falconidae

Falco rupicoloides--Greater kestrel

Family Aquilidae

Milvus migrans--Black kite
Elanus caeruleus--Black-shouldered kite
Aquila wahlbergi--Wahlberg's eagle
Polemaetus bellicosus--Martial eagle
Circaetus pectoralis--Black-breasted snake-eagle
Haliaetus vocifer--Fish eagle
Buteo rufofuscus--Jackal buzzard
Buteo buteo--Steppe buzzard
Accipiter melanoleucus--Black sparrowhawk
Accipiter badius--Little-banded goshawk
Micronisus gabar--Gabar goshawk
Circus ranivorus--Marsh harrier

Family Tytonidae

Tyto alba--Barn owl
Tyto capensis--Grass owl

Family Bubonidae

Asio capensis--Marsh Owl

Class Mammalia

Family Canidae

Canis mesomelas--Black-backed jackal

Family Mustelidae

Aonyx capensis--Clawless otter

Family Viverridae

Herpestes sanguineus--Slender mongoose
Cynictis penicillata--Yellow mongoose
Genetta sp.--Genet

Family Felidae

Felis libyca--Wild cat

Many of these predators listed were seen in or near the study grid and the capabilities, as predators, of some were examined. In January 1971 a large puff-adder was caught in the grid, and upon examination of its stomach contents a marked adult *O. angoniensis* and the remains of two other (unidentifiable) *Otomys* were found. On another occasion a spotted grass snake was found in a trap on the grid, but its stomach was empty. FitzSimons (1920) listed the following snakes as predators of *O. irroratus*: python (*Python sebae*), mole snake, rinkals, Cape cobra (*Naja nivea*), and puff-adder. It is doubtful if the python plays much of a role as a predator of *O. irroratus* as their ranges are nearly allopatric. Dixon (1966) reported finding an *Otomys* sp. (probably *O. angoniensis*) in the stomach of a black mamba, *Dendroaspis polylepis*, in northern Natal.

Black-shouldered kites were commonly seen in the study grid and on one occasion took what appeared to be a shrew or a small *Rhabdomys*. These birds appear to be too small to take anything but a juvenile *Otomys*, but in the Caprivi one was seen taking an adult *O. angoniensis* (J. Taylor, pers. comm.). FitzSimons (1920) stated that hawks were a prominent predator of *O. irroratus*, as was the secretary bird. Geldenhuys (1960) reported observing a grey heron, *Ardea cinerea*, standing patiently in wait over runways of *O. irroratus* and *Rhabdomys pumilio*.

Owls regurgitate the undigestible remains of their prey in characteristic pellets. These pellets contain many skeletal parts of the prey, including the skull, which can be used as an easy aid in identification of prey species. From the literature and findings in the study area owls appear to be the most prominent predator of the vlei rat, and *O. irroratus* is a common prey of both the barn owl, *Tyto alba*, and the grass owl, *Tyto capensis* (FitzSimons, 1920; Ranger, 1927; Skead, 1956 and 1963; Davis, 1959; De Graaff, 1960; Bateman, 1960; Vernon, 1972). They have also been reported as preying upon *O. angoniensis* (Davis, 1959; Pienaar, 1961; Coetzee, 1963; Benson, 1965; Vernon 1972). Skead (1956 and 1963) found *O. irroratus* representing 13,3 and 10,7 per cent respectively of the total prey in pellets of the barn owl. Davis (1959) found vlei rats (both *O. angoniensis* and *O. irroratus*) representing nine per cent of the total prey at one locality and 17 per cent at another. Bateman (1960) examined approximately three year's accumulation of pellets from a pair of barn owls in King Williams Town. Of the 501 total prey animals found, 77 (15,4 per cent) were birds and 424 (84,6 per cent) were rodents. The remains of O. irroratus in these pellets represented 41,9 per cent of the total prey and 49,5 per cent of the rodents, an extremely high percentage. Vernon (1972) was uncertain of the species of Otomys in his owl pellets and mistakenly suggested that all of them were O. angoniensis. It is certain that there must have been O. irroratus among his specimens as well (see Table 7). He stated that Otomys formed the dominant prey species at two barn owl localities and was recorded in their pellets from 15 of his 28 collecting sites. He also stated that Otomys was especially numerous in the prey of the grass owl from the Transvaal where it was the dominant prey, forming between 34 and 48 per cent of the diet.

Pellets from both species of owls were collected during the study period at the same localities on the Reserve from which Vernon's samples (Localities 24 and 36) came, but at a later date. In April 1970 a grass owl nest was discovered in the study grid which contained one adult and four young. Subsequently there was always one individual in residence in the grid. Pellets from these grass owls found on or adjacent to the study grid were collected each month from April 1970 to January 1971. Pellets from the barn owl were collected in February 1971 from a deserted barn 1 km from the grid. Because many of the grass owl pellets were found scattered about the grid it was impossible to age all the pellets and compare the results with monthly population sizes of animals on the grid. The remains found in the grass owl pellets were, therefore, lumped together and are presented in Table 7 along with those of the barn owl. Vernon's results were summarized and included in the above Table for comparison. In the barn owl Vernon found that Otomys sp. comprised only 10,1 per cent of the total prey, whereas during the study period it was 24,1 per cent. Praomys natalensis decreased tremendously as a prey species (47,1 to 12,1 per cent) and birds increased considerably (8,3 to 44,8 per cent). It is possible that when the nocturnal P. natalensis was abundant it was a more favored prey of the more nocturnal barn owl. The trapping results in the grid showed that during the study period the P. natalensis population was rather low and declining (Fig. 19). This may indicate that when the P. natalensis population declined the barn owl shifted its diet to birds and the increasingly abundant Otomys.

The results from the grass owls can be compared more favorably to the trapping results on the grid. Vernon (1972) found that Otomys sp. comprised 37,0 per cent of the total prey, while during the study period it was only 18,6 per cent (Table 7). In 1970, when most of the pellets were collected, Rhabdomys pumilio was much more abundant than Otomys on the grid (Fig. 19). This is also demonstrated by the high percentage (36,9) of Rhabdomys in the pellets. The population of O. irroratus was quite low during much of that time (Fig. 19). It appears that from the time Vernon collected pellets to the time they were collected during the study period, the Rhabdomys population increased and the Otomys population declined. These fluctuations could well be the result of the flood in October 1969. From the pellet results there is an indication that prior to the flood, when Vernon made his collection, the population of Otomys was much greater. The flood then reduced the Otomys population. The more wide-ranging Rhabdomys (Schulz, 1953; P.M. Brooks, pers. comm.) was able to occupy the grid and increase its population more readily than Otomys. There is also an indication that this was the case following the flood in January 1972 (Fig. 19). These fluctuations in the populations are apparently reflected in the owl pellets. As can be seen in the study by Vernon the prey of owls varies from one locality to another, which may give a key to the abundance of various prey at each locale or at a specific time rather than indicating any particular prey preferences.

Other interesting features are demonstrated from the results of the owl pellet analysis. The grass owl is crepuscular and the barn owl nocturnal. On numerous occasions the grass owl was seen flying at dusk and again just before sunrise. This difference in activity pattern would explain the greater abundance of the crepuscular Otomys (see Activity) and the crepuscular to diurnal Rhabdomys in the diet of the grass owl, and of the nocturnal Praomys and Tatera in the diet of the barn owl. Vernon (1972) explained the higher percentage of Praomys in barn owl pellets as the result of both predator and prey being semicommensal with man. However, this would be meaningless if they were not active at the same times.

In the Otomys that were clearly identifiable O. irroratus outnumbered O. angoniensis 9:1 in barn owl pellets and 14:1 in those of the grass owl. The proportions in the grass owl pellets agree closely with those obtained in the trapping results on the grid (Fig. 19), and may indicate that most of the feeding of grass owls was in the general area of the grid. Vernon (1972) stated that grass owls are invariably found in vleis, which are their preferred habitat. The lower percentage of *O. irroratus* taken by the barn owl may indicate that the latter has wider-ranging habits and is not limited to a particular habitat as is the grass owl (see also Vernon, 1972). The results in any case bear out that, whichever owl is considered, *O. irroratus* greatly outnumbered *O. angoniensis* within the area. Although *O. angoniensis* lives in more open habitat this does not appear to make it more susceptible to predation, indicating that its lighter color may conceal it better in its preferred habitat.

From examination of molar toothwear on skulls found in owl pellets, general patterns of age preference (or abundance) of prey may be determined. Of the 28 skulls of *O. irroratus* that could be aged in the grass owl pellets there were 10 juveniles (35,7 per cent), 4 subadults (14,3 per cent), and 14 adults (50,0 per cent). Comparing these results to the numbers of each age group present on the grid (Fig. 16) suggests that juveniles are the most heavily preyed upon. The large size of an adult male does not deter the owls; on two occasions a very large, marked, adult male *O. irroratus* was found partly eaten next to the grass owl nest site. The number of known-age *O. irroratus* in the barn owl pellets is probably too small to indicate anything conclusive about age structure of prey. Of nine known-age *O. irroratus* in barn owl pellets one was a juvenile (11,1 per cent), three were subadults (33,3 per cent), and five were adults (55,6 per cent).

Otomys has been reported by several authors as a prey item of numerous carnivores. FitzSimons (1920) reported the following carnivores as predators of *O. irroratus*: mongoose (species unrecorded), African polecat (*Ictonyx striatus*), genet (*Genetta* sp.), serval (*Felis serval*), wild cat (*Felis libyca*), jackal (*Canis* sp.), fox (species unrecorded) and honey badger (*Mellivora capensis*). *Otomys* sp. were found in the stomachs of black-backed jackals, *Canis mesomelas*, from the Transvaal (Grafton, 1965). A present investigation of serval, *Felis serval*, scats collected each month for a year at a montane grassland locality in the eastern Transvaal indicates that *O. irroratus* is by far the most prominent prey item. Smithers (pers. comm.) said that *O. angoniensis* is also a common prey of the serval in Rhodesia. In Botswana *O. angoniensis* was found in the stomach contents of the side-striped jackal, *Canis adustus*, the black-backed jackal, and the small-spotted genet, *Genetta genetta* (Smithers, 1971). Smithers also recorded *O. angoniensis* from stomachs of the large grey mongoose, *Herpestes inchneumon*, and the water mongoose, *Atilax paludinosus*, in Rhodesia. Dieterlen (1968) listed quite a number of carnivores as predators of *O. tropicalis* in east and central Africa.

Black-backed jackals and a slender mongoose, *Herpestes sanguineus*, were seen near the study grid and both could be considered potential predators of *O. irroratus*. Several scats of the black-backed jackal from near the grid were examined but they were never found to contain rodent remains. Numerous scats of the clawless otter, *Aonyx capensis*, were seen along the banks of the stream running beside the grid, but all contained crab remains. On one occasion scats of an otter were found in the grid over 100 m from the stream. Shortridge (1934) reported that they may occasionally prey upon swamp rodents up to the size of a cane rat, *Thryonomys swinderianus*, so it is very likely that *O. irroratus* may occasionally be taken by this otter. It is doubtful if the yellow mongoose, *Cynictis penicillata*, which was seen in the Reserve, would prey upon *O. irroratus*. If they prey upon *Otomys* at all they would be more likely to take *O. angoniensis*, as both predator and prey prefer a drier habitat.

The indigenous peoples in various parts of Africa have been reported capturing and eating *Otomys* (Shortridge, 1934; Dieterlen, 1968). Shortridge (1934) stated that the local people burned off the reed-beds during the dry season and, with the aid of dogs, captured enormous numbers of *O. angoniensis*, *Dasymys*, and *Thryonomys*, which they ate.

Dispersal, Home Range, and Territoriality

A mammal must move in order to find food, shelter, and mates, and to escape from enemies. Some of these movements may develop into a regular pattern with minor variations (home range and territory) and others may be quite irregular (emigration and immigration).

Emigration and immigration are essentially the same phenomenon, the only difference being in point of view. Both imply a one-way movement. Emigration (i.e. dispersal) is of great importance in the lives of mammals, but when it occurs is not necessarily extensive. In January 1971 trapping was conducted around the grid in two concentric rings 30 and 60 m from the outer trap rows. ~~On this occasion~~

On this occasion 11 marked *O. irroratus* from the grid were captured in the 30 m ring. Four of the 11 had not been captured in the grid two weeks previously. Twenty seven new *O. irroratus* were marked in the two rings and only two of these were later captured in the grid. These two had been captured previously only in the 30 m ring. Trapping was conducted at distances of 100 to 200 m from three sides of the grid and only two marked *O. irroratus* from the grid were captured, one of which had crossed the stream. This tends to indicate either that emigration in *O. irroratus* is only over short distances, or that those individuals that disperse over long distances commonly end up in unsuitable habitat and die or fall prey to predators. Schulz (1953) found that *O. irroratus* readily moved into a depopulated area, which indicates that population pressure in this case was the underlying factor in their dispersal. The habitat of *O. irroratus* can often be quite isolated, therefore any dispersal would be into unfavorable habitat and the result probably fatal. It is also evident from the ring-trapping reported above that dispersal takes place in both directions.

One form of emigration is that of young animals at maturation dispersing from the home site. The high rate of disappearance of *O. irroratus* from the grid after one month (Fig. 18) is a good indication that not only transients are involved, but that dispersal of recently matured animals is also occurring. It was possible to obtain a measure of the dispersal distance of individuals that were caught in one area a few times as juveniles and later established a definite home range in the grid. The mean distance of dispersal for 21 individuals from the area of their birth site to the center of their established home range was only 18,3 m. Males dispersed a distance of 35 m compared to only 8 m for females.

The area over which an animal moves in its normal activities of feeding, mating, and raising of young is termed the home range. There exist numerous methods for the study and determination of home ranges. The most common method of revealing the home range of rodents is by repeated recaptures. Various authors differ in the minimum number of captures necessary to make an accurate assessment of the home range, but it is generally considered the more captures the better. In this study the requirements postulated for recognition of a home range were a minimum of 10 captures over a period of at least two to three consecutive months without any apparent shift of home range and no captures in any of the outer trap rows. The maximum number of captures of an individual considered for home range calculation was 34.

The trap-revealed home range and the true home range are recognized as not necessarily being the same. Stickel (1954) compared various methods of calculating home range and concluded that the exclusive boundary strip method, being only two per cent larger than the actual home range, was the most accurate. This method was utilized in the calculation of the home range size of *O. irroratus*. The home ranges of 40 *O. irroratus* (16 males and 24 females) were calculated. The mean home range size was 1 443 m^2, and varied from 675 to 3 038 m^2. The home range size of males averaged 1 730 m^2 and was highly significantly different ($P<0{,}01$) from the home range size of females (1 252 m^2). In rodents males generally have larger home ranges than females, which may in part be due to the larger size of males and their more widespread movements in searching for mates.

The size of the home range has, in itself, very little significance. More important are the effects of habitat upon home range size, the increase or decrease of home range size as a reflection of population density, and, in general, the reasons why an animal is at a particular place at a particular time. The home range of *O. irroratus* was calculated for two different seasons and compared. In the first example a home range for the same four individuals of each sex was calculated from four captures in June, and again in October, 1970. The means of these calculations (in m^2) are given below (sample size in parentheses);

June 1970		October 1970	
male	female	male	female
984(4)	647(4)	956(4)	844(4)
816(8)		899(8)	

The sample sizes were not large enough for a statistical analysis so a few more home ranges of unrelated animals were added to the sample. The results of this analysis are as follows:

June 1970		October 1970	
male	female	male	female
769(6)	619(10)	999(10)	836(7)
675(16)		926(17)	

The difference in mean home range size of males between the two seasons was not found to be significantly different (P>0,10), while for females the difference was significant (P=0,02). The home range size of the combined sexes in June and October was compared and the differences found to be very significant (P<0,01). The reason for a change in home range size between June and October is difficult to determine. The main differences occurring between June and October would be a much lower temperature in June, a better quality and greater quantity of food in October, and breeding and the birth and care of the young occurring in October. In general, males seeking mates during the breeding season tend to wander more widely, and conversely, females caring for young tend to limit their movements so as not to be away from the nest for too long. Certain species of rodents may also have to wander more widely during the winter in search of food. None of these, however, appeared to be the case in O. irroratus. Although the home range of males did increase from June to October the activities associated with breeding did not cause it to increase significantly. The home range of females in both of the above examples was considerably larger during October when breeding and the rearing of young was going on. It is possible that their activity increased as a result of an increased need for food. Also, because the nest site of O. irroratus tends to be of a more temporary nature than that of most rodents, there would not be the necessity to always remain near a permanent nest site. The overall impression appears to be that activity, and with it home range size, is suppressed during winter as a result of low temperatures.

Both species of vlei rats, O. irroratus and O. angoniensis, have been reported to change their ranges seasonally (Davis, 1942; Hanney, 1965; Smithers, 1971). Davis (1942) reported that O. irroratus moved from a natural habitat into adjacent pine plantations at the onset of winter and remained there throughout the winter. During this time they inflicted considerable damage upon the young pine trees by eating the bark. It appears that this shift was purely in relation to food requirements. Hanney (1965) stated that O. angoniensis shifts its range as a result of veld fires and may move as much as 1 km to unburnt areas. For this reason he stated that the concept of home range is not applicable to *Otomys*. Hanney (1964) also found that burning of the habitat caused the harsh-furred rat, *Lophuromys flavopunctatus*, to move towards moister areas. Smithers (1971) stated that *O. angoniensis* in Rhodesia makes seasonal movements associated with the water level.

The home ranges of *O. irroratus* were compared at different population densities. An inverse relationship between population density and size of home range has been shown in other studies of rodents and is probably typical, but not invariably true. Home ranges were calculated from captures in May 1970 and in May 1971, when population size was approximately double that of May 1970 (Fig. 14). The home range size (in m^2) is again based upon four captures of each individual:

May 1970		May 1971	
male	female	male	female
546(7)	578(15)	506(4)	450(6)
567(22)		473(10)	

It was not possible to statistically compare the home range sizes of the males as the sample size in May 1971 was not large enough. Female home ranges did not differ significantly ($P>0,10$) as a result of the population density. Considering the combined sex home range there was a decrease in size as a result of the greater population density in 1971, but the difference was not significant ($P>0,10$).

It has been shown that after a flood the majority of the individuals were retrapped within the boundaries of their originally noted home ranges (McCarley, 1959). Eighteen previously marked *O. irroratus* were captured in May 1972 following the flood of the study grid in January of that year. Twelve of the 18 (66,7 per cent) were captured within the boundaries of their previously determined home range. Thirteen of the 18 were females and 10 of these 13 (76,9 per cent) returned to their original home ranges. Of the five males only two (40,0 per cent) returned to their original home range. Owing to the small number of males concerned any discussion of the discrepancy in return rates between the sexes would be presumptuous.

Animals with a fixed home within the home range generally maintain an area around the home site that they defend against other individuals of the same species. This defended area is called territory. When plotting the home ranges of the large and probably territorial males of O. irroratus there usually existed areas of overlap of adjacent ranges, but at the same time there was usually an area exclusive to each individual. While this exclusive area may not indicate the territory of each, it may nevertheless indicate that they are territorial. There may be considerable overlap of adjacent territories, because each individual was not usually in a position to survey the whole of its territory all the time in order to spot intruders or trespassers. For this reason it is exceedingly difficult from trapping results alone to determine whether animals are territorial, let alone the extreme difficulty of actually defining certain limits of territories.

Adult males frequently shifted their home ranges but this rarely occurred with adult females. This shift, sometimes just an extension of the home range, of certain males could usually be associated with the death or disappearance of a large adult male from the area. The new area that then became occupied was that which this individual had previously occupied. This shifting or extension of the home range can be interpreted as the result of the removal of territorial pressures. Females, unlike males, rarely shifted their home ranges. Therefore, it may not be justifiable to assume that they are territorial. The territories of females generally are much smaller and limited to just the close vicinity of the nest. Compared to the activities of females, males have larger home ranges and are more inclined to wander. The inclination to change or extend the home range would, therefore, be much greater for males. Further discussions regarding territoriality can be found below under Social Behavior.

REPRODUCTION

Reproductive Capacity

The reproductive capacity (e.g. litter size, gestation period, and number of litters per year) of rodents varies considerably. Very little is known of the reproductive capacity of O. irroratus, but what is reported in the literature for members of the Otomyinae tends to be in general agreement. Basically, all that is known of the Otomyinae is that they are polyestrous and the number of offspring per litter rarely exceeds four. Powell (1925), in reference to the vlei rat (probably both O. angoniensis and O. irroratus) in Southern Africa, stated that they produce three to five young per litter, breed three times per year, and begin breeding at four months of age. This comment has served as the basis for most ensuing references to the breeding capacity of the Otomyinae and for all references to O. irroratus (see Schulz, 1953; Asdell, 1964).

Litter Size

It has been stated that the number of offspring per litter of O. irroratus does not exceed four (Roberts, 1951). Because it is believed that Powell (1925) did not distinguish between O. angoniensis and O. irroratus, the above reference by Roberts is the only information in the literature on litter size specifically referring to O. irroratus. FitzSimons (1920) stated that O. irroratus produces five to 12 young per litter and that on one occasion he found a nest containing nine young. He also reported observing seven young clinging to the fur of the mother (nipple-clinging?). I must agree with Shortridge (1934) that this note by FitzSimons is out of place, and in reality refers to some other more prolific rodent. All species of Otomys, including O. irroratus, have only two pairs of inguinal mammae. The observations of FitsSimons are, therefore, highly improbable.

The number of embryos or offspring per litter reported in the literature for other species of *Otomys* ranges from one to five. Vesey-FitzGerald (1966) recorded *O. anchietae* in Zambia and Tanzania as producing only one offspring per litter. *Otomys angoniensis* has been reported from South West Africa usually with three young, but ranging from two to four (Shortridge, 1934); in Zambia with two to three young (Ansell, 1960); in Kruger National Park (one specimen) with three embryos (Pienaar, 1964); in Malawi with one to three embryos (Hanney, 1965); and in Botswana with three to five embryos (Smithers, 1971). *Otomys denti* has been reported from Kenya with usually three young (Copley, 1950); in Malawi with one to four embryos (Hanney, 1965); and in eastern Zaïre with a mean litter size of 1,07 (Dieterlen, 1968). *Otomys tropicalis* has been reported from Uganda with a litter size of one to three and one to two embryos (Delany, 1964; Delany and Neal, 1966); and in eastern Zaïre with a mean litter size of 1,37 embryos from 73 gravid females (Dieterlen, 1968). The litter size of *O. angoniensis* in 10 cases (including embryo counts in gravid females) from the study area was one to four, with a mean of 3,10.

Thirteen gravid female *O. irroratus*, usually in late stages of pregnancy, were brought into the laboratory from the study area in order to study postnatal growth and development. In the 13 litters born in captivity to these females, litter size averaged 2,77. Also during the study period seven litters were either born or aborted in traps, in which there was an average of 1,86 young per litter. The combined mean litter size of these 20 litters was 2,45. Nineteen gravid females were dissected which contained a mean of 2,21 embryos per litter. The mean litter size of all 39 *O. irroratus* pregnancies from the study area, combining numbers of embryos and numbers of young born per female, was 2,33 with a range of one to four. Of the 39 litters 6 had 1 young (15,4 per cent), 19 had 2 (48,7 per cent), 9 had 3 (23,1 per cent), and 5 had 4 (12,8 per cent). Dieterlen (1968) recorded the following numbers of embryos per female in *O. tropicalis* as: 48 with 1 embryo (65,8 per cent), 23 with 2 (31,5 per cent), 2 with 3 (2,7 per cent), and none with 4.

Although the number of embryos does not necessarily indicate the size of the litter because embryos are occasionally resorbed in the uterus, no indications of resorbtion of embryos were found in *O. irroratus*. It therefore appears valid to include the number of embryos into the calculation of a mean litter size for *O. irroratus*. Dieterlen (1968) also stated that the litter size and the number of embryos in *O. tropicalis* compared favorably. The low mean value of young born or aborted in traps (1,86) possibly resulted because not all had been either aborted or born at the time of observation of the female. Alternatively, it may reflect merely sampling error due to the small sample size. In any event, it was not the result of young having been eaten by the mother as this was never observed. Only rarely was a small portion of a newly born dead young eaten by the mother. Unlike some other rodents with cannibalistic tendencies *Otomys* does not appear to eat flesh.

Litter size and many environmental variables are often correlated with latitude. Generally, the size of the litter increases away from the equator to compensate for a higher mortality in winter. This may be the reason for what appears to be a larger litter size of *O. irroratus* compared to the more tropical *O. anchietae*, *O. denti*, and *O. tropicalis*.

Generally, mammals bearing precocial young usually have smaller litters than those bearing altricial young. In part this is because precocial young have a longer gestation period during which the fetus grows larger before birth. This limits the number of young a female of a given size can carry. The young of *O. irroratus* are definitely precocial and large at birth (see Postnatal Growth and Development), which may account for the small litter size. Spiny mice of the genus *Acomys* also bear precocial young and have a correspondingly small litter size of two to three (Dick, 1959; Dieterlen, 1962 and 1963). The number of young is also generally lower in rodents with a better survival potential. Meester and Hallett (1970) associated small litter size with nipple-clinging in the rodent species they studied, and Davis (1963) ascribed the high survival rate of young *Mystromys albicaudatus* to their habit of persistently clinging to the nipples of the mother. Because the young of *O. irroratus* are nipple-clingers (see Postnatal Growth and Development) their survival potential is no doubt improved, which means that fewer young, and therefore smaller litters, are required to ensure adequate recruitment into the population.

The implantation position of 100 embryos in 78 gravid female *O. tropicalis* was as follows: 45 embryos in the right horn of the uterus and 55 in the left horn (Dieterlen, 1968). In three gravid female O. angoniensis from Botswana a total of 11 embryos were found, eight on the right and three on the left (Smithers, 1971). Among a sample of 14 gravid female O. irroratus from the study area nine (64,3 per cent) had all of the embryos implanted in one uterine horn while only five (35,7 per cent) had embryos in both horns. In seven gravid female O. angoniensis from the study area six had embryos in both uterine horns while only one had embryos in one horn.

Gestation Period

In rodents there generally exists a relationship between the size of litter and length of the gestation period. Those animals with small litters usually have a longer gestation period. Dieterlen (1963) reported two species of Acomys, which produce comparatively large precocial young and have a small litter size, with gestation periods of 36 and 38 days. Because O. irroratus failed to breed in captivity only circumstantial evidence from a few females on the study grid can be used to estimate a gestation period. In O. irroratus it was noted to be longer than 35 days and probably was closer to at least 40 days in length. Usually the larger the rodent the longer the gestation period. Because O. irroratus is larger than Acomys (approximately 140 g versus 50 g) it is possible that the gestation period is much longer than the 36 and 38 days of Acomys. The guinea pig, Cavia porcellus, which weighs about 500 g as an adult and produces (in the wild) one to four precocial young, has a gestation period of between 60 and 70 days (Walker et al., 1964). Dieterlen (1968) was unable to determine a gestation period for O. tropicalis, but stated that it is apparently long because the young are precocial and the litter size small.

Sexual Maturity

The vlei rat (probably both O. angoniensis and O. irroratus) in Southern Africa probably reaches sexual maturity at four months (Powell, 1925). Schulz (1953) added to this by saying that O. irroratus at that age would weigh approximately 100 g. Dieterlen (1968) stated that O. tropicalis matures sexually at about 90 g or five months of age. He also stated that males mature sexually at between 80 and 100 g while females mature around 90 g.

The change from a nonperforate to a perforate vaginal orifice in females and from abdominal to scrotal testes in males was used to determine the approximate weight of O. irroratus at sexual maturity. An approximate age could then be assigned to the time of sexual maturity by comparison with Fig. 23 (weight increase) and from ageing criteria based on toothwear. Data from O. irroratus in the study grid indicate that there is a differential rate of maturational development in males and females. On the average females become sexually mature at a weight of 76 g (approximately nine to 10 weeks of age) and males much later, at a weight of 96 g (about 13 weeks of age). The smallest perforate female weighed 45 g (four weeks old) and the smallest scrotal male weighed 67 g (eight weeks old). One female that weighed 70 g (eight to nine weeks old) gave birth one month later.

Another measure used to determine the age of sexual maturity for females was to establish the age at first lactation and from that to subtract the approximate gestation period. The weight of 11 females at first lactation ranged from 88 to 135 g with a mean of 109 g. The age at a mean weight of 109 g was approximately four to five months, and subtracting five or six weeks for gestation it appears that many females may begin breeding around three months of age.

From the above, O. irroratus in the study area matured sexually at an approximate age of three months. This agrees reasonably well with the age of four months stated by Powell (1925) or that of five months for O. tropicalis (Dieterlen, 1968).

The sexual maturity of O. irroratus on the grid was calculated from data obtained prior to May 1971 when the population was increasing. It is possible that they matured slightly early as a result of this increase. Failing this, and despite the fact that Dieterlen was referring to another species in a different climate and the species Powell was referring to is uncertain, it appears that their estimates of age at sexual maturity may be somewhat conservative.

The age at sexual maturity becomes a complex problem in short-lived rodents with a long breeding season. An O. irroratus born in the spring or early summer may breed in the same year at an age of three months; but an individual born in late summer or autumn may not mature before the winter and, therefore, not breed until spring at an age of six to eight months. These individuals are very different in chronological age but are the same physiological age in respect to reproduction.

Breeding Season

It has been stated that *O. irroratus* breeds nearly all year but usually stops during the winter (FitzSimons, 1920). FitzSimons also stated that occasionally they may continue breeding throughout the winter. In South Africa nothing is known of the breeding season of *O. angoniensis* with the exception of the recovery of three well-developed embryos in August (Pienaar, 1964). From the literature it appears as if north of South Africa *O. angoniensis* has no fixed breeding season. Dieterlen (1968) found that *O. tropicalis* in eastern Zaïre breeds continuously, but that it slows slightly between June and October.

The reproductive status was noted of all *O. irroratus* captured in the study grid during each trapping period. Males with scrotal testes and females with perforate vaginal orifices were considered to be in breeding condition. The status of the adults of each sex is presented in Fig. 20 as the percentage in breeding condition during each trapping period. The percentage of animals in breeding condition was either low or nonexistent in May, June, and July (Fig. 20). This period of nonbreeding corresponds very closely with winter time when the nighttime temperatures are low, day length is short, and food is in short supply.

In May 1970 and 1971 less than 10 per cent of the males were scrotal (Fig. 20). During the same months the percentage of perforate females had declined, but only to around the 50 per cent level. This indicates that breeding was terminating at that time but had not completely stopped. Five females collected on 14 May 1970 were gravid with small embryos, which may have been conceived in early May. In June a few juveniles were captured, but in July there were none (Fig. 16), indicating that breeding had stopped for nearly all of May. The trapping period in the second week of May 1972 was immediately preceded by a sudden two-week cold spell, which apparently terminated virtually all breeding activity.

Breeding was in full force during the second week of August 1970 with 95 per cent of the females perforate and 65 per cent of the males scrotal (Fig. 20). Five of the 20 females captured in August were secreting blood from the vaginal orifice, an indication that they were in estrous. Of the 16 females captured in early September, four were lactating and one was clearly gravid, again demonstrating that breeding had begun in early August.

Another means of determining the reproductive season of *O. irroratus* was an analysis of the weight of the testes and ovaries. The paired reproductive organs from 56 specimens (28 males and 28 females) were dissected and weighed. Weights are represented in Figs. 21 and 22. Again it is quite evident that breeding was generally lacking in May, June, and July, as there was a considerable decrease in weights of these organs during that period.

From the above information the breeding season of *O. irroratus* in the study area can be stated to be approximately nine months in duration, from early August to late April or early May. Breeding appeared to be continuous for the nine months with no obvious peaks or breaks in activity.

Numerous environmental factors have been suggested as controlling reproduction, but little actually is known owing to the complexity of isolating each limiting factor in experiment and analysis. To add to this complexity, Delany and Neal (1969) found that breeding seasons of the various species of rodents from one locality were not closely synchronized. Some of the following factors have been implicated in varying degrees in previous rodent studies: temperature, precipitation, food, and photoperiod. The mean temperature in August is considerably lower than in April and even May (Table 2). It therefore appears that temperature on its own can be ruled out as a limiting factor. As mentioned above it appeared that an early onset of low temperatures in late April and early May 1972 terminated breeding slightly earlier than in May of the two previous years. The mean monthly rainfall is lowest in the study area during August (Table 1). The effect of rainfall is usually expressed through the vegetation, which in the case of *O. irroratus* is their only food. Because of the exceptionally low mean rainfall in August, the vegetation, and in turn the food of *O. irroratus*, is at its poorest in quality and quantity. Therefore, it appears as if precipitation and food can also be ruled out as limiting factors to the onset of breeding. This is not to say that the decline of precipitation and food in autumn is not a terminating factor, however.

The photoperiod (number of daylight hours or number of hours of darkness) has been studied more than any other factor in relation to breeding and is known to control reproduction in some mammals. Considering the winter solstice of 21 June as the central point, it appears that the onset of breeding occurs 40 to 50 days after and the termination of breeding 40 to 50 days before the solstice. Because onset and termination occur approximately the same length of time before and after the solstice photoperiod may be the most important underlying factor in the control of reproduction. At the same time temperature, precipitation, and food may play a role as accessory factors that exert control only at specific times or in specific situations.

Reproductive Potential

The vlei rat has been reported as being polyestrous, producing three litters per year (Powell, 1925). Considering that the breeding season of O. irroratus in the study area is nine months long and the estimated gestation period is approximately 40 days, it is possible that a maximum of seven litters could be produced per breeding season. Females have been dissected that were simultaneously gravid (with small embryos) and lactating. This indicates that they probably conceived at first postpartum estrous and continuous production of litters is possible. It seems reasonable to believe that O. irroratus, in nature, could produce approximately four to five litters per breeding season. Taking into consideration the mean litter size of 2,33 and the estimated production of four to five litters per season, the total young produced per season would average nine to 12. This breeding potential would be increased somewhat as a result of their longevity, which could extend their breeding through two seasons.

Comparing litter size of O. irroratus with that of an altricial and more prolific rodent such as the multimammate mouse, Praomys natalensis, the reproductive potential of O. irroratus appears low. Coetzee (1965) reported an average litter size of 9,46 for wild-caught P. natalensis, which is equivalent to what one female vlei rat might produce in a year. Several other factors should, however, be taken into consideration. Firstly, the young of O. irroratus are born in a precocial state and development is rapid. This generally ensures that their survival rate will be greater than for altricial young which are more dependent and take longer to develop. Secondly, the breeding season of prolific species may not be as long as that of *O. irroratus*. Although Coetzee (1965) reported *P. natalensis* as having a breeding season closely corresponding to *O. irroratus*, it is not uniform and only reached a peak at the end of the season. Delany and Neal (1969) reported that in Uganda *Lophuromys* produced small litters (3,2) and had a high percentage of females pregnant for 10 months, while *Praomys*, with particularly restricted breeding periods, produced the largest litters (12,6). Thirdly, the more prolific rodents generally have a maximum longevity of one year as opposed to a possible two years in *O. irroratus*. The above three factors all work together to balance the differences in reproductive potential between species producing small and large litters. Spencer and Steinhoff (1968) stated that the contribution to the total rate of increase of litters produced in the additional time afforded by long breeding seasons is greater for producers of small litters, because a large proportion of parents survive to produce throughout the breeding period. The increment provided is sufficient to overcome the initial advantage of parents producing large numbers of young in their first litters.

From the above it appears that the reproductive potential of *O. irroratus* could be great, despite their small litter size. FitzSimons (1920) stated that *O. irroratus* is a rapid breeder and if it were not for its many predators there would be an irruption of this species. Roberts (1935), in reference to all Otomyinae, stated that despite litters of only two to four young, they are, nevertheless, prolific.

Attempts to breed *O. irroratus* in captivity proved fruitless, so no comparisons between field and captive reproductive data were possible. Pitchford and Visser (1962) and Visser (pers. comm.) stated they were able to breed *O. angoniensis* only in large outdoor enclosures. Davis (1963) was unable to breed *O. irroratus* in captivity and Dieterlen (1968) was also unsuccessful with *O. tropicalis*. The possible reasons for their nonbreeding in captivity will be discussed below under Social Behavior.

POSTNATAL GROWTH AND DEVELOPMENT

Gravid females from the study area were live-trapped and brought into the laboratory for the study of growth and development of young *O. irroratus*. This was necessitated by the difficulties encountered in attempts at breeding in the laboratory (see Social Behavior). Thirteen gravid females were brought in and from these 36 young were born (two to four per litter, mean 2,77). Four individuals were stillborn and two litters (five young) were premature and did not survive. Several instances of premature birth occurred in traps and those in the laboratory were within two days of capture, indicating that abortion resulted from stress caused by capture or captivity. A disproportionate number of young which were weighed each week (Fig. 23) died or stopped growing, probably a result of conditions of captivity (see Mortality and Social Behavior).

Description at Birth

Nothing has been reported in the literature regarding the appearance of *O. irroratus* at birth. Vesey-FitzGerald (1966) reported that the young of *O. anchietae* are born in an advanced state of development. Ansell (1960) reported that *O. angoniensis* in Zambia are born with hair and with incisors erupted, and Delany and Neal (1966) recorded the same for *O. tropicalis* in Uganda. Dieterlen (1968) reported that *O. tropicalis* is precocial at birth and supplied a brief description of morphology and size at birth.

The young of *O. irroratus* are precocial at birth and the neonatal appearance is much like that of a miniature adult. The head and body are well-furred and almost fully pigmented (black as in adults). The general coloration of the pelage is very similar to that of adults, but the texture is finer and fluffier. The dorsal surface of the head is fully covered with fur 3 mm in length. Vibrissae are present and long (13 mm). The ears are pigmented black and have a covering of sparse, short, buff and black hairs on the inner surface of the pinnae; behind they are nearly hairless with the exception of a few short hairs near the upper margin. The fur on the dorsal surface and sides of the body is generally blacker and shorter than on the head (2 mm in length). Scattered over the body and along the sides and hindquarters are longer guard hairs (5 mm). The underside of the head and body has the general black pigmentation of the rest of the body, with the exception of slightly lighter areas on the chin and inguinal region. The fur is darker, shorter, and sparser on the underside and is relatively sparse on the more lightly pigmented areas on the chin and inguinal region. In the center of the chin there are a few long hairs extending from a "mole". The upper surfaces of the feet are sparsely haired and resemble the sides of the body in color. The soles of the feet are naked and pigmented black as in adults. The tail has black pigmentation dorsally with short black hairs. The ventral surface of the tail is less pigmented, having a slight pinkish color, especially near the base, and is sparsely covered with short dark hairs.

The incisors of _O. irroratus_ are erupted, which enables them to cling to the nipple (see Social Behavior for further discussions of nipple-clinging). The upper incisors project beyond the gumline 1 to 2 mm and the lower ones 0,5 mm.

Generally, the eyes are not open, but in a few individuals they were slightly open or one was open and the other closed. In the individuals with the eyes yet unopen their position was obvious as a slight bulge beneath sealed slits of black pigmented skin.

The ear pinnae are erect and like the ears of adults. The auditory meatus is open and there is weak response to sound.

The feet are nearly of adult form and the digits are fully separated. The claws are present and measure 1 mm in length. Locomotion is possible but is uncoordinated.

The mean and extreme body measurements (length in mm and weight in g) of 28 _O. irroratus_ at birth are as follows: head-body length 71,1 (64-76); tail length 33,4 (30-37); hind foot length 19,5 (17,5-22,0); ear length 8,6 (7,5-10,5); total weight 12,5 (9,6-15,5). The following are the mean measurements of the newborn represented as a percentage of the mean of adult measurements: head-body length--44,1 per cent; tail length—33,8; hind foot length--61,8; ear length--40,8; total weight--8,7.

The above descriptions and measurements of newborn O. irroratus are in close agreement with what Dieterlen (1968) found in O. tropicalis. The following are the extreme measurements he recorded for newborn O. tropicalis: head-body length, 65-85; tail length, 25-45; hind foot length, 17-22; ear length, 8-12; total weight, 10-17. He stated that the newborn weight was about 10 per cent of the adult weight.

Physical Growth

Physical growth and behavioral development was recorded every day or every other day during the first two weeks of life and at weekly intervals thereafter. Growth and development rates are presented in Figs. 23, 24, and 25.

Because young O. irroratus are so well-developed and precocial at birth there is little obvious change in pigmentation of the skin and color and proliferation of hair as they develop. Those areas that were seemingly unpigmented at birth rapidly became pigmented black by day two. The same was true for hair proliferation in those areas where hair was absent or sparse at birth. The incisors continued to grow and by one week of age had begun to take on the yellow color of adult incisors. The eyes were usually open by day two, but in a few individuals were not open until as late as day four. Hearing generally became acute by day two.

The young grew rapidly during the first 10 weeks of life, showing an average weight increase of 1,29 g per day or 9,0 g per week (a mean total increase of 90 g). The body weight at 10 weeks averaged 71,5 per cent of the adult weight, and the other body measurements between 80 and 85 per cent of adult size. The rates of increase for the body measurements up to eight and 10 weeks of age can be seen in Figs. 23 and 24.

It was found in comparing the weight increase of captive young to those in nature that the increase was comparable during the first five weeks, but became increasingly disparate by 10 weeks. At 10 weeks of age the mean weight of captive animals was approximately 33 per cent greater than that of those captured in nature. There are several basic problems in making the above comparison. Firstly, the age of the animal in nature was estimated and their weight-correlated age may therefore be inaccurate. At a time when individuals are gaining an average of 9 g a week a slight miscalculation in weight could result in a considerable misjudgement in age. Secondly, the sample size at 10 weeks in both laboratory and field study was exceptionally small.

The pelage of both young (from about two weeks of age) and adult O. irroratus was long, soft, and shaggy as described above under Morphology. The hairs on the back varied in length from 15 to 25 mm. The basal 10 mm of the dorsal hairs were a dark slate-gray. These hairs were sometimes tipped with buff, other times with black, and occasionally with both buff and black, giving the dorsal color a speckled appearance. In bright sunlight there was a yellow, green, and purple iridescence to the pelage which was also present in the juvenal and subadult pelages.

Two types of molts are usually recognized in rodents: one associated with seasonal changes (seasonal molt) and the other with ontogeny (developmental molt). Few observations of molting in O. irroratus were made so it is difficult to draw any definite conclusions. No adult individuals were observed undergoing molt, so it is surmised that O. irroratus is one of those mammals that have no definite seasonal molt, but rather seem to be continually losing a few hairs as new ones develop.

In most rodents there are three major developmental pelages (juvenal, subadult, and adult) and a definite molt usually occurs between each. The postjuvenal molt in O. irroratus appeared to begin quite early, with its first obvious appearance on the dorsal surface of the head on day 14. It did not become apparent on the shoulders and back until day 28 and proceeded in a posterior direction until day 42. Molting on the venter was not observed. Layne (1968) stated that the ventral phase of the molt of Peromyscus is a more subtle process, therefore the possible reason it went unnoticed in O. irroratus. In contrast to many rodents the color differences between juvenal and subadult pelages of O. irroratus were never obvious. The only difference appeared to be in texture, the subadult pelage being slightly coarser.

The postsubadult molt was first observed between days 56 and 70. The venter first appeared to undergo molting where it proceeded in a posterior direction. Molting began slightly later on the back with a narrow strip down the middle, progressively extending onto the sides. The differences between the subadult and adult pelages were clearly obvious. The new fur was shorter and darker. The intensity of speckling of the normal pelage appeared to be lacking in the new pelage but in time became apparent. The duration of this molt was uncertain but could be complete by day 84.

The occasional occurrence of semialbino specimens of O. irroratus was noted by Hewitt (1931). Shortridge (1934) made reference to a true albino specimen of O. irroratus as well as several semialbinos. I have seen a semialbino specimen (pinkish fur but with normally colored eyes and skin) in the Transvaal Museum collection that had produced three normal-colored young. Pirlot (1958) recorded a female albino O. tropicalis with a normal-colored young. Melanistic forms of O. irroratus have also been recorded (Roberts, 1951).

Five O. irroratus on the study grid were noted with one or two small patches of white fur. As a result of handling, two of these individuals had lost a piece of skin and fur from the back of the neck. The place where this injury occurred later grew in as white fur. It is therefore suggested that the occasionally observed patches of white fur are the result of prior injury or skin loss from that particular area.

Behavioral Development

The development of the precocial young of O. irroratus is rapid. Most of the individual and social behavior patterns of adults become manifest in the young by two weeks of age (Fig. 25).

FitzSimons (1920) reported that young O. irroratus cling to the nipples and also to the long fur with teeth and claws. It appears that what he reported as young clinging to the fur was probably also nipple-clinging. Dieterlen (1968) reported nipple-clinging in O. tropicalis. Nipple-clinging is a very prominent feature of young vlei rat behavior during the first two weeks of life. The young cling to the nipples almost constantly during the first seven days and are seldom seen unattached. To remove the young for measuring it was necessary to block off the nasal openings, together with a gentle but constant pull of the animal. During the first week, detachment took an average of 30 seconds, but soon they became detached in only 10 seconds and occasionally fell off of their own accord. The principal adaptive value of nipple-clinging has been suggested to be the reduction of litter losses through predation (Davis, 1963; King, 1963; Layne, 1968). This could be especially true in an animal using an open, unprotected nest such as O. irroratus. (See the section below on Social Behavior for further discussion of nipple-clinging.)

Solid food is eaten by the second day but does not become a regular part of the diet until day six or seven. Weaning appears to be nearly complete by day 13.

Young O. irroratus at birth are capable of locomotion with the body partly raised off the substrate. The hind limbs are splayed out and movement is uncoordinated until about day five. By then the hind limbs are held under the body and the young are capable of a coordinated run. The righting response is immediate at birth. A strong grasping reflex of the forepaws exists at birth enabling the young to cling.

As in most rodents coordination for locomotion purposes developed in an anterior to posterior direction, the forelimbs becoming fully coordinated before the hind limbs. An interesting difference in limb coordination (unrelated to locomotion) occurred in O. irroratus, i.e. the appearance of the scratching reflex with the hind foot (day 0) prior to face washing (day 2). Cleaning the hind foot with the teeth following scratching was observed as early as day two. Regular grooming sessions began the seventh day.

When the young were placed in a group, a weak form of investigational behavior began by day one or two, probably associated with the opening of the eyes.

Play was an independent activity consisting of racing about the cage, often while carrying an object in the mouth. This began during the first week and was a common activity by the end of the second week. Play in previous studies of rodents is usually described as a social behavior, but in O. irroratus it involved only single animals. This may be related in some way or another to their strongly antisocial behavior as adults.

During the first five days of life, the littermates huddled when they came in contact, pushing and crawling over and under each other. When separated during this period, a sharp squeaking noise was produced which aided in bringing them together and would enable the mother to locate them if lost. As this contactual urge began to diminish around day five there ensued the defensive upright warding posture (Fig. 32) and threatening "chit" found in adults. The elongate posture (Fig. 31) was seen about day seven and well-coordinated tail shivering by day 12. Social grooming between littermates and between the young and the mother was observed as early as day four but did not become a common activity until day 14. For references to adult behavior and for further explanation of the defensive upright warding posture, the threatening "chit", the elongate posture, and tail shivering see the discussion below under Behavior.

ACTIVITY

Activity is a form of behavior distinguished from sleep or quiescence. The term denotes movement, usually locomotion, although feeding, drinking, elimination, and other functions are often referred to as activities. This section will deal primarily with locomotion in order to demonstrate activity patterns.

In the natural life of a rodent, locomotor activity serves in social behavior, obtaining food and water, exploratory movements within the home range, dispersal, escape from enemies, and exercise. It is not within the scope of this section to discuss the many motivating factors involved in all these forms of behavior, or the end results in terms of home range, territoriality, and dispersal movements. This section will be limited to information on the amount and timing of general daily activity and the effects of certain abiotic environmental factors upon activity.

Daily Cycle

In South Africa O. irroratus has been described by some authors as diurnal (C.H.B. Grant in Thomas and Schwann, 1905a and 1906a; Roberts, 1956), and by others as primarily nocturnal, although somewhat active in daytime as well (Hewitt, 1931; Shortridge, 1934). Ranger (1927) stated that it was seen at all times of the day and Shortridge (1942) later stated it as being both diurnal and nocturnal. Further support for the belief that it is nocturnally active comes from the abundant remains of this animal in the pellets of barn and grass owls (FitzSimons, 1920; Ranger, 1927; Skead, 1956 and 1963; Davis, 1959; De Graaff,1960; Bateman, 1960; Vernon, 1972). Evidence from owl pellets found in the study area indicates that O. irroratus is a common prey of both owl species (see Mortality).

Information on the activity rhythms of other species of Otomys in the literature is as contradictory and confusing as for O. irroratus.

Roberts (1951) stated that the Otomyinae of Southern Africa are mainly diurnal. *Otomys anchietae* from Zambia and Tanzania was found to be mainly diurnal (Vesey-FitzGerald, 1966). Ansell (1960) in Zambia believed *O. angoniensis* to be diurnal but perhaps also nocturnal; while Hanney (1965) in Malawi caught them only at night. Smithers (1971) stated that *O. angoniensis* in Botswana is predominantly nocturnal but to some extent also diurnal. Several authors have reported *O. angoniensis* from owl pellets (Davis, 1959; Pienaar, 1961; Coetzeé, 1963; Benson, 1965; Vernon, 1972), and they have also been found in pellets from the study area (see Mortality). Copley (1950) and Bere (1962) reported *O. denti*, in Kenya and Uganda respectively, as active both day and night. Delany (1966) stated that *O. tropicalis* was seen running about during the day in Uganda. On the Cameroun Mountain they were often seen during the day but their remains in owl pellets indicate that they are partly nocturnal (Rosevear, 1969). Dieterlen (1968) stated that *O. tropicalis* in eastern Zaïre and Rwanda has a polyphasic day and night activity cycle. He found that 21 per cent of the catches were between 0800 and 1600 hours. Although Dieterlen included no specific times he stated that including the early morning and late afternoon catches the percentage increased to 30 to 40 per cent. Presumably his reference to early morning was from sunrise to 0800 hours and late afternoon, from 1600 hours to sunset.

The daily activity cycle of *O. irroratus* was examined in the field and superficially in the laboratory. Falls (1968) stated that while laboratory studies are necessary to determine effects of individual factors and define relationships which may be significant to animals, it is also necessary to study activity in the field. He also stated that live-trapping has been the method most frequently used in the field, but the following are the inherent disadvantages: traps restrain animals, animals either may avoid or habitually visit traps, and only a very limited number of events can be recorded.

The traps in the study grid were examined every two hours for a 24-hour period in October 1970, February 1971, and July 1971. Each time the traps were examined the identifying numbers of the captured animals were recorded and the animals released. This tended to restrain their activity less and also served as a record to determine if any individuals habitually returned to the same trap (which none did). The results showed activity occurring throughout much of the

24 hours but with two prominent peaks of activity, the smaller peak in early morning and the major peak in late afternoon (Figs. 26-28). Judging from these data _O. irroratus_ could be considered primarily crepuscular. The results also give a possible reason for the diversity of activity times reported in the literature. Despite insufficient capture data it appears as if activity of _O. angoniensis_ in the study grid corresponds closely to that of _O. irroratus_. It is likely that crepuscular activity cycles predominate throughout the Otomyinae, but with varying degrees of nocturnal or diurnal activity possible.

In studying the activity of animals in the laboratory it is desirable to use samples taken directly from the field (Falls, 1968). The activity of 12 recently wild-caught animals was tested over a cumulative period of 49 days in the laboratory under controlled conditions of light (12 hour on-off cycle), temperature (20°C), and relative humidity (50 per cent). These animals were tested in the enclosure described above in Materials and Methods and locomotor activity was recorded on an event recorder. The summarized results are presented in Fig. 29. The activity occurring between 0400 and 0600 hours, although not forming a distinct peak, was sustained for a longer period than at most other times of the day. The most distinct peak of activity occurred between 1800 and 1900 hours. Both of these active periods were followed by a characteristic sharp decline in activity, similar to that recorded in the field. Although activity periods in the laboratory situation were not as easily discernible as in the field, they corresponded closely (Fig. 30).

Variations and Relationships

Owing to the many contradictory reports on activity of _Otomys_ in the literature, Shortridge (1934) suggested that activity may vary with season or locality. The activity of _O. irroratus_ in the study area was recorded during different seasons. The results of the studies undertaken in October and February were very similar and the general climate during the two months closely comparable. Therefore, the results of the two months were combined as a summer (October-February) activity pattern and are compared and contrasted with winter activity during July (Fig. 30). Although _O. irroratus_ maintains a crepuscular cycle in both seasons there exists a difference in amount and timing of activity. The two peaks of activity during the summer trials accounted for 42 per cent of the total recorded activity. The two peaks of activity during the winter trial were more extended and accounted for 82 per cent of the total recorded activity, nearly twice that seen during summer. The total recorded nocturnal activity between the two peaks accounts for a major difference between summer and winter in amount of activity. During summer 25 per cent of activity occurred at night while only four per cent occurred at night during winter. The obvious reason for the virtual lack of nocturnal activity during winter was the extremely cold, below-freezing temperatures (Fig. 28), which caused more activity to occur during the daylight hours. The timing of activity also differed in winter and in summer; during winter the peaks in activity occurred later in the morning and earlier in the afternoon (Fig. 30).

There exists no evidence to confirm or disprove the suggestion of differences in activity according to locality, but it is doubtful if any great variations in activity of O. irroratus exist. Possibly minor local or seasonal variations may occur but a basic crepuscular pattern would be expected throughout the range.

Numerous abiotic environmental factors have been examined to determine their effect upon activity of rodents. Some factors have been shown to control the general activity pattern while others cause only minor variations. Getz (1968), in studying the activity of the red-backed vole, Clethrionomys gapperi, discovered that light was the primary factor in regulating activity patterns; changes in atmospheric conditions (temperature and humidity) influenced only the level of activity. Other authors have found wind, rain, and the moon (in nocturnal species) influencing the activity pattern. Little attempt will be made here to elucidate variation in activity as a result of atmospheric conditions as this would require a longer and more continuous study. The main reason for including temperature, humidity, official sunrise and sunset, and various other factors in Figs. 26-28 is to indicate (if possible) the primary factor(s) regulating the basically crepuscular pattern.

It appears that in Otomys light is possibly the major underlying factor. Twilight actually begins before official sunrise, hence the early morning peak in October and February began before sunrise. Temperature appeared to play a minor role in the onset of activity in July as the morning activity began later in relation to sunrise than during the summer, probably because of extremely low temperatures.

In all three trials the morning peak of activity occurred at or slightly before sunrise and the afternoon peak before sunset. Despite the apparently inconsistent relationship of activity to the timing of official sunrise and sunset, the light intensity during the two peaks of activity appeared closely comparable. Activity, therefore, basically occurs during the two periods of twilight.

In the October trial a strong breeze was blowing between 2100 and 2400 hours causing a decline in humidity and a rise in temperature (Fig. 26). The activity during this time increased slightly and remained at that level during the change. Activity then suddenly declined following cessation of the wind and the accompanying change in temperature and humidity. Hammer (1969) found that although wind did influence the activity of Peromyscus maniculatus the combined forces of wind and temperature exerted a still greater influence. It appears as if wind and other atmospheric changes may have caused the activity level to increase slightly.

In the February trial it was cloudy and overcast between 1000 and 1400 hours causing the temperature to remain low and the humidity high (Fig. 27). During that period it appears as if activity increased slightly. The suppression of the normally hot midday temperatures (Fig. 27) and the diminished light conditions may have been responsible. Gentry and Odum (1957) found nocturnal species to be caught more frequently on warm, cloudy nights with conditions of diminished light.

A light rain between 1600 and 2000 hours in February (Fig. 27) occurred at the time of the normal late afternoon peak. It is unknown whether this affected activity, although it does not appear to have done so. Gentry and Odum (1957) found catches to increase during a light rain. Becuase O. irroratus readily dies from loss of body heat when it becomes wet (see Mortality), activity during heavy rainfall would be expected to be greatly reduced.

Due to the lack of adequate facilities in the laboratory and the difficulties of maintaining vlei rats in captivity, it was not possible to conduct extensive studies under different conditions of light, temperature, and humidity. An obvious feature of activity in the laboratory (Fig. 29) was the immediate decrease in activity when the lights came on and the sudden increase when they went out. It would be interesting to ascertain what would happen to the activity pattern under conditions of constant light or darkness. Because the vlei rat requires a constant supply of fresh food the introduction of food at a specific time each day could influence activity.

BEHAVIOR

Individual Behavior

The following individual behavior patterns refer to adults only. For juvenile behavior and its development see the section on Postnatal Growth and Development.

Locomotion.--The vlei rat is quadrupedal and in walking and running uses a diagonal sequence of alternate limb movements. Walking is the main form of locomotion and is frequently interrupted by hesitations. Running is quick with the body kept close to the substrate in a flat posture, seemingly an adaption for rapid movement through runways.

These animals are capable of swimming but do not appear to readily take to water. Shortridge (1934) stated that they are not expert swimmers and only enter water to cross from one reed patch to another. Ansell (1960) stated that O. angoniensis is partly amphibious. Copley (1950) reported that O. denti in Kenya was not a strong swimmer. He stated that if hard-pressed it will take to water and dive, but does not remain under the surface for long; generally it swims only as far as the nearest vegetation. Coe (1967) observed O. typus readily taking to water and swimming. Otomys tropicalis was found to swim very well (Dieterlen, 1968). Dieterlen described the swimming as primarily performed with the hind limbs while the forelimbs lie alongside the chest; only near land does it assume a walking movement with the forelimbs. A hard-pressed Otomys sp. (either O. angoniensis or O. irroratus) was observed to swim a short distance and then dive under the surface of the water (J.E.L. Wahl, pers. comm.). The discovery of bilharziasis in O. angoniensis (see Relationships with Man) is evidence that they probably take to water. One marked O. irroratus from the study grid was found to have crossed a flowing stream at least 5 m in width..

The vlei rat is basically terrestrial but is known to occasionally climb trees to eat bark and terminal buds from the upper branches (Davis, 1942 and 1966; MacKellar, 1952; Schulz, 1953 and 1962; P.J. Geldenhuys, pers. comm.).

Exploration.--When an individual is placed in a strange enclosure it demonstrates its extremely shy and retiring habits by moving to a side wall or near corner, facing inwards with its back to the wall, and then often not moving for several hours on end. When it finally decides to investigate its surroundings the body is tense and in an elongate posture. In this posture the body is very much extended and flattened, the tail very stiff, sticking straight out behind or with a very slight upward tilt, and the ears erect and slightly forward (Fig. 31). The animal moves with very slow, cautious steps, occasionally stopping to rise on its hind limbs and test the air. Its nose and vibrissae are constantly exploring and testing the air, ground, and any object in its path. Any slight sound or movement causes it to beat a hasty retreat and some time may elapse before it resumes exploration. Occasionally it may suddenly retreat without any evident cause.

After becoming familiar with its surroundings the animal moves with a more relaxed posture, the body being higher off the substrate, with more rounded body contours, and with the tail more relaxed, dipping slightly at the base and giving the appearance of being dragged.

In the natural state O. irroratus was found to be very shy, greatly disturbed by noise and movement (Roberts, 1956). Coe (1967) stated that O. typus was also shy by nature.

Investigative behavior was tested by subjecting an animal to a new object in familiar surroundings. The elongate posture is resumed when contacting such new objects. Motivation for investigation of a new object is seldom immediate or a direct action, but arises during a regular reconnaissance of its surroundings, which apparently "refreshes its memory" and helps keep a check on its environment. Shillito (1963) and Ewer (1967) found this same behavior in Microtus agrestis and Cricetomys gambianus respectively.

Rest and sleep.--The resting animal normally adopts an elongate posture with the hind limbs under the body, the forelimbs forward and curled under the neck, and the chin resting on the ground. Occasionally an individual will rest on its side in a slightly curled posture with hind limbs out to the side.

The typical sleeping posture resembles the resting posture, the only difference being that the eyes are closed. Individuals sometimes sleep like many other rodents, in a sitting posture with the head tucked ventrad. Although the tail comes forward it is not curled around the body as in many other rodents. During sleep the eyes are seldom closed for more than a few seconds to minutes at a time, and at the slightest disturbance they are immediately opened.

Stretching, by extending the limbs and de-arching the back, usually occurs as the animal leaves the nest upon awakening or after rest. Stretching is not always followed by grooming as in *Peromyscus* (Eisenberg, 1962), but is often accompanied by yawning.

Grooming.--Washing begins with several rapid alternate motions of the forepaws under the mouth. This is followed by several rapid movements of the arms and paws, usually simultaneously, up the face to the level of the eyes and back down to the nose. This motion is interrupted often to repeat washing of the paws. After repeating this sequence several times the arms and paws are extended back behind the ears. Accompanying the action of the arms and paws over the face is a bobbing motion of the head. Washing of the sides, flanks, and inguinal region frequently follows face washing. This action involves combing the fur with the forepaws while mouthing the same area with rapid head bobbing. Cleaning of the tail as in *Cricetomys gambianus* (Ewer, 1967) and *Peromyscus* (Eisenberg, 1962) has never been observed. Washing is always done while sitting slightly upright with the weight on the hind legs.

Scratching of the head, ears, sides, and back is done with the hind foot and from a three-point stance. Scratching of the back is accomplished by ventrally shifting the skin of the back and side, thereby exposing it to the reach of the hind foot. Biting at the claws of the hind foot following scratching occurs occasionally.

Feeding.--All authors have reported *O. irroratus* as being strictly vegetarian, eating primarily young shoots, leaves, stems, roots, and rhizomes of grasses and other vlei herbage. Evidence in the study area supports this view with the exception that roots and rhizomes were not found to be part of the diet. The roots of grasses were, however, eaten by captive animals. Cursory examination of the stomach contents of dissected specimens from the study area demonstrated only vegetable matter. In areas of forest plantations they are known to eat the bark from young trees, especially pines (Davis, 1942; MacKellar, 1952; Schulz, 1953 and 1962). MacKellar (1952) reported that the eating of tree bark appeared to be in response to a craving for a particular food constituent rather than the adoption of bark as a normal food. For further discussion of bark eating and damage to trees see Relationships with Man. In relation to controlling damage to trees it was found that the vlei rat in nature will eat dry maize meal, especially during and just after winter when the veld is at its poorest and food is in short supply (Schulz, 1953 and 1962; Geldenhuys, 1960).

All other Otomyinae have also been reported as being herbivorous, with food habits similar to those of *O. irroratus*. Shortridge (1934) and Smithers (1971) reported *O. angoniensis* as also eating grain and seeds. Dieterlen (1968) found primarily young shoots, stems, and leaves in the stomach contents of *O. tropicalis*, but also found small bits of roots, seeds, fruit, and insects. He further confirmed that they occasionally eat the bark of young trees.

Evidence from plant cuttings in the study area and from what was determinable in stomach contents, indicates that *O. irroratus* ate nearly all of the plant species common to its distribution in the grid (see Table 4). Because the grass *Arundinella nepalensis* was the most abundant and widespread plant in the study grid it was commonly eaten. Green seeds of the grass *Paspalum dilatatum* were found in the stomach contents of one specimen. Young shoots of the reed *Phragmites australis* and the weed *Tagetes minuta* (both found in vlei rat habitat in the study area but not in the grid) were found eaten. The fact that they eat the weed *T. minuta* and the nonindigenous thistle, *Cirsium vulgare*, indicates that they readily eat any palatable vegetation occurring in their habitat.

When *O. irroratus* eats, the food item is picked up with the teeth and lips and held in the forepaws while it sits in the typical hunched upright position (Fig. 31). This upright posture is not as erect as that of a squirrel, but more like that described for the cane rat, *Thryonomys swinderianus* (Ewer, 1968), or the woodrat, *Neotoma floridana* (Poole, 1940), with the forelimbs barely raised above the ground. Small items of food are sometimes held with only one forepaw while the other rests on the ground, as seen in *O. tropicalis* (Dieterlen, 1968) and again as in *T. swinderianus* (Ewer, 1968). Feeding is usually followed by a period of grooming.

In feeding upon grass the vlei rat bites through the stem close to the ground, picks up the cut piece in the mouth, sits back on its haunches, grasps the grass on either side of its mouth with a paw, and bites off a 2 to 5 cm piece. If the piece of grass is young and tender the vlei rat sticks the end in its mouth, bites off a series of small pieces, and then grinds the previously cut series of small pieces with its molars. If the grass is coarse it moves the piece back and forth through its mouth from one end to the other, stripping off the outer part to get at the tender pith.

Tell-tale piles of plant cuttings are left along runways, some of which are the result of attempts to get at and eat the tender upper parts of the vegetation. In typical vlei rat habitat a piece of grass or other plant cut at the base will not topple over, which makes it necessary to continue cutting off basal pieces until the more tender parts are reached.

Little piles of grass cuttings composed of about 20 pieces 3 to 4 cm in length were found in O. tropicalis feeding places (Dieterlen, 1968). Dieterlen found no cuttings in the most regularly used runways, but in some of the less used runways he found piles consisting of 10 to 15 cuttings. He also occasionally found apparently uneaten pieces 3 to 5 cm long, but did not understand their significance. It is suggested that these uneaten pieces are the result of attempts to reach the upper, more tender, parts of certain plants, as mentioned above for O. irroratus.

The following foods were fed to captive animals: lettuce, carrots and carrot tops, cabbage, beet tops, spinach, lucerne (alfalfa), green grasses, and standard mouse cubes. All of these were eaten but lettuce and lucerne were preferred. Individuals have survived as long as six months in captivity on such a diet. A few individuals readily took to eating mouse cubes but most did not. If animals are kept on a mouse cube diet they must receive a weekly supplement of fresh vegetation. Schulz (1953) found that they did not survive well in captivity upon a diet of maize meal, but greatly improved their chances of survival with supplements of lucerne meal and pine needles. Animals kept on a diet of fresh vegetation were never observed drinking water and survived well without it.

Vlei rats eat large quantities of fresh vegetation in captivity, an adult often consuming as much as half a head of lettuce and a carrot, complete with its top, every day. Pitchford and Visser (1962) said that O. angoniensis also required large amounts of food. Vlei rats generally require a fresh supply of food each day. For these reasons they are expensive and time-consuming to keep in captivity.

In the laboratory food is consumed sporadically throughout the day with peaks coinciding with activity peaks (see Activity and Fig. 30).

Coprophagy, the eating of feces, is very common in the vlei rat and has also been recorded in several rodents (Ewer, 1968), lagomorphs, and shrews. From the hunched, upright, feeding position the feces are removed from the anus with the teeth and then eaten. This habit is very important in vegetarian species during transition of the young from milk to solid food, in order for them to obtain the proper bacterial flora for digestion from the adults (Ewer, 1968). It has also been shown to be a source of vitamins otherwise unobtainable. Coprophagy appears to be more common during a shortage of food. When an abundance of food is present feces are discarded after removal from the anus. Eating of feces when there is a lack of food may have additional survival significance during the winter months when there is a shortage of green vegetation. It was suggested that in shrews coprophagy occurs only at a time of food shortage (Crowcroft, 1957; Sharma, 1962).

Elimination.--During defecation in captivity no special posture is assumed nor is there any specific place for this activity. It appears to occur at any time while walking or feeding. Defecation also occurs in the nest and feces are rarely cleaned out. In the field feces were found scattered everywhere in runways, feeding sites, and nests (Powell, 1925; Schulz, 1953; pers. obs.) Dieterlen (1968) found the same in *O. tropicalis*.

Poole (1940) reported that the woodrat, *Neotoma floridana*, makes piles of dung on flat or slightly concave rocks, often in exposed places. This trait is occasionally seen in *Otomys* where accumulations of feces can be found on small exposed bare spots of earth or flat rocks about 10 to 30 cm in diameter. Schulz (1953) referred to these dung patches of *O. irroratus* as "sun parlours", as they were devoid of a protective canopy of vegetation and were used for lying in the sun. Feces were also very commonly deposited on top of traps. The significance of the above defecation practices is unknown unless they serve as a means of marking.

Urination generally occurs in a specific corner in captivity, which indicates its possible use as a marking device. During urination the animal backs into the corner with its tail extending up the corner and remains motionless until finished.

Owing to the large amount of fresh vegetation eaten by vlei rats, copious amounts of wastes are produced and cages with solid bottoms and absorbent floor litter are quickly soiled.

Marking.—A prominent marking movement becomes evident when an individual is placed in a new or clean cage. This movement, unlike the perineal drag of many other rodents, is performed by placing the region at the side of the base of the tail against a side wall. By extending and lowering the hind limbs this area is rubbed up and down on the wall where scent is presumably deposited from a pair of prominent anal glands. In nature this movement would presumably be used to mark the vegetation along the sides of the runways.

The possible use of feces and urine as a means of marking has been discussed above (see Elimination).

Nest building, burrowing, and runway formation.—The nests of *O. irroratus* in the study area were usually open and shaped like a shallow bowl, approximately 15 cm in diameter and 3 cm deep, with normally two runways leading away. They were always placed where the canopy of vegetation was heavy so that a sufficient protective covering was available. They were composed of the most readily available vegetation which was chopped, shredded, and placed directly on top of the substrate. FitzSimons (1920) stated that the nest is composed of fine grasses or nearby materials which have been bitten and shredded. Dieterlen (1968) found that *O. tropicalis* generally built a simple nest similar to that described above for *O. irroratus*. He concluded that these nests are merely temporary and that *O. tropicalis* leads a nomadic type of life. The same conclusion was arrived at for *O. irroratus* in the study area. Vesey-FitzGerald (1966) stated that *O. anchietae* constructs no nest.

In captivity a similar type of nest is formed with carrot tops or shredded paper or lettuce (finely shredded with the teeth), which is placed in a shallow depression in the soft litter. The nesting material is either carried to the nest in the mouth or simply pulled into the nest and under the animal with the forelimbs. Final placement of nesting material is performed with sideways and backward motions of the forelimbs, and undesirable items are discarded from the nest with the mouth.

It has been stated that *O. irroratus* never occupies burrows (C.H.B. Grant in Thomas and Schwann, 1905a and b), although occasionally they nest under large rocks (C.H.B. Grant in Thomas and Schwann, 1905a). Powell (1925), Shortridge (1934), and Davis (1953) stated that they dig shallow burrows in which to live. In the eastern Cape Province, where reeds are scarce, they often live in burrows or crab holes near the banks of rivers (Shortridge, 1934). Shortridge (1942) reported that at another locality they normally live above ground, making no regular burrows. Roberts (1951) stated that they generally live above ground but occasionally take refuge in burrows in banks and in dry ground. FitzSimons (1920) suggested that they burrow only in exposed situations. Vesey-FitzGerald (1966) reported that O. anchietae does not burrow. Kershaw (1922) stated that O. angoniensis in Malawi nests above ground, and not in burrows. Shortridge (1934) stated that they normally live above ground because the soil is too wet to burrow. Otomys angoniensis has been reported to take refuge under large rocks supplied in large outdoor enclosures, but later dug their own burrows (P.S. Visser, pers. comm.). Copley (1950) and Bere (1963) reported O. denti nesting above ground inasmuch as the soil was too wet to burrow. Dieterlen (1968) found that O. tropicalis constructed burrows only where vegetation was sparse. Coe (1967) reported that O. typus does not burrow into the soil, but excavates a cavity in the persistent leaves at the base of giant senecios.

In the study area only a few burrows occupied by O. irroratus were found. One was in the side of a ridge of dirt running alongside a stream and was composed of three tunnels leading to a central nest chamber. The main tunnel extended horizontally into the bank for 30 cm, ending in a nest chamber 20 cm in diameter. The other two tunnels (0,5 and 1 m in length) led upwards and out the back of the bank. These latter two tunnels seemed very little used and probably existed only for escape. The nest was simple, like the one built above ground. Another burrow, found in an exposed situation, made use of part of an abandoned burrow system of a mole rat, Cryptomys hottentotus. The tunnel, 2 m long and 15 cm below the surface, had a vertical entrance at either end. The simple nest was in a small chamber 40 cm from one end. The other entrance did not appear to be actively used and again probably served only for escape. In another exposed situation large rocks provided a place under which they nested. No burrows were formed; the soil was simply excavated from directly beneath the rock and there a simple nest was built.

Again there was more than one entrance. The use of crab holes was not observed in the study area, but this could be the result of a high water table. Dieterlen (1968) found a similar type of burrowing situation regarding O. tropicalis. Firstly, the burrows generally had several openings. Secondly, the entrance, although steep, was found to be relatively short (30 to 50 cm) and led directly to the nest chamber. Thirdly, the nest was of a simple type.

It would appear from information in the literature and observations in the study area that O. irroratus does not burrow in situations where there is adequate cover or the soil is too wet. Burrows appear to be occupied only in dry and exposed situations. Because these animals are generally found in moist habitats with good vegetative cover it is believed that they normally nest above ground. The other species of Otomys mentioned above probably also occupy burrows only in dry and exposed situations.

In captivity, digging takes place with alternate motions of the forelimbs. After a small pile of floor litter has developed under the body from this movement a concerted effort of the hind limbs expels the material with considerable force. A characteristic sideways motion of the forelimbs, which was often seen, may be useful in eliminating debris from a runway. Since their burrows, when built in nature, are neither intricate nor extensive they are probably not very efficient at digging.

The vlei rat uses its extensive runway system for most of its activities. Runways are probably formed as a direct result of feeding, the individuals more or less eating their way through the vegetation. The tops of the cut vegetation are sometimes left uneaten and help to form a protective covering. In captivity vlei rats eat often the underside first and then the inside of a head of lettuce, which provides them with a hollowed-out, protective canopy. They have also frequently been seen pushing upwards vigorously with the head and shoulders as they crawled under vegetation. This behavior no doubt aids in the formation of runways.

During a study of runway activities of the meadow mouse, Microtus californicus, and the harvest mouse, Reithrodontomys megalotis, in California, both species actively utilized the same runways (Pearson, 1959). As with Otomys, meadow mice actively kept the runways cleared, because in their absence the runways quickly became overgrown despite continued activity of the smaller harvest mice. In the

Van Riebeeck Nature Reserve study area, all of the rodent and shrew species present used many of the same runways. It is obvious that neither the shrews nor the few Praomys natalensis in the study area would be able to keep the runways clear. Other than Otomys, only Rhabdomys pumilio occurred in significant numbers. Because R. pumilio if often found with the vlei rat throughout its range it would be interesting to determine the extent of multiple use of runways and whether R. pumilio can form and keep clear, runways on its own.

Response to traps.--Like other members of the genus, O. irroratus seldom takes the bait of snap-traps and is usually caught only by accidentally running over traps placed in runways (C.H.B. Grant in Thomas and Schwann, 1905a). Schulz (1953) and Geldenhuys (1960) found that O. irroratus will take small quantities of dry maize meal bait, but their tests were conducted in winter when food was scarce. Hanney (1965) found in Malawi that neither O. angoniensis, O. denti, nor O. typus were attracted to a bait of peanuts or peanut butter. Dieterlen (1968) stated that trapping of O. tropicalis was successful only because of their curiosity. Eisentraut (in Rosevear, 1969) found that O. tropicalis in Cameroun never took bait and entered traps placed in runways only by accident. Eisentraut found that the best way to capture them was by snaring them with a noose in their runways. Neal and Cock (1969), in a test of selectivity of two sizes of snap-traps, caught so few O. tropicalis that they were unable to analyze the results.

The best means of capturing a vlei rat with a snap-trap is by placing a rat-size trap at a right angle to a runway with the trigger end directly across the runway. An individual then has an equal chance of being caught regardless of the direction it comes from. Whether bait is necessary and, if so, what type would be best, is unknown. If Dieterlen (1968) is correct in his assumption that they are caught out of curiosity then some sort of bait should help. Stickel (1948) found Peromyscus leucopus much more attracted to baited live-traps than to unbaited ones. Most rodents are attracted to bait as a possible source of food. Most conventional baits, such as peanuts, rolled oats, or maize meal, would, therefore, undoubtedly be unappealing to a strictly herbivorous vlei rat. This possibly suggests that granivorous types would probably be attracted to normal baits, while browsing or grazing types would be relatively unattracted.

Snap-traps have been shown to be ineffective for certain species of small mammals by Edwards (1952), who also stated that trapping results with one kind of trap may give biased results as to the relative abundance of certain species. Cockrum (1947), in trapping experiments with two species of shrews and seven species of rodents, found live-traps to be two to three times more effective than snap-traps. Dieterlen (1968) stated that because of the difficulty of capturing O. tropicalis conclusions concerning their population structure must not be drawn from trap success.

In the study area, away from the grid, approximately 5 000 trap nights were conducted with snap-traps (both rat traps and Museum Specials), and only 10 O. irroratus were captured. Approximately 500 trap nights were conducted with live-traps and 60 vlei rats were captured. This represents a 60-fold increase in trap success using live-traps. On one occasion 40 snap-traps (20 rat traps and 20 Museum Specials) captured four vlei rats over a period of three days. Two weeks later the same area was trapped with 20 live-traps and over a period of three days 18 vlei rats were captured and removed. It therefore appears that live-traps are far more successful in capturing vlei rats, and their use is suggested even for removal trapping.

During the first six trapping sessions on the study grid two different types of live traps, hardboard and wire mesh, were used (see Materials and Methods and Fig. 2 for descriptions). This provided an opportunity for a comparison of their success in capturing O. irroratus It was obvious that the vlei rat has a highly significant ($P<0,01$) preference for the hardboard trap (Table 8). L.R. Wingate (unpublished data), in an area adjacent to the study area, studied the trap preference of six different live-traps. He found that the vlei rat had a decided preference for the wire mesh trap over the hardboard trap. Examination of the results in Table 8 suggests an explanation of the apparently conflicting results obtained in the two studies. Apparently there is a seasonal preference or avoidance of certain traps. In March there was no preference between traps in the present study, but as the temperature decreased in winter (May, June, and August) the hardboard traps were preferred. As the temperature warmed in September the preference for the hardboard trap decreased. Wingate conducted his study in January and February during the summer when a decided preference could be detected for the wire mesh trap. The vlei rat either prefers the closed, more protected hardboard trap during the winter and the open more ventilated wire trap during the summer, or avoids the open trap in the winter and the closed trap in the summer. Rain during the summer months would, however, have a more detrimental effect upon vlei rats caught in wire traps (see Mortality).

During the entire study period 333 *O. irroratus* were marked and released on the study grid. These 333 individuals were captured a total of 2 613 times, averaging 7,9 captures per animal. The most commonly caught animal was captured 62 times, and 83 (25 per cent) of the marked animals were captured 10 or more times.

Only 42 *O. angoniensis* were marked and released and they were captured 93 times, an average of 2,2 captures per animal. The most commonly caught animal was captured 33 times. Although the numbers of *O. angoniensis* were rather meager the above tends to indicate that both species of vlei rats are not shy of entering live-traps.

Trapping was conducted on the study grid twice a day for four consecutive days during the first six trapping sessions (March-September 1970). The number of new *O. irroratus* captured in the morning and afternoon of each day were totalled, and are shown below as the per cent of new animals trapped on each successive day during the four day session:

Per Cent Trapped on Successive Days

<table>
<tr><th>1st Day</th><th>2nd Day</th><th>3rd Day</th><th>4th Day</th></tr>
<tr><td>64</td><td>18</td><td>13</td><td>5</td></tr>
<tr><td colspan="2">82</td><td></td><td></td></tr>
<tr><td colspan="3">95</td><td></td></tr>
</table>

Because 95 per cent of the total captured during four days was captured during the first three days, it was decided to limit the remaining trapping sessions to only three days. In that way there would be less undue stress placed on the animals. A brief survey during one month demonstrated that individuals continuously recaptured showed a progressive loss in body weight.

It has been suggested above (under Composition in the section on Population Dynamics) that a differential in trapability may possibly exist in vlei rats of different ages and between the sexes. It has been recorded before in rodents that adults may inhibit the approach to traps by juveniles (Davis and Emlen, 1956; Watts, 1970; Wiley, 1971).

It has also been found in *Peromyscus maniculatus* that one sex was more susceptible to capture than the other (Beer *et al*., 1958). However, there is little evidence to support either of these possibilities in the vlei rat.

Social Behavior

Social behavior includes any behavior patterns involving two or more interacting individuals. C.H.B. Grant reported *O. irroratus* as living singly or in pairs (in Thomas and Schwann, 1905b). Powell (1925) and Shortridge (1934) stated that *Otomys* is by nature rather antisocial. *Otomys irroratus* was described by Roberts (1956) as being very shy. The same was also said of *O. typus* (Coe, 1967). Dieterlen (1968) believed *O. tropicalis* to be antisocial, and suggested that it is usually found singly but may occasionally occur in pairs. In captivity *O. irroratus* was shy, retiring, and antisocial.

Communication.--Communication is by means of the following senses: visual, auditory, olfactory, and tactile. The eyes of the vlei rat, although very large, appear to be rather ineffective, as individuals are not visibly affected by the activity of others in adjoining glass-sided cages nor by slow movements of an observer only 30 to 60 cm away. However, Roberts (1956) stated that in nature movement did disturb them.

Observations on their response to sound involved sounds only within the range of human hearing, but there was nothing to suggest the occurrence of frequencies above that range. Only two adult sounds were heard, the first being an alarm squeal heard infrequently from animals held for measuring. The second was a metallic "chit" repeatedly uttered as a threat directed by the upright individual at an approaching animal during conflict. The closer the intruder approached the more rapid and intense became the "chits". Hearing seemed quite keen but only loud noises and an imitation of the "chit" elicited immediate response. Roberts (1956) stated that in nature noise greatly disturbed them. Chattering of the incisors together, common in many murid and cricetid rodents (Ewer, 1968), was not observed. Ewer (1968) suggested that this behavior is absent in species which rarely attack by biting, possibly being replaced by vibration of the tail. This would not appear to be the case in the vlei rat as both tail shivering and biting attack occur.

Although the olfactory sense appeared to be the most highly developed, the role of glandular secretions, urine, and feces in olfactory communication is not fully understood. An intruder, actively smelling the substrate and anything in its path, did not seem overly interested in investigating these means or areas of communication. Recognition of conspecifics was naso-nasal and very rarely naso-anal. When individuals (male and female or mother and young) were returned to their cleaned cage there normally followed a period of nonrecognition, confusion, and threat. Recognition did not take as long as in new encounters but they had to repeat all sequences, and only when the "new" cage had been fully explored did confusion cease. If this same procedure was repeated but with familiar floor litter returned to the cage, recognition of cagemates was immediate, indicating that unfamiliar surroundings caused or contributed significantly to breakdowns in recognition patterns.

Although defecation and occasional urination are indiscriminate these would occur more often in the most actively used runways, which would help to mark these pathways. Defecation and urination, accompanied by marking with the anal glands, probably serves only as an indication of the use of specific runways and not as a deterrent to conspecifics. Despite the lack of positive evidence it seems likely that olfactory communication may exist in one form or another (see also Elimination and Marking).

Tactile communication by use of the vibrissae appeared to be a means of supplementing olfactory information when investigating new surroundings and objects. The vibrissae probably aid the animal when moving rapidly through the narrow runways. Contact of the vibrissae did not occur in social nose to nose contact.

Adult-offspring behavior.--Because successful breeding did not occur in the laboratory behavioral interaction between the male and young was not observed. J. Meester (pers. comm.) made brief observations on one successfully bred pair and their young in which the male appeared to be fully tolerated by the female, often huddled with the female while the young were suckling, and seemed oblivious of the young.

For the first few days after birth a high-pitched squeak was emitted by the young when separated from the mother. This squeak could be heard easily from 10 m away and probably served as an aid in finding lost and helpless youngsters.

Nipple-clinging by the young, a phenomenon previously reported in O. irroratus by FitzSimons (1920) and also known in Aethomys, Tatera, Thallomys, Mystromys, and Neotoma (Donat, 1933; Lawrence, 1941; Davis, 1963; Meester and Hallett,1970) among other genera, was prominent in the vlei rat and was aided by the presence of incisors at birth. Even though the young were mobile at birth their clumsiness caused them to be dragged about hanging onto the inguinal mammae. As their coordination quickly improved they were soon seen running along behind the mother while firmly attached to the nipples (Fig. 31). For the first few days the young were seldom found unattached, but probably did let go at times as it does not seem likely that the female transported the young while foraging for food. Instead they are presumably left in the nest. On a few occasions a mother with a nipple-clinging baby was captured in a trap. Because these cases involved the mother and only a single, advanced young it appears more likely that the youngster followed the mother into the trap and was not transported there. The discovery of very young and helpless individuals wandering aimlessly in the study area also gave credence to the suggestion that they detach at an early stage. Dieterlen (1968) stated that he observed several female O. tropicalis in nature transporting one to two young about on the nipples. This could easily have been the result of females with young being disturbed from their nest.

While suckling the young the mother would crouch over them with her back arched and hind legs extended, or lie on her side with the upper hind limb raised to accomodate the young. The mother detached the young by very slowly rising and moving off the nest like Peromyscus (King, 1963). When detached in such a manner the young remained quiet and undisturbed in the nest, but if startled they remained firmly attached to the nipples. The mother was never observed mouth-carrying the young as has been seen in species producing large litters, such as Rhabdomys pumilio and Praomys natalensis (Meester and Hallett, 1970). Nipple-clinging would appear to be an adaptation in which the survival rate of the young is greatly increased, especially in O. irroratus which uses an open, unprotected nest.

When the young were returned to the cage after measuring the mother seldom made an attempt to collect them, but because of their mobility they would soon locate her. There was apparently olfactory recognition on the part of the mother after which the young were pulled under her body with the forepaws. This pulling-in action was identical to that used in nest building. The young were then groomed only very briefly, possibly because they were capable of grooming themselves at an early age. By the age of three to four weeks there was a reversal of roles, after which the young were often seen grooming the mother.

When the young began actively eating solid food they often came into conflict with the mother over a particular food item. The result would be a brief tugging match, with the mother rather violently jerking the food from the young, then sometimes turning her back to eat the morsel undisturbed. Occasionally one of the young would become perturbed over a conflict with the mother and give a threatening "chit".

Adult interactions.--The behavior patterns and postures discussed in the following categories are essentially the same for both sexes, unless otherwise stated. Allowance has been made for a certain amount of individual variation.

1. Approach behavior. Approach to a strange individual is conducted with the body in an elongate posture. This elongate posture is characterized by the body being tense, extended, and somewhat flattened, with the tail rigid and horizontal, the nose and vibrissae active, and the posterior margin of the ears extended outward to direct the ear pinnae more forward (Fig. 31). Movements are normally very slow, with much hesitation.

2. Contact behavior. Contact is made in the elongate posture and is nose to nose. Naso-anal contact seldom manifests itself in male-female encounters and such close proximity is never allowed in male-male or female-female encounters. Any naso-anal contact is initiated by the male from the elongate posture with the female in a threatening upright posture. Unlike several other rodents (Eisenberg, 1962 and 1963) naso-anal contact is infrequent and no change in the opening of the eyes has been noted in the vlei rat.

During initial contacts lateral shivering movements of the tail are usually displayed. This behavior is manifested in a number of rodents and represents a high state of general excitement (Ewer, 1968). These movements are of large amplitude in the house mouse, *Mus musculus*, and create a rustling sound against the substrate which constitutes a threat to a rival (Clark and Schein, 1966; Ewer, 1968). In some rodents this movement is a sign of aggression, but in male cane rats, *Thryonomys swinderianus*, it is a sexual display during courtship

(Ewer, 1968). Tail shivering is definitely associated with a high state of excitement in the vlei rat but no association with mating behavior is known to exist. Because, in vlei rats, it occurs during conflict situations and is primarily demonstrated by dominant individuals it probably serves as a threat display.

3. Grooming behavior. Owing to either the antisocial behavior of the vlei rat, or because of a low or nonexistent motivational stimulus, social grooming between adults has seldom been observed in either inter- or intrasexual encounters.

Certain animals have body areas of specialized sensitivity where they enjoy being groomed. Scratching and rubbing the vlei rat just under the chin will cause it to turn the head, close the eyes, and remain motionless until manipulation is stopped. A similar area of sensitivity under the chin exists in Thryonomys (Ewer, 1968) and in the black-tailed prairiedog, Cynomys ludovicianus, (King, 1955). Ewer (1968) stated that this area is briefly groomed when two friendly cane rats meet and that this behavior forms a sort of greeting ceremony. Grooming of this area, along with general social grooming, has been frequently witnessed between juvenile littermates but appears nearly nonexistent in adults, perhaps as a result of a breakdown of sexual behavior in captivity (see Sexual behavior).

Displacement grooming is common in conflict situations and is usually displayed by the dominant individual.

4. Upright postures. The upright posture is normally associated with defensive threat and submissiveness and is often accompanied by a threatening "chit". When the upright posture becomes mutual (Fig. 32), "boxing" and pushing ensue after which the dominant and submissive roles are established. In the upright position the angle of the body to the substrate depends upon the amount of aggression involved or upon the persistence of the aggressor. Usually the more vertical the body, the greater the level of submissiveness. When the angle of the body with the substrate is near 45° the forepaws are held together and close to the body, but when in a more vertical position the forepaws are outstretched to ward off attack. A female, when approached by a male, readily goes upright but seldom into the vertical position. Attack is seldom initiated from an upright posture. Eisenberg (1962) stated that in Peromyscus the upright posture is either transitory to flight or maintained as a defensive posture. This appears to be the case in the vlei rat but it is also transitory

to another posture, that of submissive appeasement (see Submissiveness).

5. Threat. Threat displayed by the dominant, approaching individual is characterized by the low, elongate, approach posture (Fig. 32), with ears flattened against the head, shivering of the tail, and occasionally a slight exposure of a side to the rival. This lateral display (Fig. 32) is a transition behavior occurring only briefly after mutual upright posture and before approach followed by direct attack (see Intrasexual encounter). As in Peromyscus (Eisenberg, 1962), the elongate posture during threat appears similar to that during investigation and in both cases is expressed by "confident" individuals.

6. Chasing. This consists of the dominant animal running after the submissive one, making frequent attempts to bite the rump, which results in numerous minor wounds and much fur loss. Damage does not seem to be inflicted upon the tail and there is never a shift to sexual behavior with attempted mounts as in Peromyscus (Eisenberg, 1962) and some other rodents. If the individual being pursued makes a sharp turn or quick stop the pursuer often loses contact with him. This disappearance of the releaser stimulus (the fleeing animal) results in a shift of behavior by the pursuer to such displacement activities as feeding and grooming.

7. Fighting. Fighting generally occurs following a chase when the pursued animal is caught. Fighting is characterized by rolling and struggling about on the ground, head to head, with bodies adpressed. It is of short duration, ending with one having a bite hold on the rival's shoulder, cheek, or lip. They then break apart and chasing again ensues. Unlike some other rodents during locked fights, serious wounds are often inflicted. Also, there does not appear to be a struggle for a superior position.

Eisenberg (1963), referring to heteromyids, stated that locked fighting is more common in quadrupedal rodents while sparring predominates in the more bipedal Dipodomys and Microdipodops. In the confined conditions of the laboratory there does not appear to be any predominance of either locked fighting or sparring in the quadrupedal vlei rat. During agonistic tests a submissive female was killed by the dominant female and a submissive male was so badly wounded by the dominant male that it had to be destroyed, the major wounds occurred during locked encounters. Although occasional individuals in the field, usually large males, have similar wounds it seems likely that under natural conditions locked fighting, and especially mortal wounds, would occur less frequently inasmuch as opportunities for escape would not be limited as in the laboratory. Impressive vocal displays of threatening "chits", similar to those heard during sparring bouts, have been heard a few times in the study area.

8. Dominance. Several characteristics are associated with dominance in vlei rats. Dominant animals approach a rival in the elongate posture, with ears flattened against the head. This approach by the dominant animal is sometimes followed by a lateral display (see Fig. 32 and Threat), but more often by an outright attack. No variation in degree of eye opening has been observed as in other rodents. Tail shivering and displacement grooming are more common in dominant animals. Usually individuals with greater body weight will be dominant over those lighter in weight, but on one occasion a male with 15 per cent lower body weight proved far superior to his heavier rival. Males are generally dominant over females.

9. Submissiveness. Submission is characterized by the animal who assumes an upright defense posture (Fig. 32) accompanied by chitting. The more vertical the body posture and more extended the forelimbs the more submissive the animal. The intensity of the vocalization is dependent upon the amount of aggression involved, male-female encounters eliciting less aggression than male-male or female-female encounters. Appeasement sometimes follows the vertical upright posture and is demonstrated by nearly falling over on the back, exposing the vulnerable belly (Fig. 32). When this occurs even a persistent attacker will desist and move away. A similar type of appeasement posture is also found in the vole, _Microtus agrestis_, (Clarke, 1956) and the golden hamster, _Mesocricetus auratus_, (pers. obs.).

Sequences of behavior during encounters.--Behavior patterns in intrasexual, male-male and female-female, encounters are essentially the same, differing only in frequency. Sequences in intersexual encounters are different in some respects and will be described separately.

Because of the shy and retiring nature of the vlei rat several weeks of familiarization to laboratory conditions are necessary before tests can begin, and when animals are placed in a mutually unfamiliar enclosure another period of two to three days is required to again familiarize.

1. Intrasexual encounter. After being placed in the observation

chamber there is a period of quiet sometimes lasting five hours. Finally one animal begins slowly to move about in the elongate posture making a thorough investigation. After several false starts, which involve racing back to the point of departure, it finally makes contact with another animal. Because no overt aggression exists at this point the first contact with the other animal by the approaching individual usually results in a hasty retreat. There now remains curiosity on the part of both individuals which may cause the inactive animal to begin investigating. During the highly excitable periods of initial approach both animals come nose to nose in an elongate posture with much retreating, reapproaching, and tail shivering. Eventually one individual, usually the more "confident" (who began investigating first), presses the approach too close, causing the other to go upright and begin chitting. This may happen once or twice, followed by retreat of the approacher, but eventually ends in mutual upright posture with much sparring. Sparring may occur several times until it appears that one animal becomes more sure and aggressive and the other either goes into the appeasment posture or flees, usually the latter. When the appeasement posture occurs the rival usually retreats, but when one animal flees chasing is initiated by the other, resulting in one of the following: locked fighting, a return to an upright defense posture by the submissive animal, or escape. The dominant animal continues his approaches in the elongate posture with tail shivering and at this stage may perform the lateral display. This seldom seen exposure of the side usually precedes a direct attack. From a certain point in the sequence the lateral display is eliminated entirely and approach leads to direct attack. The submissive animal maintains an upright defensive threat posture during approaches and lateral displays by the dominant animal, but is ready to make a quick escape leap when the approacher gets too close or attacks. During approach, the dominant animal may suddenly stop his aggressive activities and begin displacement grooming or feeding or turn and leave in a relaxed walk to resume eating or grooming elsewhere. Aggressive activity may be resumed as quickly as it ceases, however, resulting in the dominant animal returning to the rival. The sudden cessation of aggressive activity may be due to a low level of aggression at that time, absence of aggression-stimulating movements on the part of the rival, or a combination of both. In time, the aggression level appears to dwindle in the dominant animal and it tries to investigate the rival more closely. The tension becomes too great in the submissive animal who then assumes an upright defense posture, thereby causing conflict to be renewed and persecution to be continued.

2. Intersexual encounter. Male-female encounters begin in the same way as the intrasexual encounters just discussed, the essential difference being a markedly lower level of aggression following recognition. Recognition appears to occur in the nose to nose position, inasmuch as once that contact has been made no attack follows. The male is generally the one approaching and shows much interest. The male assumes the elongate posture when approaching the female and shows a great amount of nervousness in the form of tail shivering. The female rises upright, "chits", and, if the male approaches too close, attempts to ward him off with the forelimbs. The male attempts to sniff her genital area but the threat of the female becomes too intense and he retreats. The assumption of typical agonistic postures, but with no hostile action, is similar to that seen in the African giant rat, *Cricetomys gambianus*, (Ewer, 1967). The male appears greatly interested and moves persistently closer until the female develops a tolerance. Brief and infrequent mutual grooming on the neck and head has been observed but no mountings were attempted. Following this there develops what could be referred to as a mutual tolerance or platonic relationship, during which the two animals merely rest and sleep huddled together.

Sexual behavior.--Little information regarding sexual behavior can be contributed as mating did not occur under laboratory conditions. J. Meester (pers. comm.) has knowledge of a successful mating in the laboratory, but the act was not observed nor is any history of the adults involved available. Davis (1963) reported that *O. irroratus* failed to breed in the laboratory. Pitchford and Visser (1962) and Visser (pers. comm.) stated that *O. angoniensis* bred successfully in large (3 m square) outdoor enclosures.

On a single occasion a three-week old juvenile was observed to climb onto the back of one of its siblings. It rather appressively bit at the fur of the neck and head of the youngster underneath which struggled to escape but for a moment ceased its struggles and closed its eyes. Although these animals were far from sexually mature this action could well represent a development of sexual behavior, as grooming the female about the head and neck during courtship occurs in a number of rodents.

Reproductive success was found to increase in captive pine voles, Microtus pinetorum, with length of time in captivity (Kirkpatrick and Valentine, 1970). Vlei rats have been kept in captivity for as long as six months and maintained as pairs for periods of one to six weeks during which no successful matings occurred. Kirkpatrick and Valentine (1970) suggested the following factors as contributing to nonbreeding: the presence of and disturbance by humans, change in food, restricted area of activity, and maintenance of a paired rather than colonial status. Eisenberg (1967) stated that solitary species, when forced to live in pairs in a small cage, even though compatible, do not reproduce, as a result of inhibition of the female reproductive cycle. He suggested that the failure of the female cycle is apparently the result of social contact above some minimal level, this tolerance level being exceeded by a constant pair association in intolerant and some semitolerant species. It has also been stated that less tolerant species will sometimes breed if provided with a larger space or if paired during estrous only (Eisenberg and Isaac, 1963). Donat (1933) achieved success in breeding Neotoma fuscipes only after greatly increasing the enclosure size. The same was also true for O. angoniensis (Pitchford and Visser, 1962).

Because of the shy and retiring habits of the vlei rat disturbance by humans could easily be a factor causing nonbreeding. Visser (pers. comm.) stated that the lack of any disturbance was very important for successful breeding, even in outdoor enclosures. The fact that food habits are not precisely known and the difficulty of obtaining adequate supplies of their "normal" food, as well as the use of rather small enclosures could be contributing factors, although Visser stated that his animals were fed primarily on lucerne and carrots. The maintainance of animals in colonies would certainly create difficulties owing to their antisocial character. Maintaining unbalanced sex ratios has also been considered. Visser had two males and four females in each enclosure.

In the vlei rat constant pair association in captivity would appear to create a situation which causes a breakdown of mating behavior in both sexes, and merely the effect of being in captivity itself may be enough to inhibit the estrous cycle. It is interesting to note that reproductively inactive animals (nonperforate females and nonscrotal males) when placed together show signs of becoming reproductively active by becoming perforate or scrotal. Maintaining littermates in pairs as a means of reducing social conflict has been attempted but these individuals have failed to develop reproductively. Eisenberg (1967) reported this method as ineffective in several species of typically solitary rodents.

The absence of sexual behavior and the failure to mate in the laboratory, as well as strong intrasexual aggression during encounter tests, demonstrate that O. irroratus is antisocial and tends toward adult isolation. The existence of marking behavior and the probability of territoriality, especially in dominant individuals, gives further proof of their asociality. It has been shown that the more asocial rodents have evolved complex threat and communication patterns to avoid contact except during mating (Eisenberg, 1963), and this definitely appears to be the case in the vlei rat. Mutual upright posture and sparring are methods of fighting which have evolved to avoid drawing blood, except in captivity where persecuted animals may be severely wounded. "Chitting" and tail shivering are both rather sophisticated mechanisms for threatening without physical contact, as is sand kicking in Dipodomys deserti and tail flagging in Perognathus penicillatus (Eisenberg, 1963).

Territorial Behavior.--The territory of an animal is an actually or potentially defended, static or moveable area around the individual and differs from the home range. In the vlei rat marking behavior and the habit of urinating in specific places could be means of defining a territory by odor.

An attempt was made in the laboratory to determine territoriality during tests of adult interactions. Prior to these tests the individual animals were placed in the observation chamber separated by barriers for periods varying from two to seven days. After removing the barriers a check was kept during the testing period as to the nestbox preference of each animal and its relationship to the original area occupied. It was found that the longer the animals were kept separated the greater the preference for a specific nestbox. The dominant individuals appeared to have the strongest preference for their original nestbox.

Because of a relatively high population density of O. irroratus in the study area, determination of territoriality from trapping records is rather difficult. If one considers only the very large and fully sexually mature males (usually over 160 g), there appears to be mutually exclusive areas occupied by conspecifics of similar size and sex. The data on females do not seem to be as conclusive and may depend upon their reproductive state. Trapping results show great overlap of home ranges and suggest that several individuals may use the same runways, as was found also in *Microtus californicus* (Pearson, 1960). This would mean that if an area is defended, defense affects only certain runways and more than likely only those in the close vicinity of the nest.

The occasional presence of regular defecation spots (see Elimination) is not understood in relation to territoriality unless these belong to the dominant individual of an area. The more usual habit of indiscriminate defecation and the presence of feces from animals of all sizes on top of traps raises doubts as to the use of feces in defining territories.

In areas of excellent habitat, as in certain parts of the study area, the population density of the vlei rat becomes rather high during the latter part of the breeding season. In these areas of high density it would be reasonable to assume that animals in a given area are familiar with their conspecifics and that their interactions are represented by a dominance hierarchy.

ECONOMIC IMPORTANCE

The economic importance of mammals falls into two broad categories--their value in the economy of nature and their direct importance to man.

Influence on the Environment

One obvious effect of rodents upon the physical environment is that resulting from digging in the soil. However, the vlei rat lives primarily above ground and seldom burrows. When it occupies a burrow it often utilizes abandoned ones of other animals and does little digging of its own (see Individual Behavior). What little is known from the few burrow systems found in the study area indicates that their burrows are not extensive and that their digging capabilities appear to be poor. It is doubtful, therefore, that digging in the soil by vlei rats has much or even any influence upon the physical environment.

Another activity influencing the soil is the habit of cutting, collecting, and shredding vegetation for nests and the subsequent decay of this vegetation. Also, in the process of feeding numerous unused cuttings are left lying around. These activities, as well as the production of body wastes, are relatively minor, but affect the physical environment in ways that would not normally occur if they were absent from the region.

The overall effect of vlei rats upon vegetation is very difficult to evaluate, but they are entirely dependent upon plants for food, shelter, and nests. Some of these activities could be detrimental to certain plant species if the vlei rat were highly selective. However, it appears that feeding is indiscriminate and nests are constructed of any satisfactory materials at hand.

Vlei rats influence other animals in their biotope in numerous ways, some harmful and others beneficial. They exert important effects on their community associates by providing a food supply for certain flesh-eaters, through competition for food, living space, and nest sites, and by serving as carriers of parasites and diseases.

The vlei rat has a wide range of known and potential predators, some of which appear to inflict considerable population control (see Mortality). Evidence indicates that owls are a serious predator of vlei rats. Also, a present study by myself indicates that in pine plantations in the eastern Transvaal virtually the entire diet of the serval, _Felis serval_, consists of _O. irroratus_. FitzSimons (1920) stated that if it were not for the considerable number of predators of _O. irroratus_ there would be a population irruption of them.

It is possible that the population of the striped mouse, _Rhabdomys pumilio_, may have diminished on the study grid partly through competition with the vlei rat (see Fig. 19).

The plague bacillus, _Pasteurella pestis_, has been isolated from _O. irroratus_, but it is thought that vlei rats do not play a primary role in transmission or as a reservoir of plague owing to their patchy distribution (Powell, 1925; Davis, 1964; Hallett _et al._, 1970). Davis (1953 and 1964) stated that vlei rats frequently make contact with and become secondarily infected from gerbils. The recovery of some of the same species of endo- and ectoparasites of _O. irroratus_ from other rodents and shrews in the study area indicates that some species of the parasites are not host specific. Distribution of parasites to other species occur either directly between animals or indirectly through the mutual use of runways or temporary use of vlei rat nests.

Relationships With Man

Several authors have urged that more work in South Africa be directed toward the biology of small mammals, especially rodents, as they have become one of man's greatest adversaries (Meester, 1954; Dorst, 1965; Du Toit, 1965). The many interrelationships between man and the vlei rat are discussed below in the following categories: Competition with man; Competition with domestic animals; As a source of food; As a laboratory animal; and Public health implications.

Competition with man.--The most important aspect of this competition includes the damage to and destruction of agricultural and forest products. Shortridge (1934) stated that the vlei rat does not appear to inflict much damage to any kind of cultivation, but added that they are attracted to crops of lucerne (alfalfa) where damage can occur.

At two separate localities *O. irroratus* has been found to have inflicted severe damage to trees in abandoned fruit orchards (P.J. Geldenhuys, pers. comm.). One case involved fig trees adjacent to a recently burned field. These trees were approximately 3 to 4 m in height and the trunks 20 cm in diameter at the base. The trees had been killed by girdling as a consequence of the feeding activities of the vlei rats. Virtually all of the bark through the cambial layer had been eaten, and numerous branches had been severed, some 4 cm in diameter. This damage was probably due to the destruction of their normal habitat in the adjacent field as a result of fire. The other case involved an apple orchard where vlei rats had climbed the trees and were observed eating bark during the winter months. Both cases, therefore, indicate that damage is usually inflicted during periods of below normal food supply.

Otomys tropicalis has been described as not normally harmful in agricultural areas, but has been found occasionally to eat young cereals (sorghum and wheat), stems and leaves of beans and sweet potatoes, young banana leaves, and the bark of young eucalyptus and cypress trees (Dieterlen, 1968). Smithers (1971) stated that *O. angoniensis* in Rhodesia occasionally ate grain put out as food for ducks.

In South Africa considerable damage is inflicted ~~to~~ on young trees in the pine plantations by *O. irroratus* and the striped mouse (Davis, 1942 and 1966; MacKellar, 1952; Schulz, 1953 and 1962; pers. obs.). Both species of rodents have been incriminated, but it is thought that the vlei rat is responsible for most of the damage. Schulz (1953 and 1962) stated that young pine trees, usually between the ages of one and three years, are gnawed up to 15 cm above ground level, and occasionally stems and lateral branches up to a height of one meter above ground level are damaged. There appear to be distinct types of damage: one where the bark is gnawed off the main stem; one where lateral branches are cut through; and one where thin stems are severed. Soft bark is usually preferred, but sometimes the outer corky layers are rejected. In most cases, vlei rats show a preference for the cambial layer. Pine needles are seldom eaten. The chances of completely girdled trees surviving are small. Partially girdled trees frequently recover but malformed stems or trunks generally result. In some instances where the main stem has been completely severed new shoots arise, but the effect is the production of a bush rather than a tree.

During the past 50 years vast areas of grassveld have been converted into the development of forest plantations. These grassveld areas have been allowed to develop unchecked to a lushness seldom ever attained when grazing, cultivation, and veld fires were the norm. The vlei rat and the striped mouse, for whom adequate cover is a prime necessity, have found their habitat vastly increased (Davis, 1942). From 1920 to 1950 the highest incidence of damage occurred in pine stands in low-lying areas adjacent to streams and vleis. In those areas it was not unusual to find 100 per cent damage (MacKellar, 1952). Owing to increased available habitat and increasing rodent populations damage spread beyond the fringes of the low-lying areas and into a markedly wider area to include steep slopes, ridges, and hilltops.

Damage originally seemed to take place only during July and August, but it has started appearing progressively earlier and now occasionally takes place as early as March. Damage generally ceases following the first rains in either September or October when preferred food species regenerate. M. Sommerlatte (pers. comm.), in a recent study, found damage to occur in the following months: June-33 per cent, July-35, August-24, and September-6.

About five to seven years after planting the trees automatically rid a plantation of grass-living rodents by suppressing the ground cover vegetation by the formation of a canopy. Davis (1942) suggested that control measures should attempt somewhat the same thing by removing the grass cover. By this measure these rodents would not be afforded protection from weather and predators, thus effectively limiting the population.

Schulz (1953) studied the effectiveness of various poison baits in the control of rodent populations. He found warfarin mixed with maize and lucerne meal effective in reducing populations, but that treated areas were quickly repopulated as a result of a reinvasion from fringe populations. Geldenhuys (1960) repeated the tests with a dry maize meal-warfarin mixture and again found warfarin to be effective in controlling both O. irroratus and R. pumilio. Although warfarin has been in use in pine plantations of the eastern Transvaal for the past 20 years, damage by rodents continues to be a problem. M. Sommerlatte (pers. comm.) found, upon examination of 7 200 trees in 72 random plots between 1970 and 1972, that 20,4 per cent of the trees during the first year after planting suffered damage. The maximum damage in any plot amounted to 85 per cent. During the second and third years after planting damage amounted to 13,0 and 3,5 per cent respectively. The average damage during the first three years after planting was 12,3 per cent. This compares closely with the 15,7 per cent damage that Schulz (1953) reported 20 years ago when the poisoning campaign was begun. This evidence leaves considerable doubt as to the effectiveness of this campaign.

At present young trees (9 to 12 months old) are generally planted in mature grassveld with little or no prior clearing or preparation. The small area cleared of vegetation around the base of the trees at planting is only 1 m in diameter. For various reasons clearing of the vegetation from the entire area to be planted is often unfeasible. It would be interesting to determine the effectiveness of cleared areas of various sizes around the bases of the trees. Herbicides, not effective on pines, could possibly be used to maintain clear areas around young trees. Eadie (1953) found the creation of vegetation-free areas surrounding tree bases to be effective in controlling _Microtus_ damage in orchards.

Inasmuch as owls have been found to be an effective predator of vlei rats, and the diet of the serval has been found to consist almost entirely of vlei rats in an area of pine plantations in the eastern Transvaal, these animals should be strictly protected.

Competition with domestic animals.--Wild mammals also affect man's interests in that they are frequently in competition with his domestic animals for forage and water. The older and coarser rushes and sedges of vleis are generally unpalatable to domestic ruminants, but the young tender shoots of vlei herbage are highly desired by both domestic ruminants and vlei rats. It is doubtful, though, whether the competition between ruminants and vlei rats for forage is extensive.

As a source of food.--Although Shortridge (1934) and Dieterlen (1968) gave evidence that vlei rats are occasionally eaten by the indigenous people, it is doubtful that they would, primarily due to their size, play a very prominent role as a source of protein.

As a laboratory animal.--The following diseases and conditions have been studied in many African rodents (Davis, 1963): plague, bilharziasis, cancer, poliomyelitis, histoplasmosis, leishmaniasis, several viral and rickettsial diseases, dental caries and periodontal diseases, and asbestiosis. Although various ~~diseases~~ pathogens have been isolated from vlei rats, the difficulties of maintaining and breeding ~~them~~ these rats in captivity limit their usefulness as a laboratory animal.

Public health implications.--Rodents are often involved as reservoirs or transmitters of diseases and parasites that affect the health of man and sometimes man's domestic animals.

The plague bacillus, *Pasteurella pestis*, has been isolated from *O. irroratus*, but it is not thought to play a primary role as a plague reservoir nor in transmission. Plague has also been isolated from *O. unisulcatus* in South Africa (Hallett *et al.*, 1970) and from *O. tropicalis* (Pollitzer, 1954) and *O. angoniensis* (Davis *et al.*, 1968) in East Africa. Roberts (1935) stated that members of the Otomyinae die off during epizootics of plague. Davis (1942) reported two large die offs of vlei rats but plague, although suspected, was not demonstrated.

The organism causing tick-bite fever or tick typhus rickettsia, *Rickettsia conorii*, has been isolated from *O. irroratus* (Gear, 1954). It has also been isolated from *O. angoniensis* and *O. tropicalis* in Kenya, where they have been defined as reservoir hosts (Heisch, 1957; Heisch *et al.*, 1957 and 1962; Heisch and Harvey, 1959; Timms *et al.*, 1959). Heisch (1957) also listed the following rickettsias from vlei rats in Kenya: rickettsial pox (*Rickettsia akari*), Q fever (*Rickettsia burnetii*), and murine or flea-borne typhus (*Rickettsia typhi*). Heisch and Harvey (1959) listed epidemic louse-borne typhus, *Rickettsia prowazekii*, from *O. angoniensis* in Kenya.

Bluetongue virus, which seriously affects sheep in South Africa, has been isolated from *O. irroratus*, but proof is lacking that this species plays a role as a reservoir (Du Toit, 1955).

McIntosh (1961) tested a few specimens of *O. irroratus* for arthropod-borne viruses but all proved negative. Leptospirosis is another possible disease of *O. irroratus* that has not been isolated to date.

Some interesting diseases that have been isolated from species of *Otomys* other than *O. irroratus* are as follows: bilharziasis (*Schistosoma haematobium*, *S. mansoni*, and *S. mattheei*) from

O. angoniensis (Pitchford, 1959; Pitchford and Visser, 1960 and 1962; Nelson _et al._, 1962a; Gear _et al._, 1966); two species of filariasis from _O. angoniensis_ in Kenya (Nelson _et al._, 1962b); and the Rift Valley fever virus from _O. unisulcatus_ in South Africa (Gear _et al._, 1955).

Internal and external parasites were saved from specimens of _O. irroratus_, removed from the study area, while they were being examined in the laboratory. Internal and external parasites recorded from _O. irroratus_ in the literature and from those examined from the study area (*), along with infestation rates of those from the study area are listed below.

1. Nematodes. Nematodes were the most common internal parasites found in the vlei rat from the study area. Three species from animals from the study area and another species previously recorded in the literature are as follows:

Family Physalopteridae
    Physaloptera africana
Family Trichostrongylidae
    *_Longistriata capensis_ (recorded from 30 of 44 specimens; 68,2 per cent)
    *_Paralibyostrongylus_ sp. (27 of 42; 64,3)
Family Trichuridae
    *_Capillaria hepatica_ (33 of 46; 71,7)

The three species were recovered from different parasitopes--_L. capensis_ from the duodenum, _Paralibyostrongylus_ from the stomach, and _C. hepatica_ from the liver. The _Paralibyostrongylus_ appears to represent a new undescribed species.

Capillaria hepatica was recorded from 29 of 36 adult specimens (80,6 per cent) and from 4 of 10 subadults (40,0 per cent). Four out of five vlei rats with a heavy infestation were large adults; the six negative subadults were the youngest individuals. Although no juveniles were examined it appears that the infestation rate with _C. hepatica_ increases with age.

Longistriata capensis was also recovered from _O. angoniensis_ from the study area.

2. Trematodes. About 30 specimens of the sheep liver fluke, _Fasciola hepatica_, were recovered from a single vlei rat from the

study area. This record is most interesting as it not only represents the first trematode recorded from _O. irroratus_, but is also the first record of _F. hepatica_ from a rodent in Africa. The only known records of _F. hepatica_ from rodents are from the United States and Russia.

3. Cestodes. Five species of tapeworms have previously been recorded from _O. irroratus_ in South Africa (Collins, 1972). Only one species was recovered from vlei rats from the study area and it was uncommon. The following cestodes are those listed from _O. irroratus_ by Collins (1972):

Family Cyclophilidae
    *_Paranoplocephala omphalodes_ (7 of 44; 15,9)
    P. otomyos
    Inermicapsifer congolensis
    I. madagascariensis
Family Davaineidae
    Raillietina thryonomysi

The tapeworm, _P. omphalodes_, was also recovered from _O. angoniensis_ from the study area.

Ortlepp (1961) reported three cases of human infection in Southern Africa with a common tapeworm of rodents, _I. madagascariensis_. It is interesting to note that outside Africa this tapeworm has adapted itself exclusively to man and has never been found in rodents (Ortlepp, 1961).

Ticks. Only two species of ticks were recovered from vlei rats from the study area. The following ticks are listed in the literature from _O. irroratus_ (Theiler, 1962), although only two of these species were taken from specimens from the study area:

Family Argasidae
    Ornithodoros zumpti
Family Ixodidae
    Ixodes sp.
    I. alluaudi
    Haemaphysalis leachi leachi
    H. l. muhsami
    *_H._ sp. (2 of 35; 5,7)

Rhipicephalus appendiculatus
*R. capensis (13 of 35; 37,2)
R. sanguineus
R. simus

The species of Haemaphysalis is as yet unidentified. Rhipicephalus capensis involves a complex of species which at present is undefined (J. Walker, pers. comm.). Haemaphysalis leachi, R. appendiculatus, and R. simus have been incriminated as transmitters of tick-bite fever (Gear, 1954).

The following ticks were recovered from one specimen of O. angoniensis from the study area: Ixodes sp., Haemaphysalis sp., and R. capensis.

5. Mites and chiggers. The mites and chiggers listed in the literature from O. irroratus in Southern Africa (Zumpt, 1961) and those recovered from vlei rats in the study area are as follows:

Family Laelaptidae
  Laelaps giganteus
  L. muricola
  *L. paraspinosis (=L. parvulus) (2 of 35; 5,7)
  *L. transvaalensis (15 of 35; 42,8)
  *Androlaelaps fahrenholzi (=Haemolaelaps glasgowi) (6 of 35; 17,1)
  Haemolaelaps labuschagnei
  H. murinus
  H. taterae
Family Myobiidae
  Myobia otomyia
  *unidentified
Family Trombiculidae
  Euschoengastia africana
  E. otomyia
  *unidentified (14 of 35; 70,0)
Family Listrophoridae
  Listrophoroides womersleyi
  *unidentified

The fur mites of the families Myobiidae and Listrophoridae and the chiggers of the family Trombiculidae, as yet, have not been identified.

In the study grid chiggers (larval trombiculids) were much more abundant on _O. angoniensis_ and on _O. irroratus_ from the dryer part of the grid. The lower part of the grid may be too wet for the survival of the nymphal and adult stages, therefore their prevalence on individuals occurring on the dryer part. Chiggers were also noted to be present only during certain seasons. Records indicate that they were recovered during the months December through July.

The following identifiable mites were recovered from _O. angoniensis_ from the study area: _L. transvaalensis_ and _Androlaelaps dasymys_.

6. Lice. Only one species of louse has been recorded in the literature from _O. irroratus_ and which was also found on vlei rats in the study area (Johnson, 1960; J.A. Ledger, pers. comm.):

Family Hoplopleuridae

*_Polyplax otomydis_ (21 of 35; 60,0)

Lice were the most abundant ectoparasite recovered from _O. irroratus_. In the study area _P. otomydis_ was also recovered from _O. angoniensis_. Johnson (1960) and J. Ledger (pers. comm.) listed _P. otomydis_ from the following species of Otomyinae: _O. angoniensis_, _O. denti_, _O. irroratus_, _O. tropicalis_, and _Parotomys brantsi_. The record from _P. brantsi_ is doubtful and is probably referable to _Polyplax myotomydis_ recorded from _P. brantsi_ and _O. unisulcatus_, which both occur in an arid habitat.

7. Fleas. Only three species of fleas were recovered from _O. irroratus_ from the study area but a total of 22 species has been recorded in the literature (De Meillon _et al._, 1961; Zumpt, 1966):

Family Pulicidae

Echidnophaga gallinacea
Pulex irritans
Xenopsylla cheopis
X. eridos
X. bransiliensis
X. hirsuta

Family Hystrichopsyllidae

Ctenophthalmus calceatus
Dinopsyllus abaris
*_D. ellobius_ (10 of 35; 28,6)

D. lypusus

D. tenax

Listropsylla agrippinae

L. chelura

*L. fouriei (4 of 35; 11,4)

L. prominens

Family Leptopsyllidae

Leptopsylla segnis

Family Chimaeropsyllidae

Hypsophthalmus montivagans

H. temporis

Epirimia aganippes

Chiastopsylla roseinnesi

*C. rossi (6 of 35; 17,1)

C. carus

Dinopsyllus ellobius was the only species recorded from O. angoniensis in the study area.

Several of the above fleas are important in transmission of plague. Of those fleas recovered from O. irroratus in the study area L. fouriei is of no importance as a plague vector. Plague has been isolated from D. ellobius and C. rossi, but they are not considered important in the perpetuation of plague (De Meillon et al., 1961).

Information recorded by De Meillon et al. (1961) regarding the hosts and distribution of the above flea species indicates that the following fleas should also have been obtained from O. irroratus from the study area but were not: C. calceatus, D. lypusus, and L. prominens.

SUMMARY AND CONCLUSIONS

This project was undertaken to study the ecology and life history of the vlei rat, *O. irroratus*, in a population on the Van Riebeeck Nature Reserve near Pretoria. Two main procedures were used to collect material and basic information. First, a permanent live-trapping grid was established where 333 animals were captured, marked, released, and recaptured. Second, snap-trapping and live-trapping were conducted elsewhere in the study area for supplementary material. Because *O. angoniensis*, a sibling species of *O. irroratus*, also occurred in the study area and grid, it became necessary to be able to differentiate between these two species in morphology and habitat preferences.

Otomys irroratus is often confused taxonomically with *O. angoniensis*. In this connection it was found that ~~the length of~~ the hind foot of *O. irroratus* is longer (29-34 mm) than that of *O. angoniensis* (25-28 mm). *Otomys angoniensis* has a ring of orange hair around its eye which is absent in *O. irroratus*. The number of laminae on M^3 differs between the two, *O. irroratus* usually having six laminae and *O. angoniensis* usually seven. This character, however, was not consistent and varied from the norm in 4,2 per cent of the 143 examined *O. irroratus* and 6,7 per cent of the 15 *O. angoniensis*. The baculum of the two species was significantly different in both shape and size. The base of the baculum of *O. irroratus*, in overall shape is obovate while that of *O. angoniensis* is spatulate. The detailed structure of the base also differs slightly in ventral view. Further, the baculum of *O. irroratus* is, in all respects, larger than that of *O. angoniensis*.

Age and seasonal differences were examined. Molar toothwear categories were used in order to determine the approximate age of *O. irroratus*. Each age class was found to be significantly or highly significantly different from the next age class for all cranial measurements with the exception of interorbital breadth, braincase breadth, and rostral breadth. Seasonal variation was not as clearly discernible as age variation, but analysis of monthly body weights of adult male *O. irroratus* demonstrated a sharp decline in weight during August and September, primarily the result of the poor quality and quantity of food then available.

Otomys irroratus occurs primarily in the grassland subregion of the Southern Savanna biotic zone, whereas *O. angoniensis* occurs primarily in the woodland subregion of the same biotic zone. As a result of the occurrence of both species in the study grid it was possible to determine that their ecological niches were nearly allopatric with only a small area of overlap. The distribution of *O. irroratus* on the grid was found to have a highly significant positive association with the following plant species: *Mariscus congestus*, *Eleocharis dregeana*, *Berula erecta*, *Agrostis lachnantha*, *Juncus punctorius*, *Pennisetum thunbergii*, and *Cirsium vulgare*. These plant species, in turn, had a highly significant negative association with the distribution of *O. angoniensis*.

The population size of *O. irroratus* on the study grid demonstrated a low in September, following the winter nonbreeding season and preceding the appearance of the first young of the season. The peak in the population size occurred in May, at the end of the long, nine-month breeding season. The population numbers during the study period fluctuated from one year to the next. Above average rainfall contributed significantly to an increase in numbers, and excessive rainfall, resulting in ~~a~~ flooding of the study grid, caused a sudden decline in numbers.

The ratio of juveniles, subadults, and adults fluctuated in the study grid according to season and, more specifically, in respect to the period when the young were born. Juveniles were absent from July to September, the period when no young were born. Juveniles were most abundant shortly after the onset of breeding (October-November) and at the end of the breeding season (May). Subadults were most numerous in June and July with the maturation of the peak number of juveniles in May. The percentage of adults in the population ranged from a low in June, when there was an increase in the number of juveniles and subadults, to a high in September, prior to the appearance of any new young and with the maturation of the March-August subadults to adults.

The sex ratio of the 333 *O. irroratus* trapped on the study grid did not depart significantly from 1:1. Males comprised 49,5 per cent of the total and females 50,5 per cent.

Since it was impossible to separate loss due to emigration from loss due to mortality on the study grid the data are represented as a combined rate of disappearance. After one month from first capture 41 per cent of the individuals concerned had disappeared. Such a high rate of loss during the first month indicates that a large number of transients and individuals dispersing from their birth site were involved. Excluding the high first month rate of disappearance the overall rate of disappearance averaged 3,1 per cent per month. The rate of disappearance was at its greatest between August and September, the result of the poor quality and quantity of food and cover at that time. This suggests a high mortality rate during August and September.

The longest-lived individual found on the study grid was 22 months of age when last captured. It is estimated from that individual and other information that the approximate, maximum natural longevity of *O. irroratus* is two years.

As mentioned above, one of the most important mortality factors for *O. irroratus*, on the study grid, was the inundation of its habitat by flood waters. On two occasions, within a period of two and a half years, floods considerably reduced the population and upset the social structure enough to significantly interrupt breeding.

Another factor that generally plays a primary and usually one of the most obvious roles in the mortality of rodents is predation. The predation of vlei rats by barn and grass owls was examined in detail and ~~they~~ these owls were found to be their most prominent predator. Reports in the literature give full support to this view. A study of the food habits of the serval, *Felis serval*, at a locality in the eastern Transvaal indicates that throughout the year the food of this species consists almost entirely of *O. irroratus*. Vlei rats, therefore, are a common prey of several predators. No mammalian predators were, however, identified in the study area.

Recapture data from the study grid revealed information on movements. Emigration was over relatively short distances and occurred in both directions, toward and away from the grid. The mean trap-revealed home range size of 40 *O. irroratus* was calculated to be 1 443 m^2 with variation from 675 to 3 038 m^2. The home range size of males averaged 1 730 m^2 and was highly significantly different ($P<0,01$) from that of females (1 252 m^2). The home range size in

October was highly significantly greater than during June, possibly a result of a suppression of activity in June by the cold winter temperatures. It was also revealed that home range size decreased slightly, although not significantly (P>0,10), when the population size doubled. Despite ~~the~~ flooding of the grid in January 1972, it was found that 12 of the 18 (66,7 per cent) recaptured *O. irroratus* in May 1972 had returned to their previous home ranges. Territoriality was difficult to determine from trapping results but there were some indications that territorial behavior existed in the larger males.

Various aspects of the reproductive capacity of *O. irroratus* were examined. Litter size varied from one to four and averaged 2,33. Litter size is small because the young are born precocial and large in size; the mother, therefore, is unable to accomodate a large number of young. The gestation period is known to be at least 35 days, but in all probability is 40 days or longer. The females reach sexual maturity around nine to 10 weeks of age and the males around 13 weeks of age. The breeding season was continuous for nine months, from early August to late April or early May. Despite the small litter size and long gestation period, the reproductive potential of *O. irroratus* appears to be quite high owing to their long breeding season, longevity, and precocial birth and rapid development of the young.

The young of *O. irroratus* are born in a precocial state with the head and body well-furred, eyes and ears sometimes functional, incisors erupted, ambulatory, and with the toes free and clawed. With the incisors erupted they are able to cling fast to the nipple of the mother. Solid food was taken by the second day after birth but did not become a regular part of the diet until day six or seven. Weaning was nearly complete by day 13. The young grew rapidly during the first 10 weeks of life, gaining an average of 1,29 g per day in weight. Behavioral development also proceeded rapidly with most adult behavior patterns becoming manifest by two weeks of age.

Activity studies in the field and laboratory revealed that *O. irroratus*, although active day and night, demonstrated a crepuscular activity pattern. This crepuscular pattern was maintained throughout the year, but during cold winter days activity was concentrated more during the daylight hours.

Few of the individual behavior patterns of *O. irroratus* differ from those of other rodents, especially quadrupedal species, differences being primarily related to environmental conditions. The vlei rat is shy and retiring in captivity. One interesting point is that they are not easily captured with snap-traps. It is suggested that live-traps be used to capture O. irroratus, even for removal trapping.

Nipple-clinging is a prominent feature of young vlei rats during the first two weeks of life. The principal adaptive value of nipple-clinging is the reduction of litter losses through predation. This would be especially true in an animal using an open, unprotected nest such as O. irroratus. The rodents reported to use nipple-clinging have been found to have small litters. Most of these rodents also produce young that experience a long period of dependence and have a high rate of survival. In that case the survival rate of O. irroratus young should be very great, as the young are not only nipple-clingers but are few in number and become independent quite early in life.

The absence of sexual behavior and the failure to mate in the laboratory, as well as strong intrasexual aggression during encounter tests, demonstrate that O. irroratus is antisocial and tends toward adult isolation. The existence of marking behavior and the probability of territoriality, especially in dominant individuals, give further proof of their asociality. It has been shown that the more asocial rodents have evolved complex threat and communication patterns to avoid contact except during mating, and this definitely appears to be the case in the vlei rat. Mutual upright posture and sparring are methods of fighting which have evolved to avoid drawing blood, except in captivity where persecuted animals may be severely wounded. "Chitting" and tail shivering are both rather sophisticated mechanisms of threatening without physical contact.

In areas of optimal habitat, as in certain parts of the study area, the population density of the vlei rat becomes rather high during the latter part of the breeding season. In these areas of high density it would be reasonable to assume that animals in a given area are familiar with their conspecifics. It can thus be concluded from their social habits, marking behavior, and considerable overlap of home ranges that their interactions with conspecifics in nature are represented by a dominance hierarchy.

The influence of O. irroratus upon the environment appears to be slight. However, the vlei rat does serve as a common prey item for a number of predators. Several species of both endo- and ectoparasites that could be of public health importance to man were recovered from

O. irroratus in the study area. One very interesting record from *O. irroratus* was the first recovery of the trematode *Fasciola hepatica* from a rodent in Africa.

Although considerable variation can be found in the ecology and life history of rodents, *O. irroratus* differs significantly in only a few general patterns of ecology and life history from many other rodents. However, notable exceptions involve the precocial birth and rapid development of the young and the presence of incisors at birth, enabling the young to cling to the nipple of the mother. Despite small litter size and long gestation period, the above exceptions, combined with the long breeding season and ~~longevity~~ life expectancy, give the vlei rat an exceedingly good reproductive potential which is not at first apparent.

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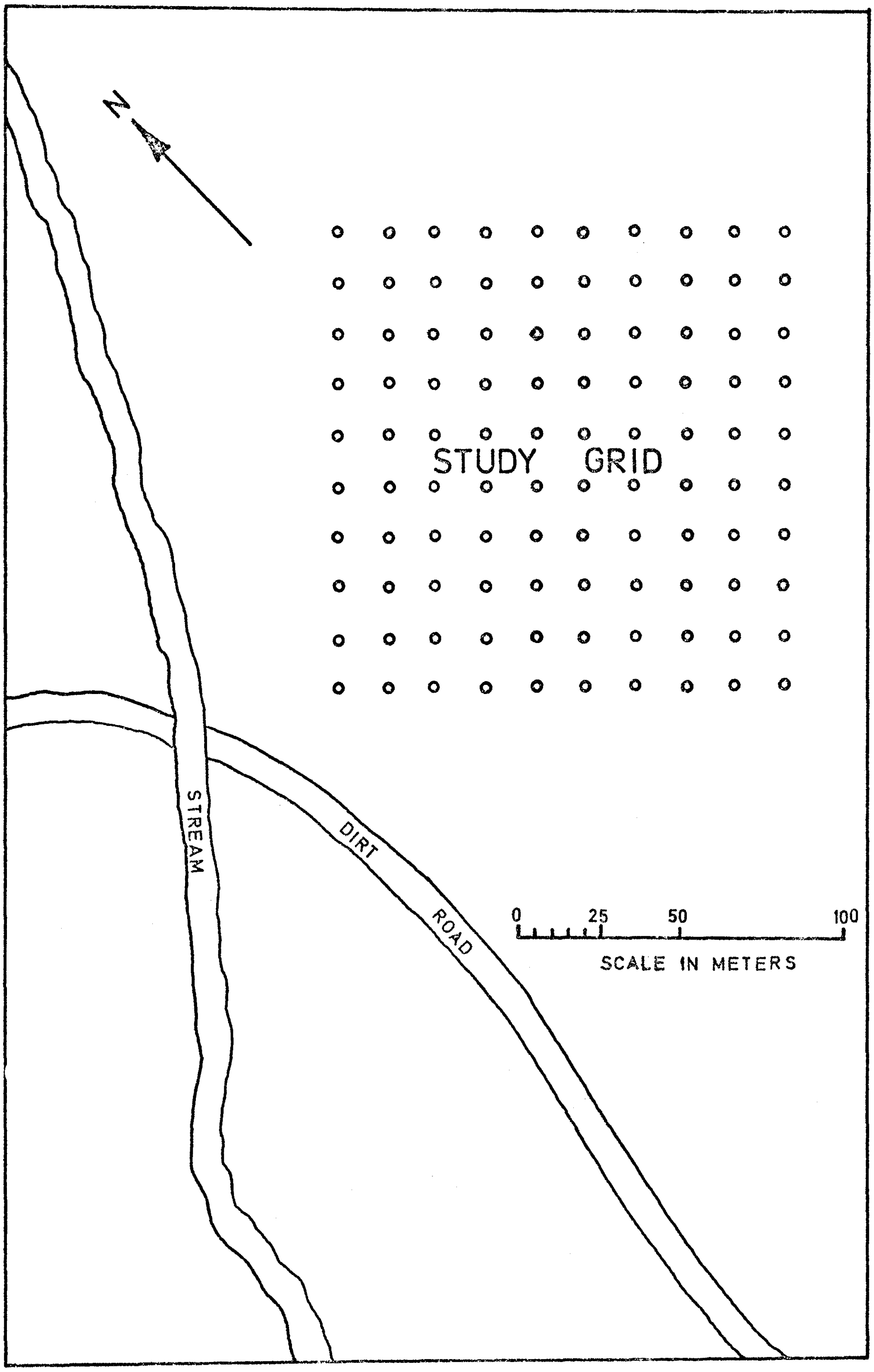


Fig. 1. Location of the live-trapping study grid in relation to physical features in the near vicinity.

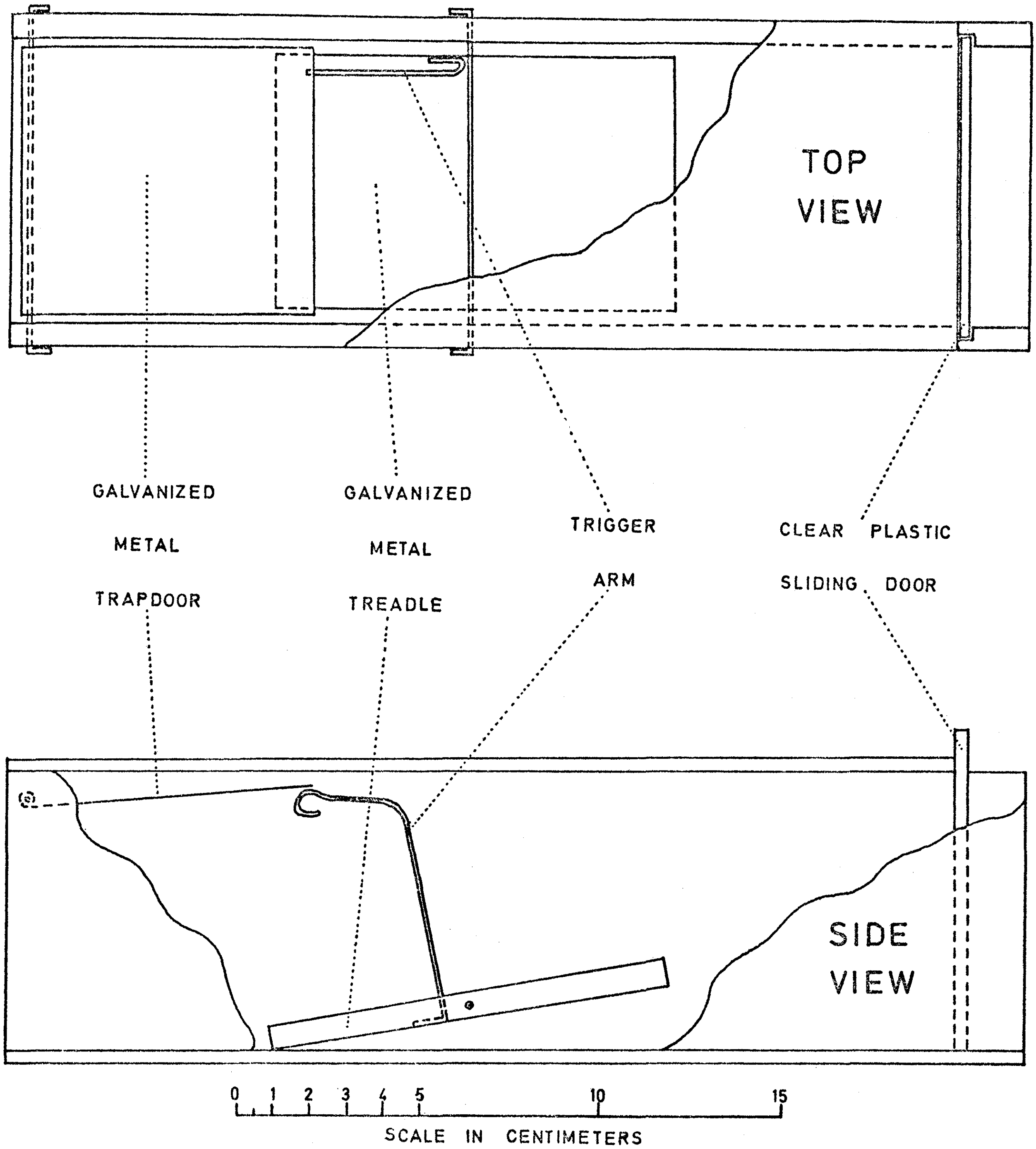
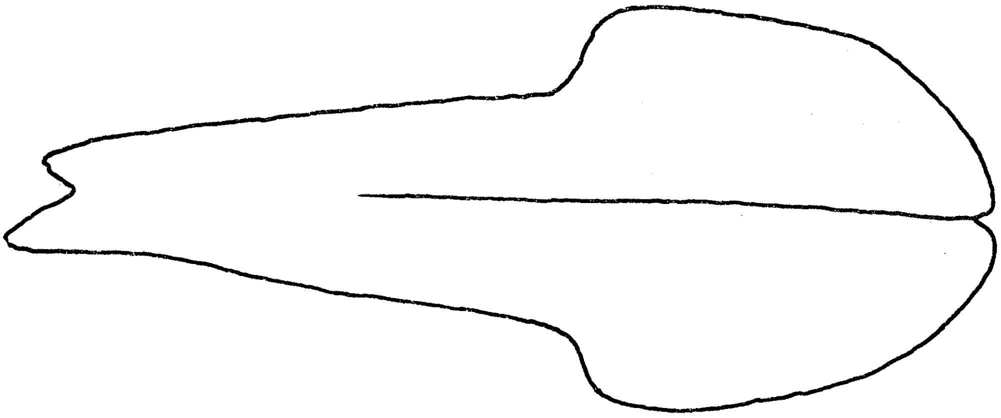
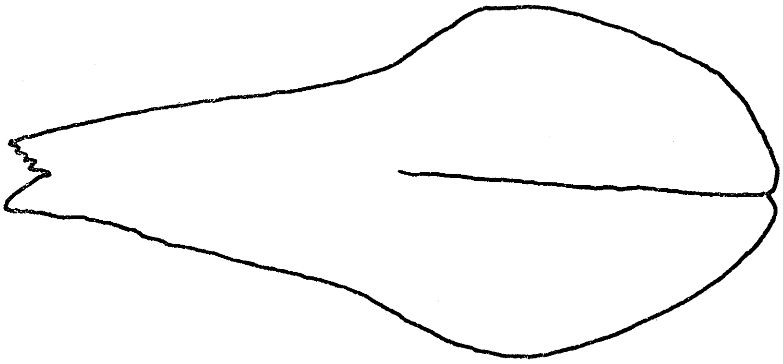


Fig. 2. Cutaway scale drawing (top and side views) of the primary live-trap used. Overall measurements are: length 28 cm, width 8,9 cm, and height 8,3 cm. Sides are made of 6 mm tempered hardboard (Masonite), top and bottom of 3 mm tempered hardboard.

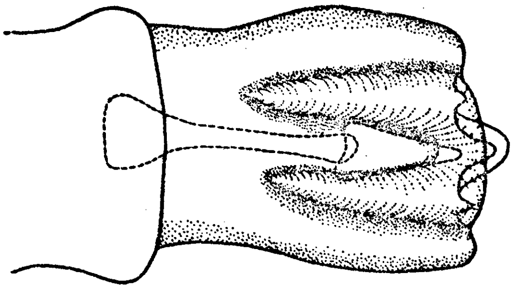


Otomys irroratus

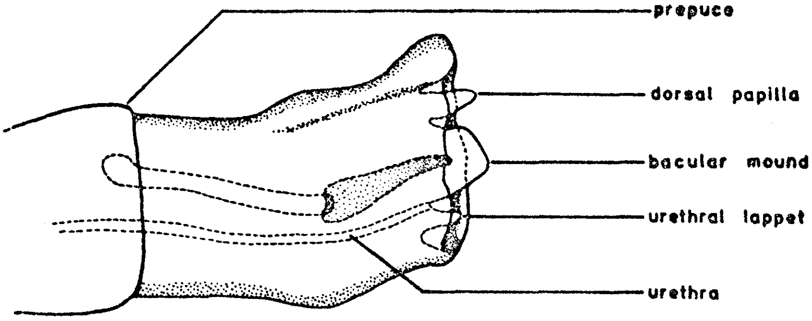


Otomys angoniensis

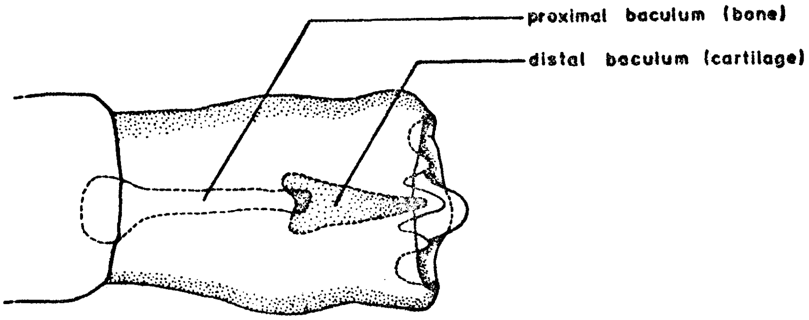
Fig. 3. Comparison of nasal bone shape in *O. irroratus* and *O. angoniensis*.



DORSAL VIEW



LATERAL VIEW



VENTRAL VIEW

Fig. 4. Phallus of *O. irroratus*.

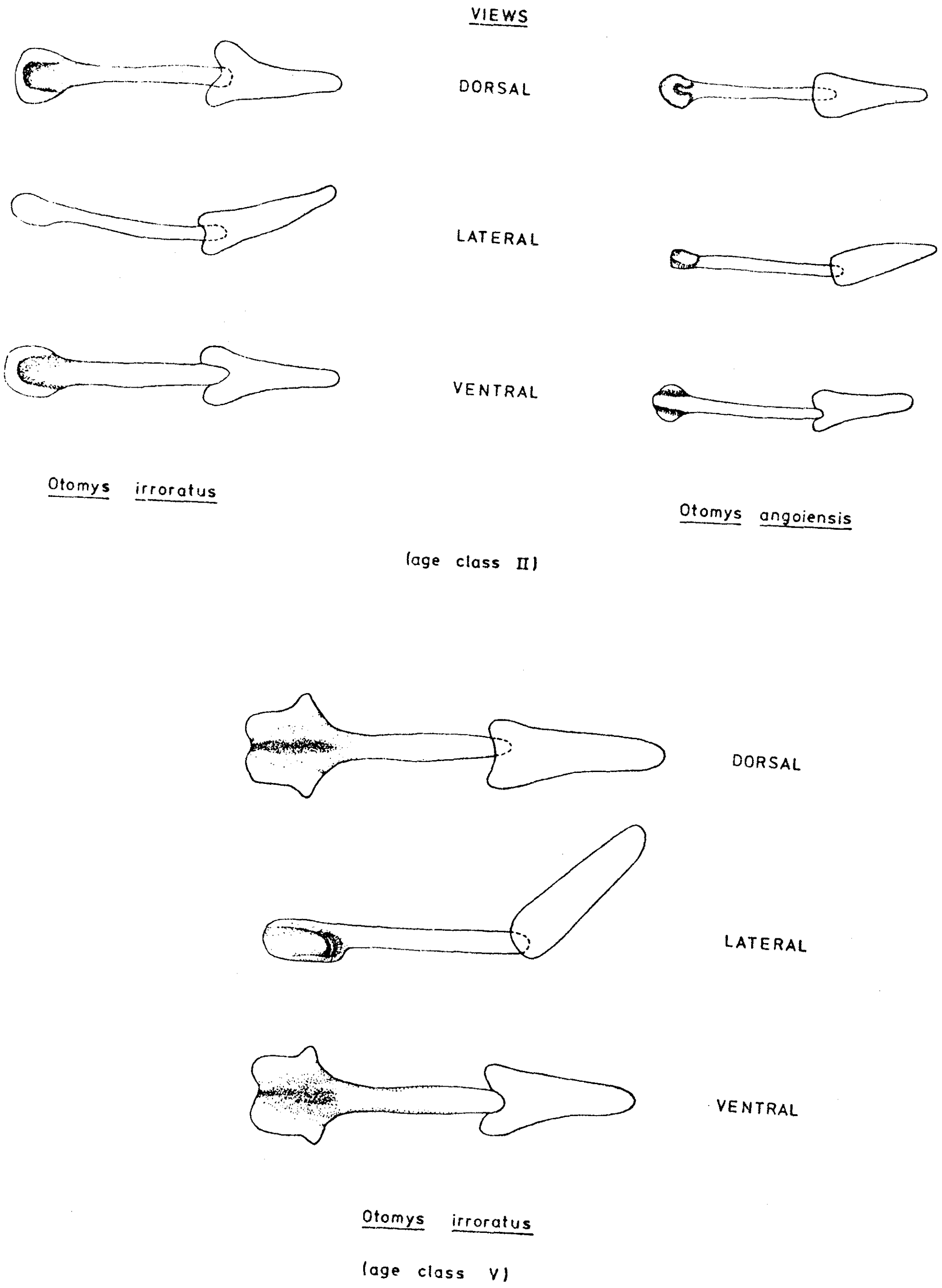


Fig. 5. The bacula of *O. irroratus* and *O. angoniensis*.

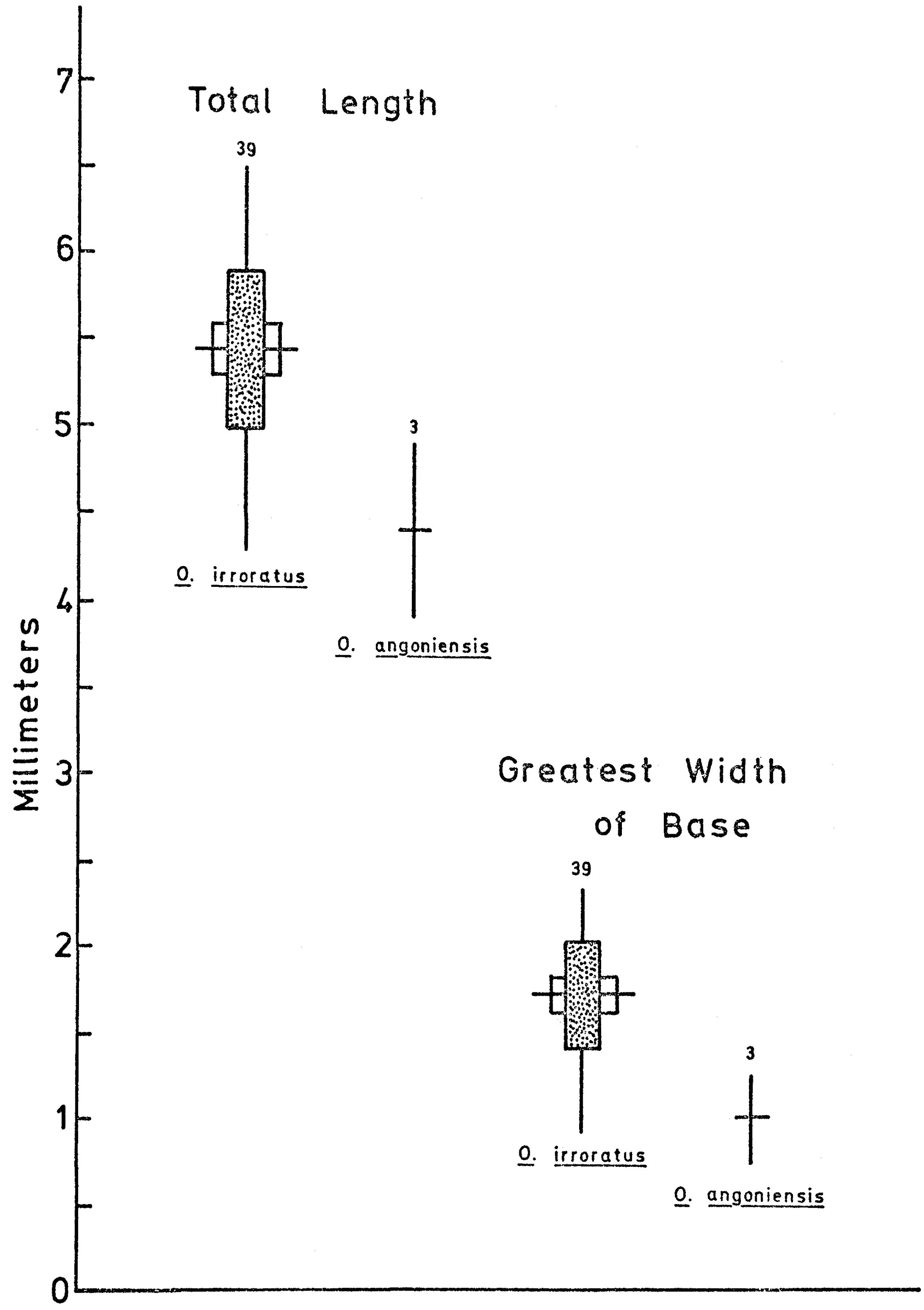


Fig. 6. Statistical analysis and comparison of two selected measurements (greatest length and greatest width of base) of the proximal portion of the baculum in O. irroratus and O. angoniensis. The vertical line indicates the total variation of the sample; the shaded bar, one standard deviation on either side of the mean; the hollow rectangle, twice the standard error on either side of the mean; the crossbar, the mean; and the number above each sample, the sample size.

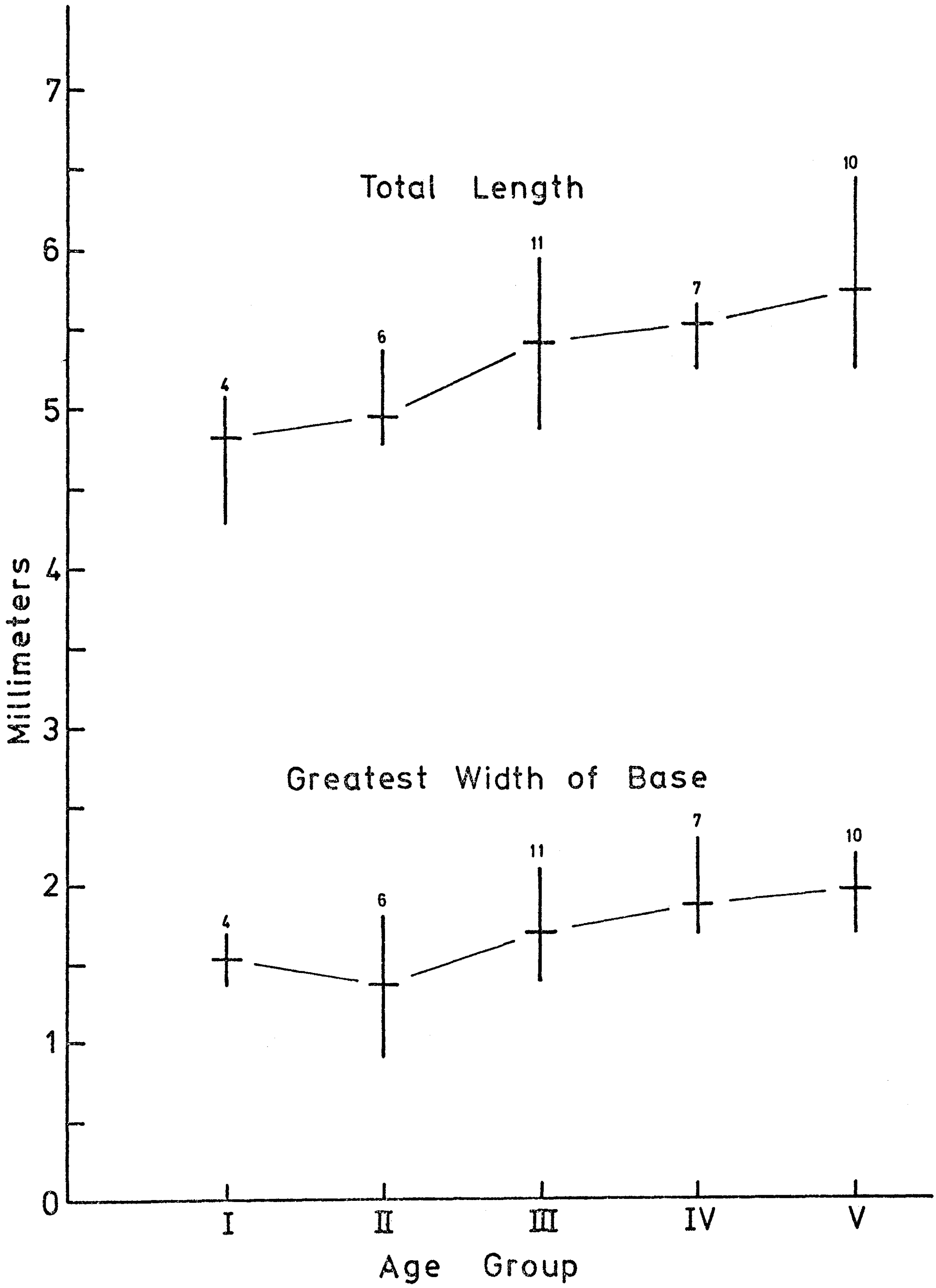


Fig. 7. Variation with age of two selected measurements of the baculum in *O. irroratus*. The vertical line indicates the total variation of the sample; the crossbar, the mean; and the number above each vertical line, the sample size.

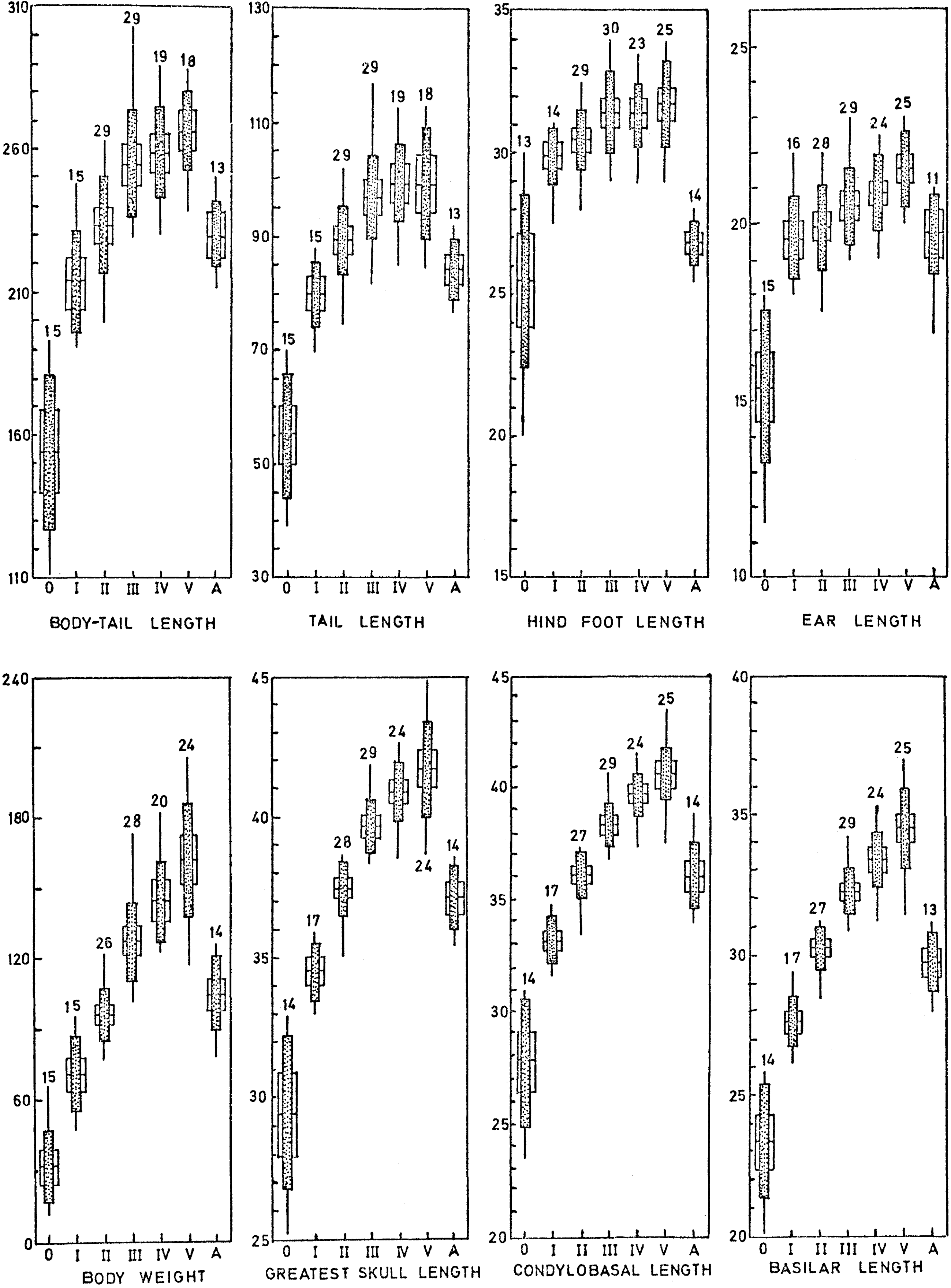


Fig. 8. Statistical analysis of weight (in g) and four external and 11 cranial measurements (in mm) of 143 *O. irroratus* representing six age classes (0-V) and 15 *O. angoniensis* (A). For further explanation see the following page (Fig. 8 continued).

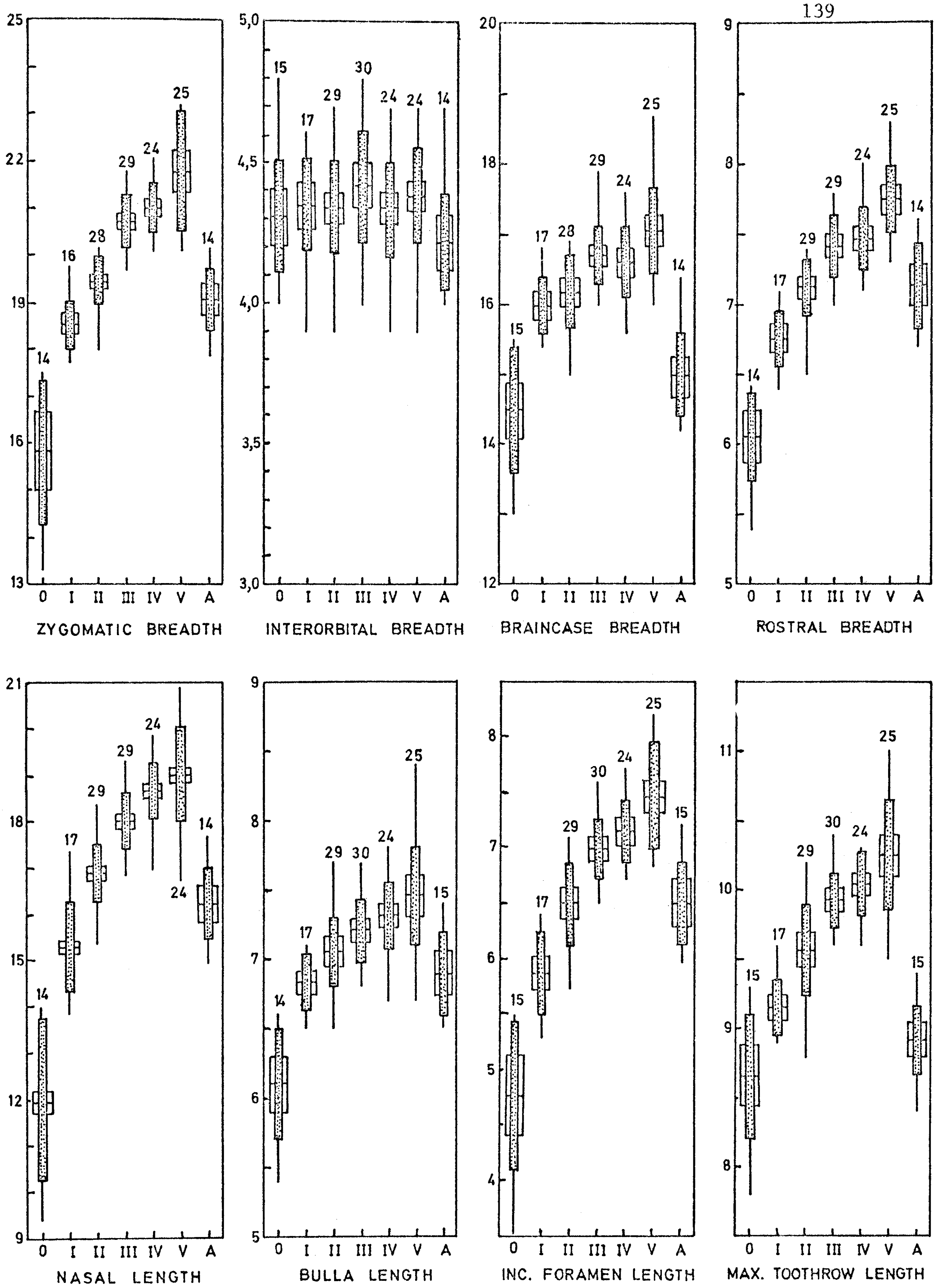


Fig. 8 (continued). The vertical line indicates the total variation of the sample; the shaded bar, one standard deviation on either side of the mean; the hollow rectangle, twice the standard error on either side of the mean; and the crossbar, the mean. Sample size is indicated directly above or below each sample.

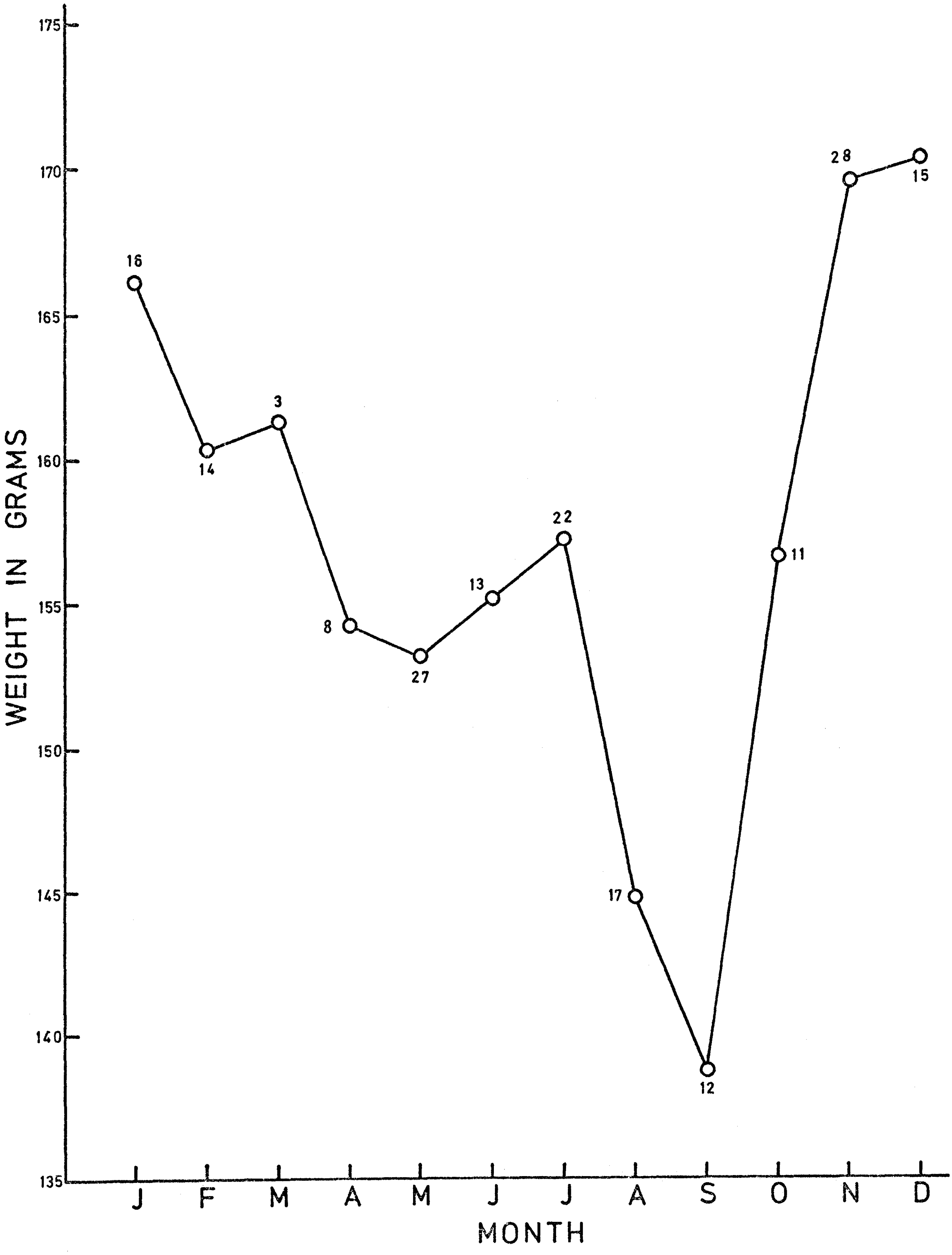


Fig. 9. Monthly fluctuation of the mean gross weight of adult males on the study grid. The numbers indicate sample size.

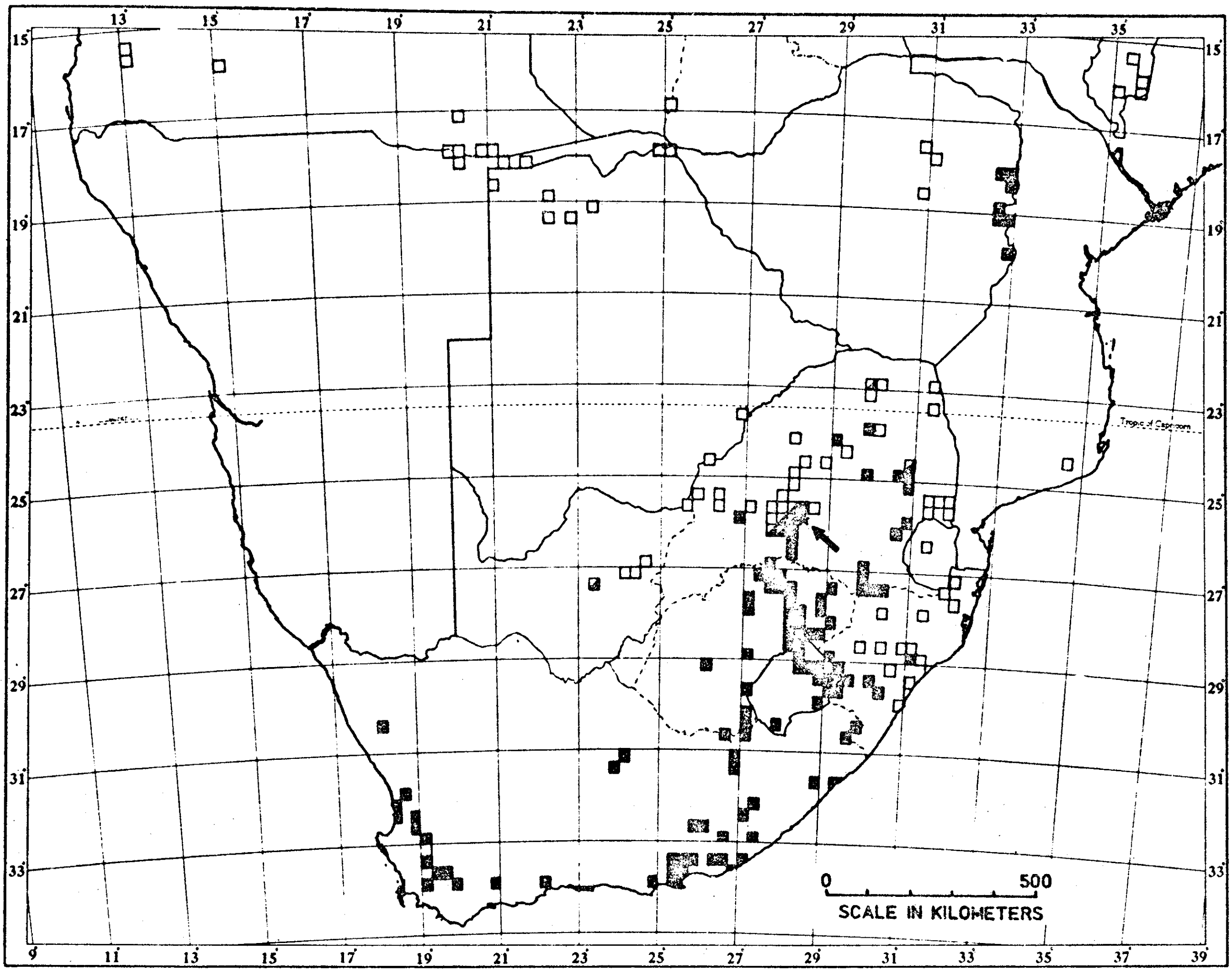


Fig. 10. Geographic distribution of O. irroratus and O. angoniensis in Southern Africa. Solid squares indicate distribution records of O. irroratus; open squares, distribution records of O. angoniensis; and squares half solid, half open, joint distribution records of both species. The arrow points to the locality of the study area, indicated by a star.

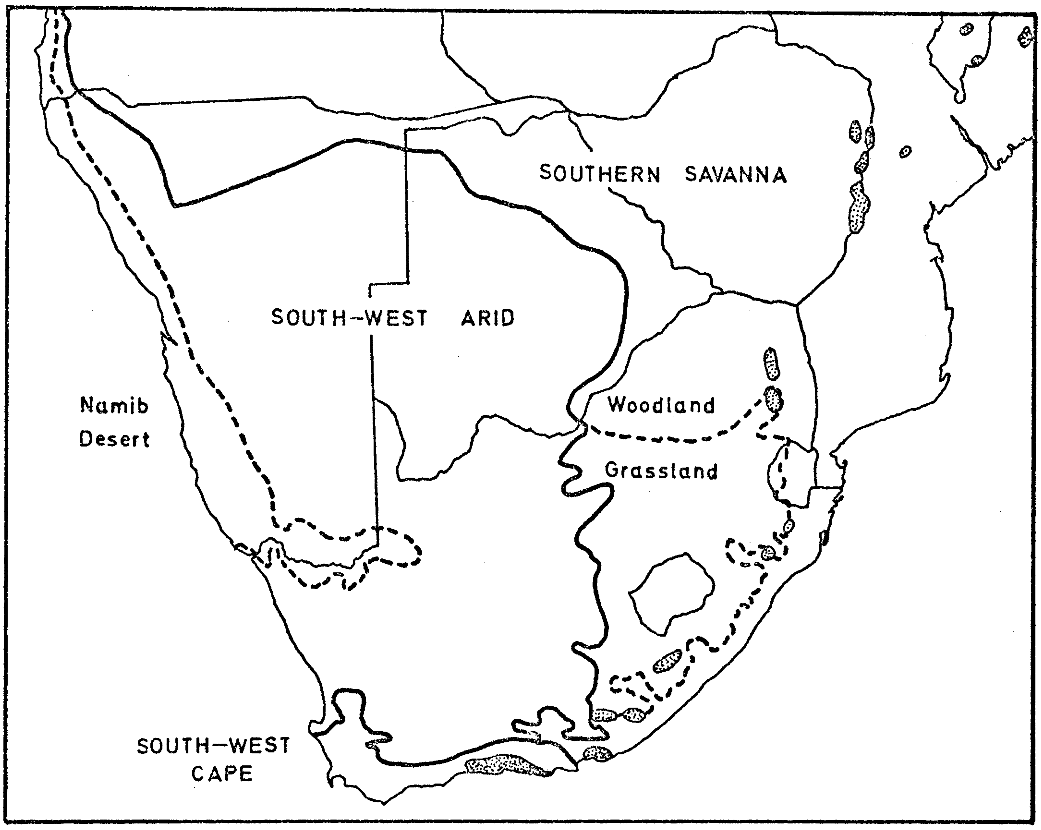


Fig. 11. Main biotic zones of Southern Africa. Forest patches are indicated by shading. (After Meester, 1965; modified from Davis, 1962.)

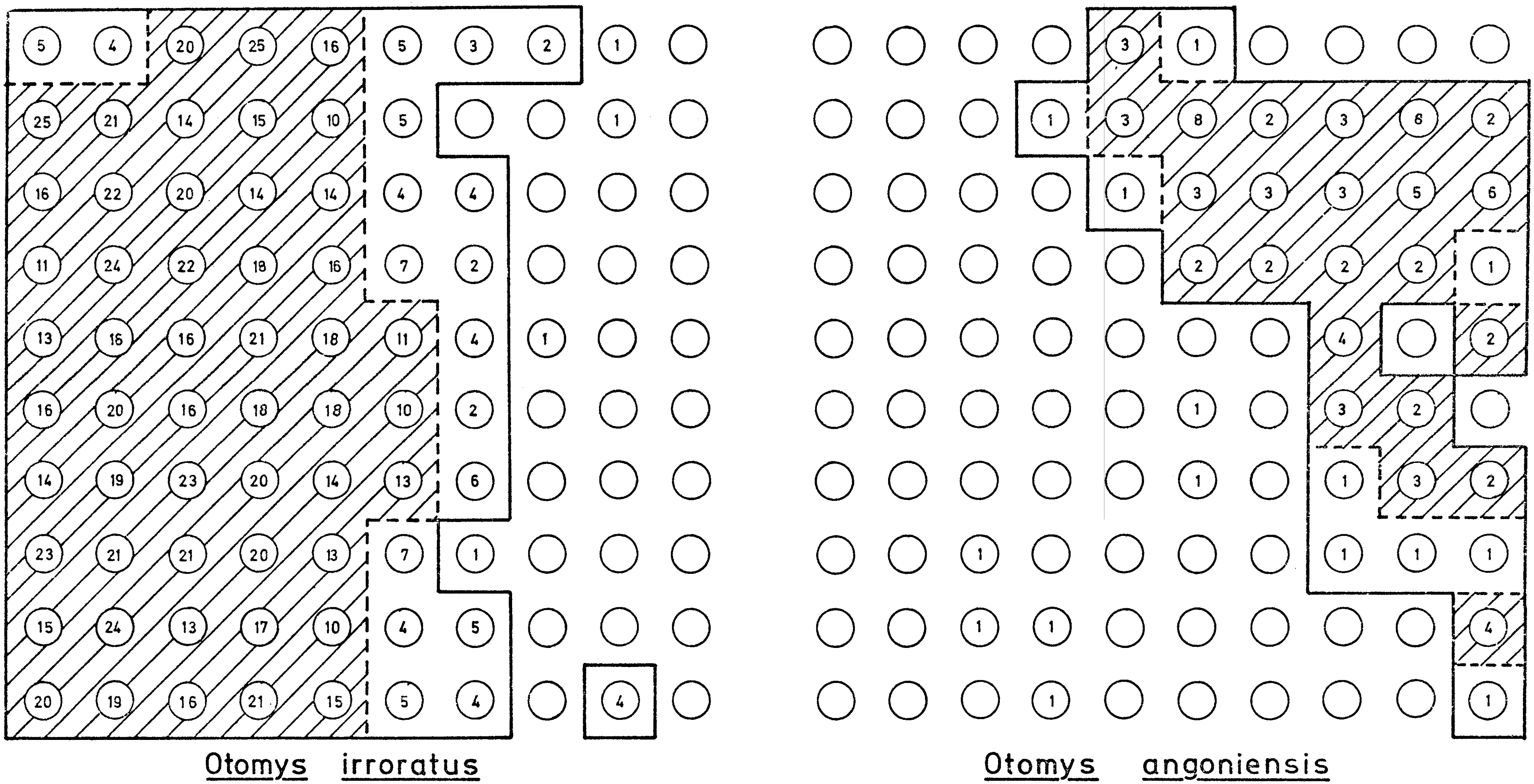


Fig. 12. Ecological distribution of *O. irroratus* and *O. angoniensis* on the study grid. The entire grid is shown twice, once for each species. Numbers in the circles indicate the number of times a different individual was captured at each trap station; the shaded area, the preferred habitat; and the remainder of the area unshaded but enclosed by the solid line, the marginal habitat.

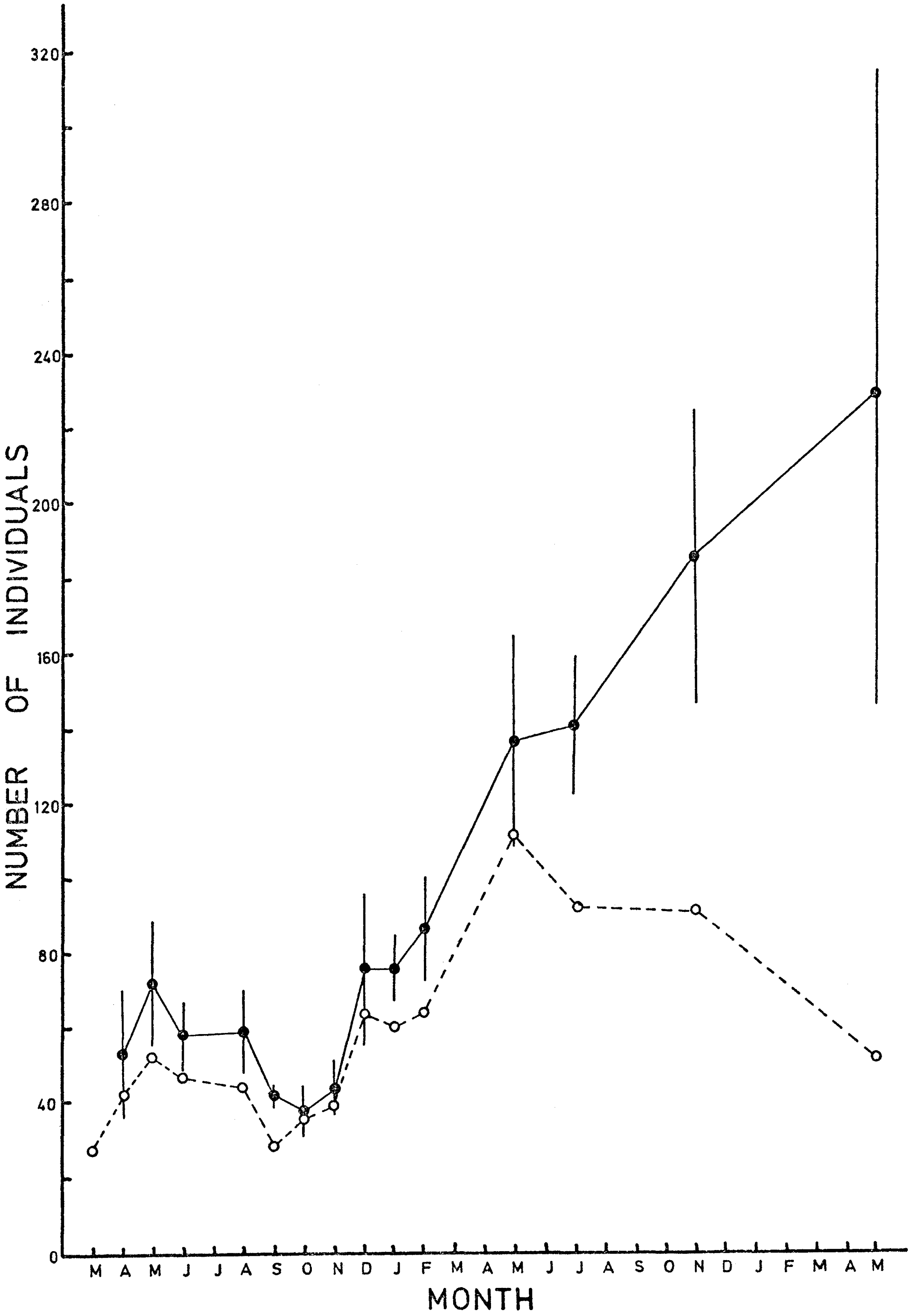


Fig. 13. Population estimates of O. irroratus on the study grid using the Lincoln Index on a cumulative basis. The vertical line indicates two standard errors on either side of the estimate and the broken line, the actual number captured.

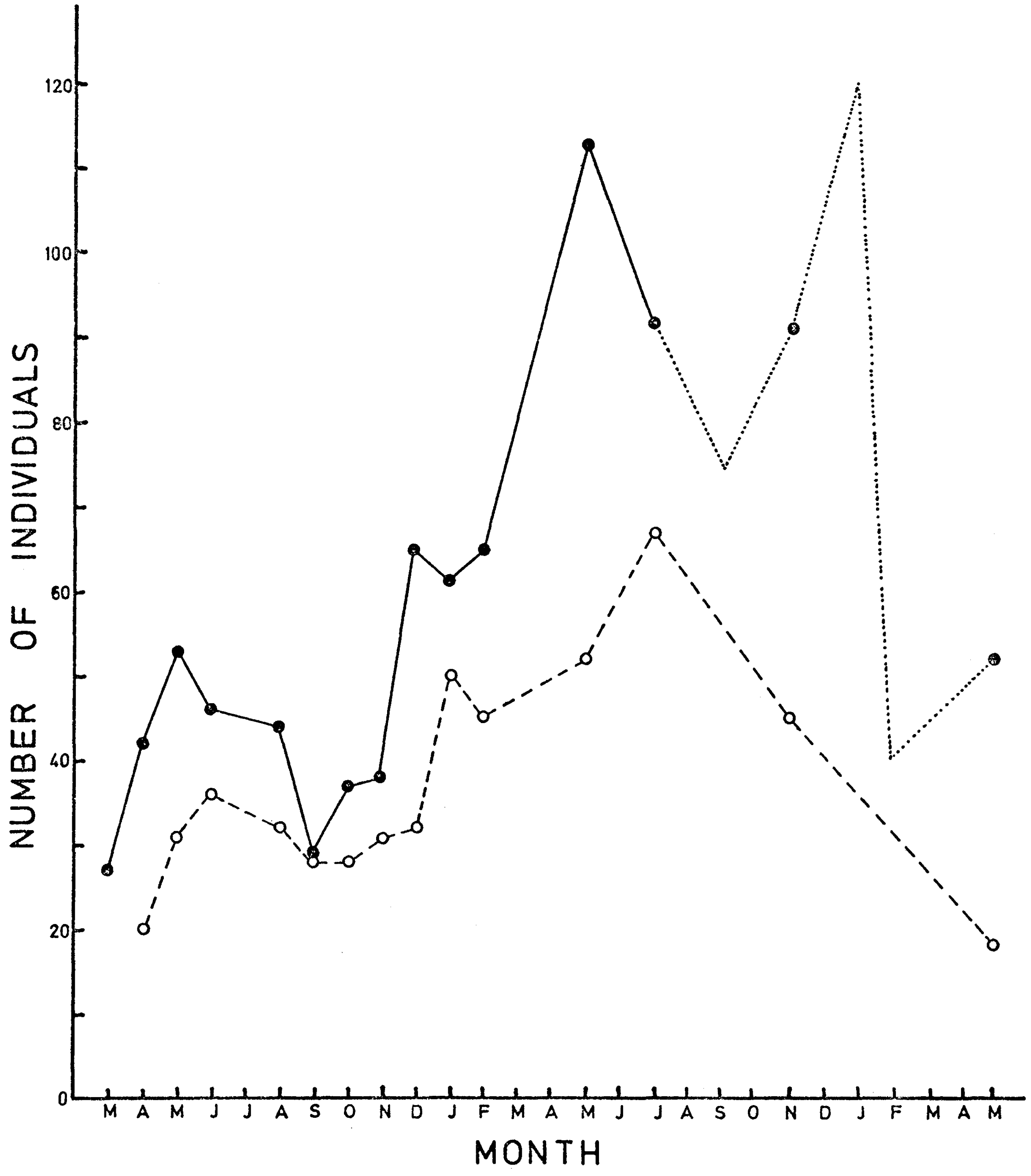


Fig. 14. Population fluctuation of *O. irroratus* on the study grid. The solid line indicates the fluctuation of total captures; the dotted line, the postulated fluctuation during long intervals; and the broken line, the fluctuation in the number of marked animals recaptured.

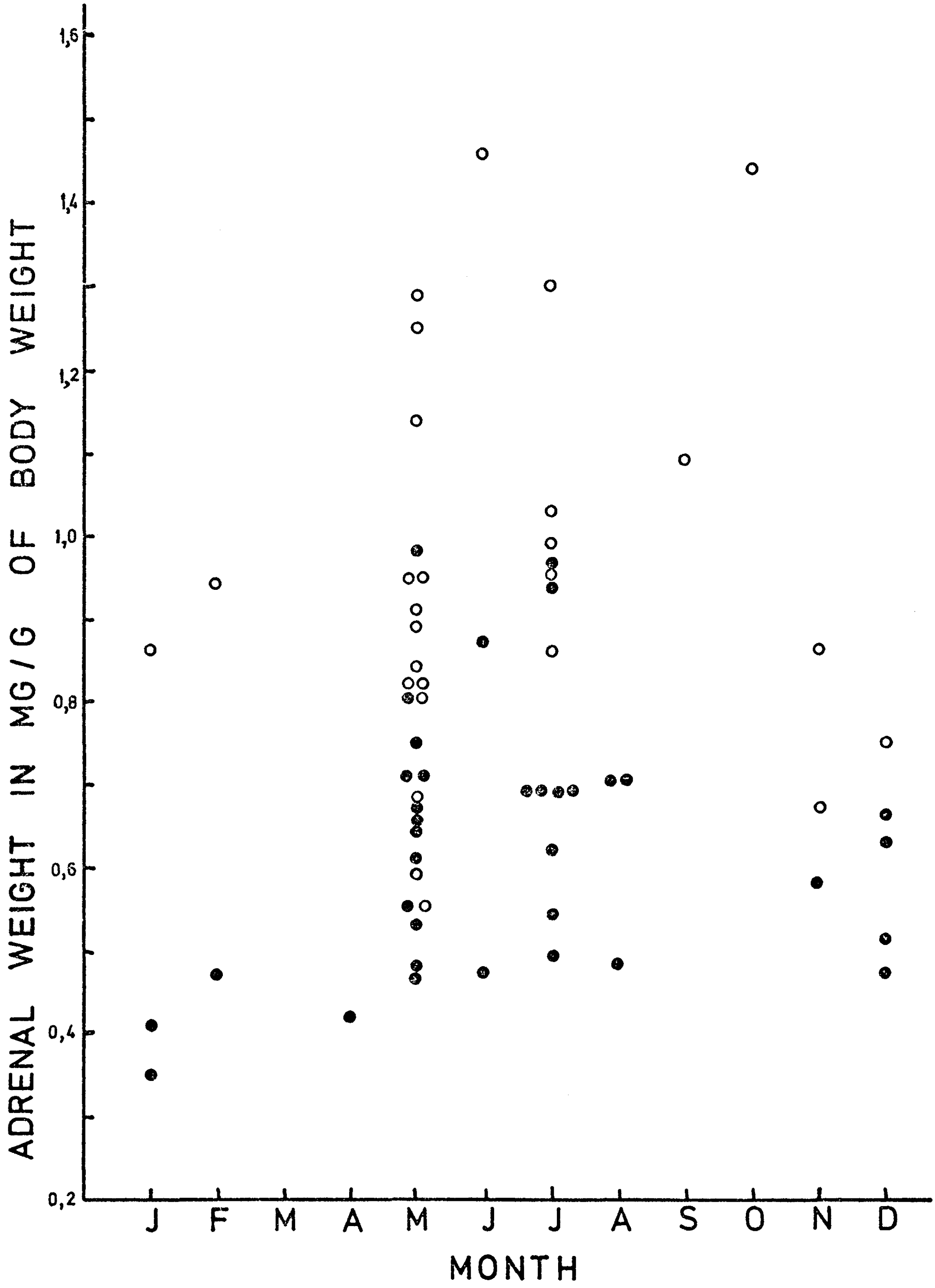


Fig. 15. Scattergram of the adrenal weights of O. irroratus during different months. Adrenal weight is expressed in mg/g of clean body weight. The solid symbol indicates males and the open, females.

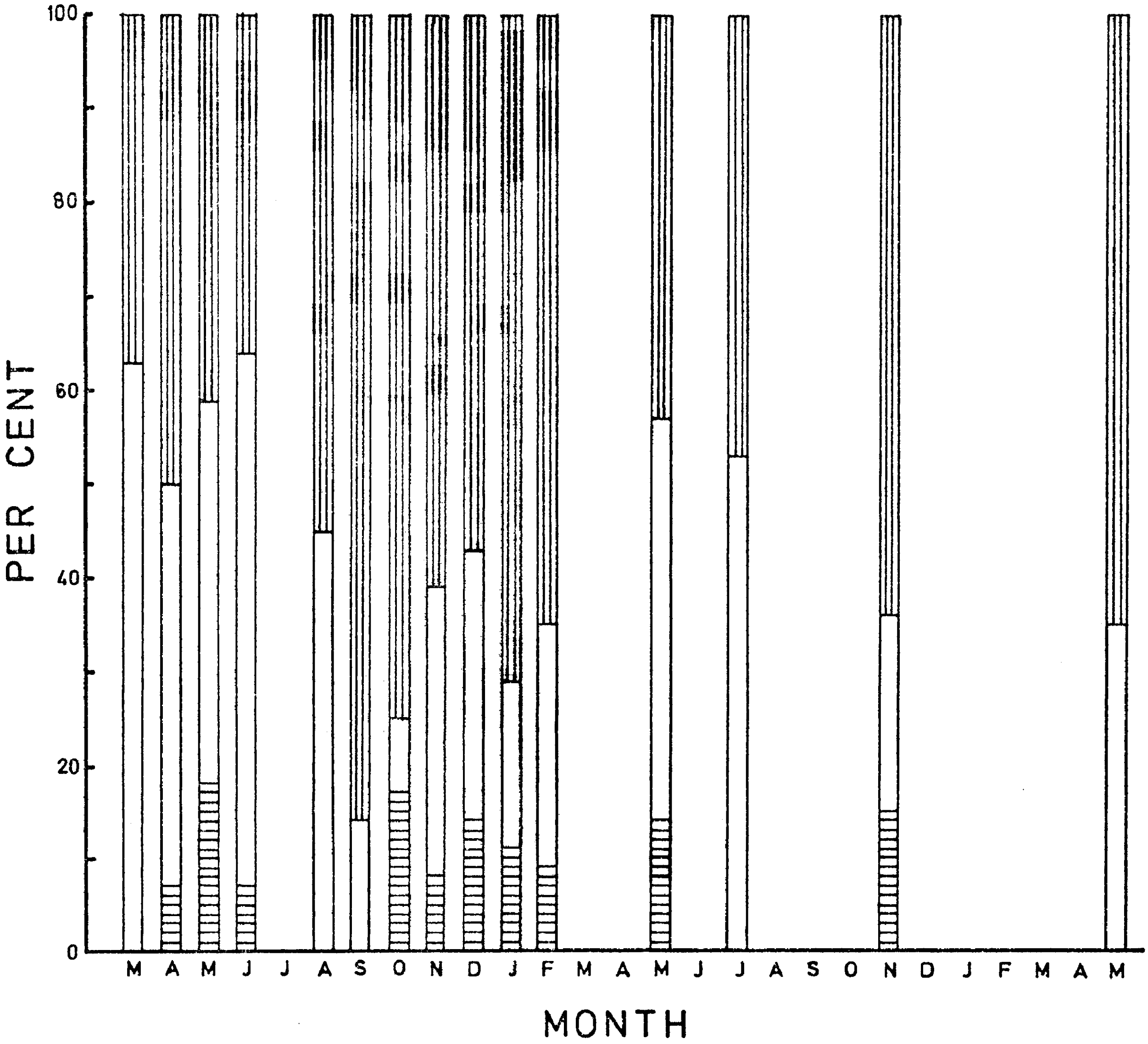


Fig. 16. Fluctuation of the age groups of O. irroratus on the study grid. Horizontal shading indicates the percentage of juveniles in the population; the unshaded area, subadults; and vertical shading, adults.

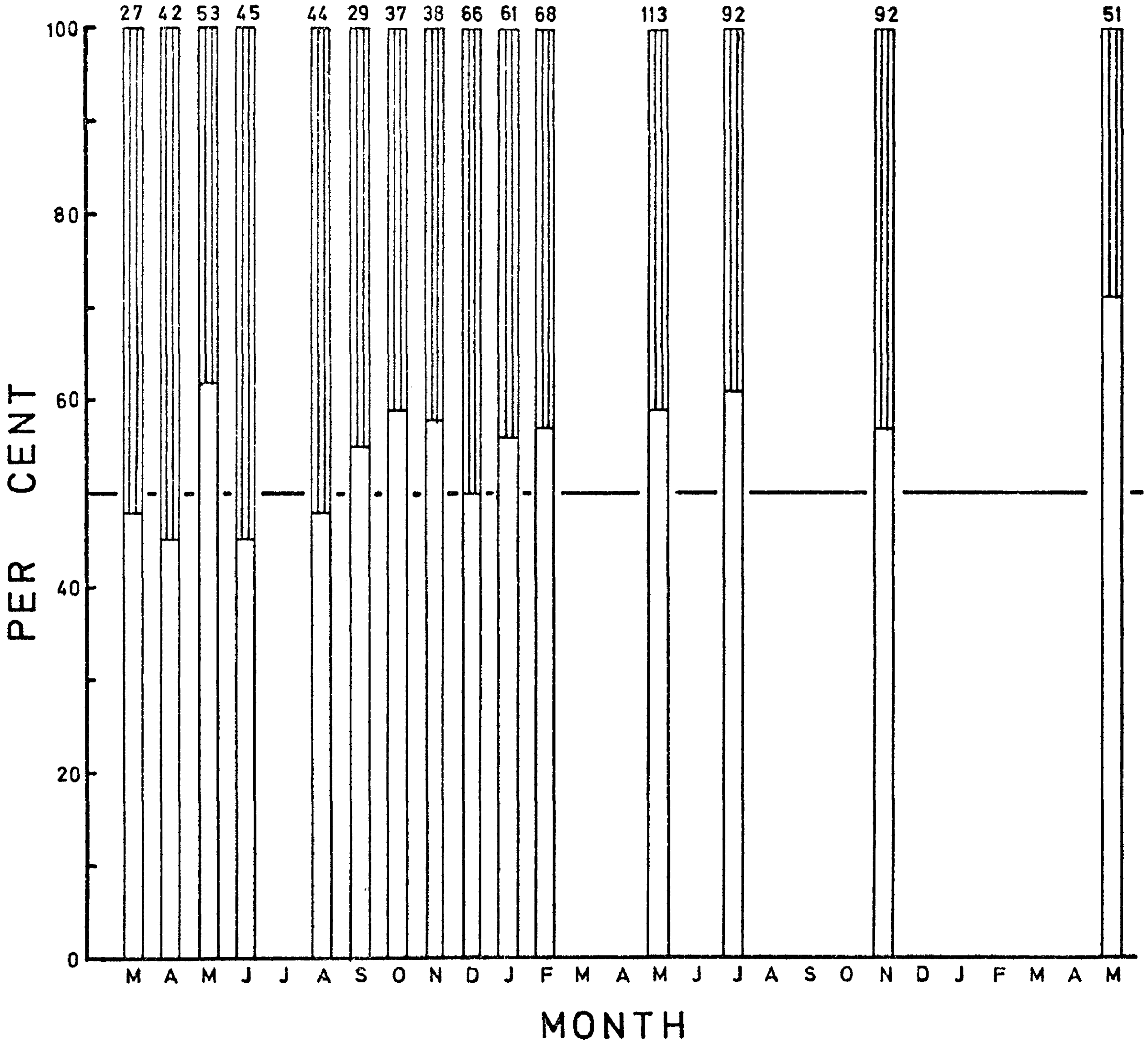


Fig. 17. Fluctuation of the sex ratio of *O. irroratus* captured on the study grid during each trapping session. The unshaded portion indicates the percentage of females; and the shaded portion, males. The number at the top of the column indicates sample size.

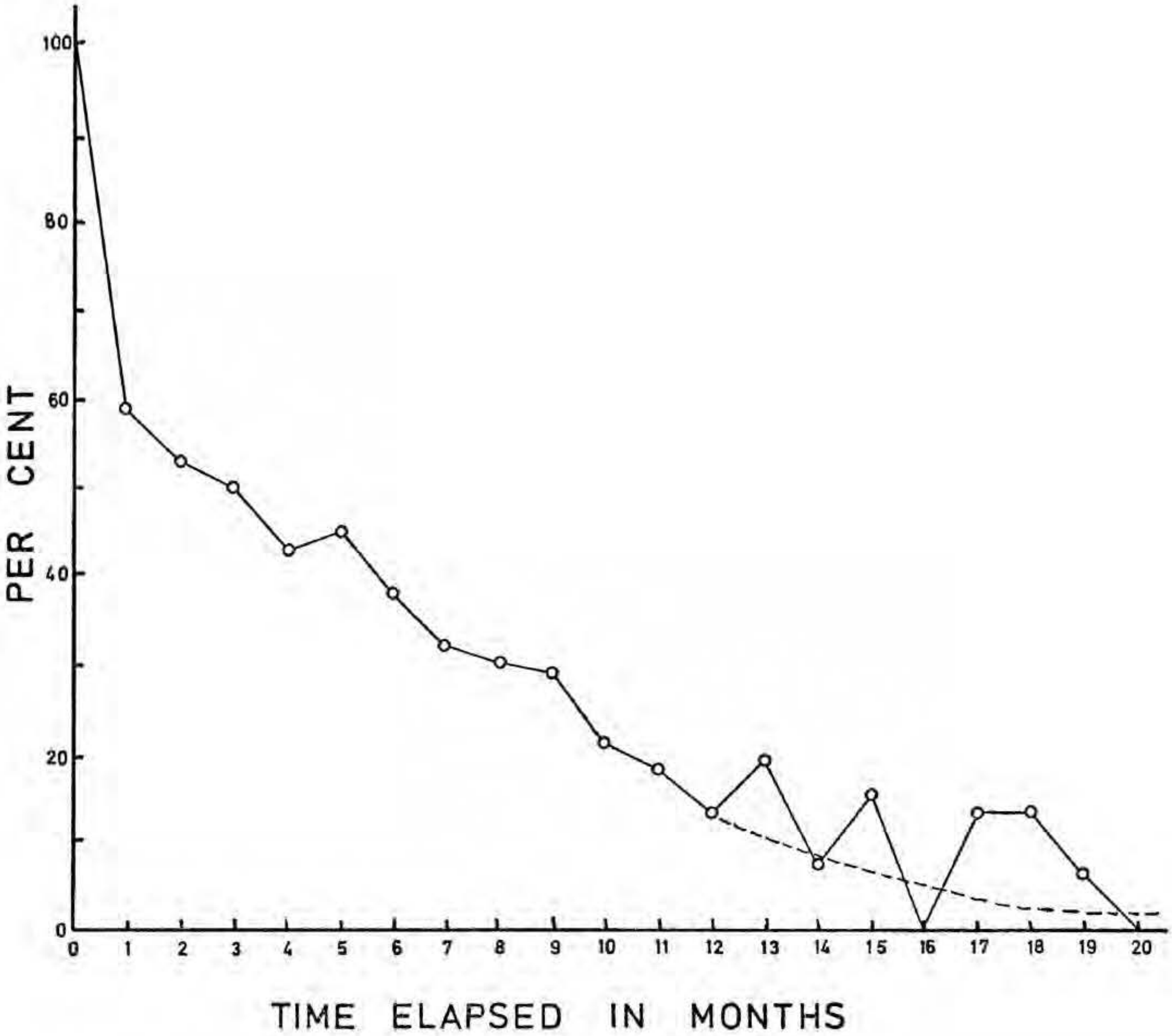


Fig. 18. Rate of disappearance of O. irroratus from the study grid. The broken line indicates the postulated curve, included because sample size from 13 to 20 months is too small for accuracy.

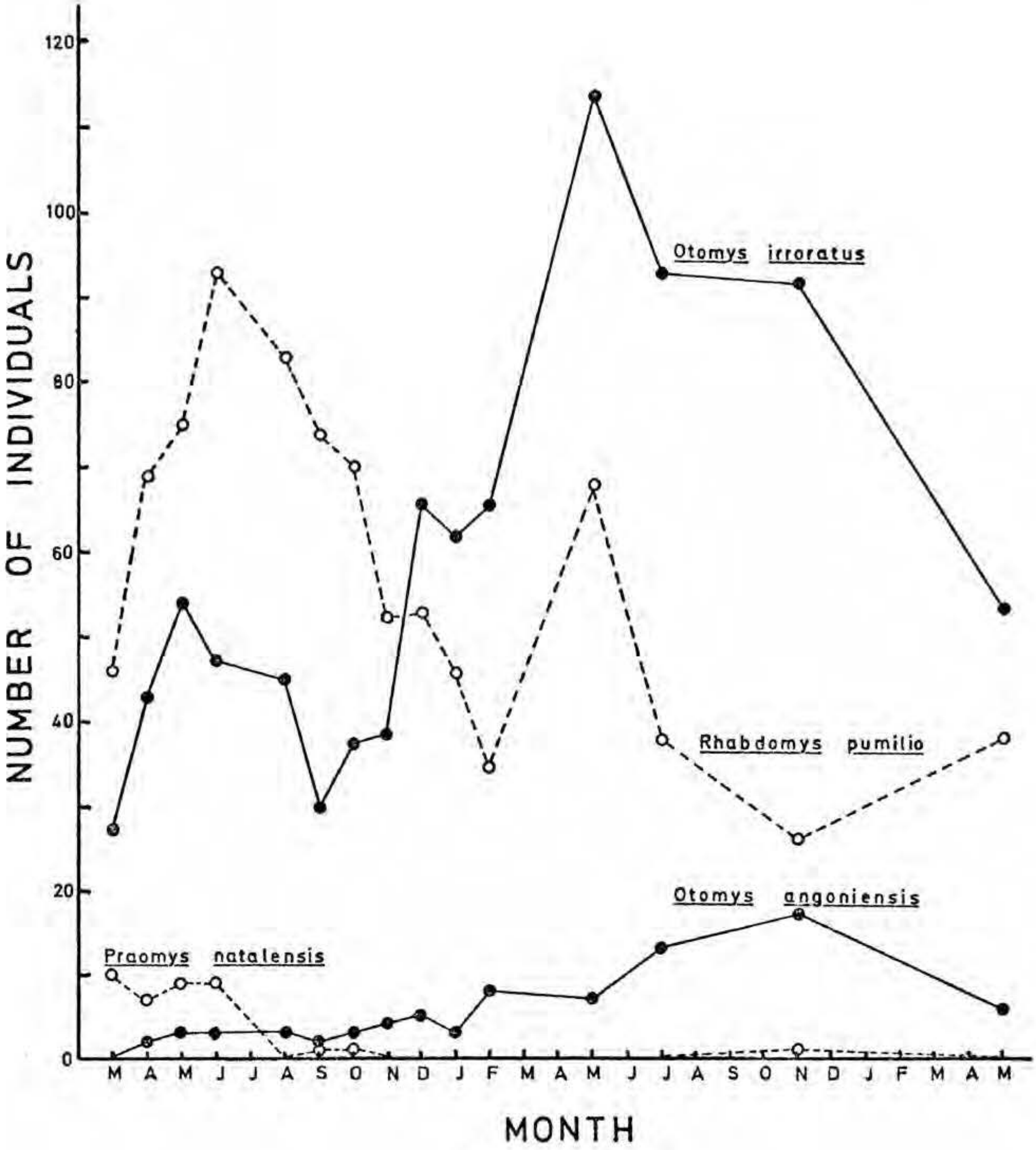


Fig. 19. Population fluctuation of the four rodent species captured on the study grid.

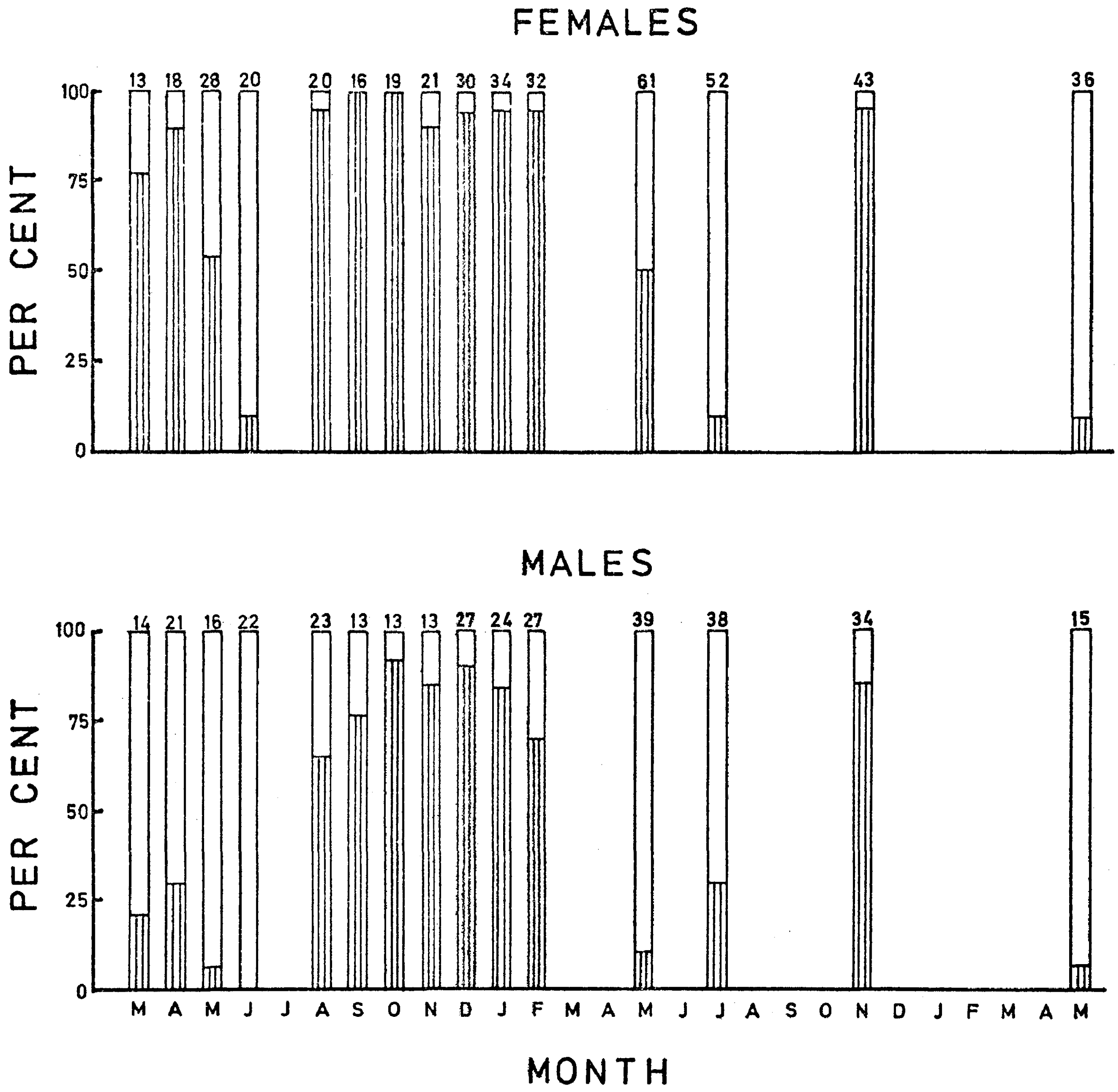


Fig. 20. Percentage of adult *O. irroratus* in breeding condition on the study grid during each trapping session. The shaded portion indicates the percentage in breeding condition (perforate vaginal orifice or scrotal testes); and the unshaded portion, the nonbreeding percentage (nonperforate or abdominal). The number at the top of the column indicates sample size.

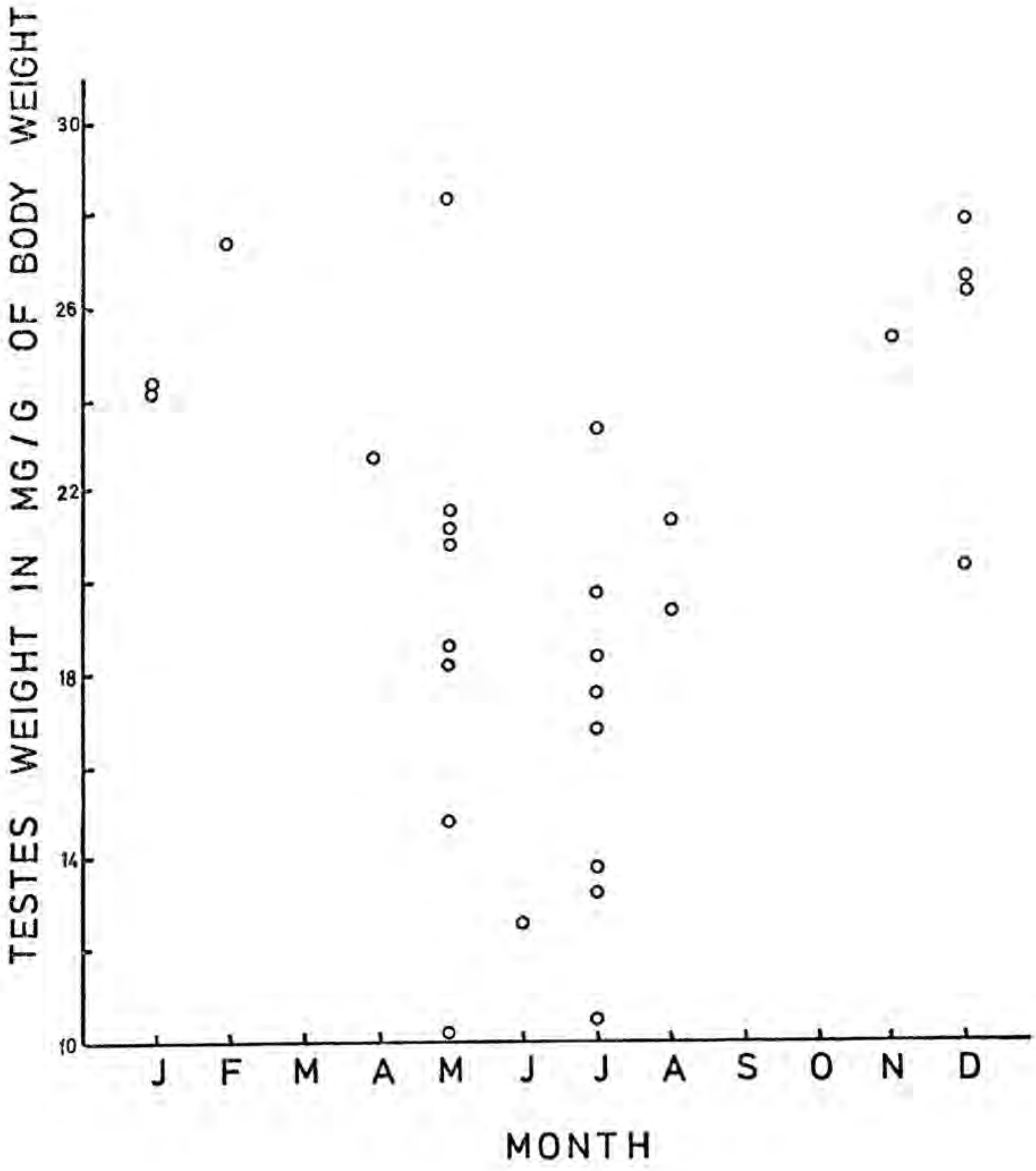


Fig. 21. Fluctuation of the weight of the paired testes of adult *O. irroratus*. Testis weight is expressed in mg/g of clean body weight.

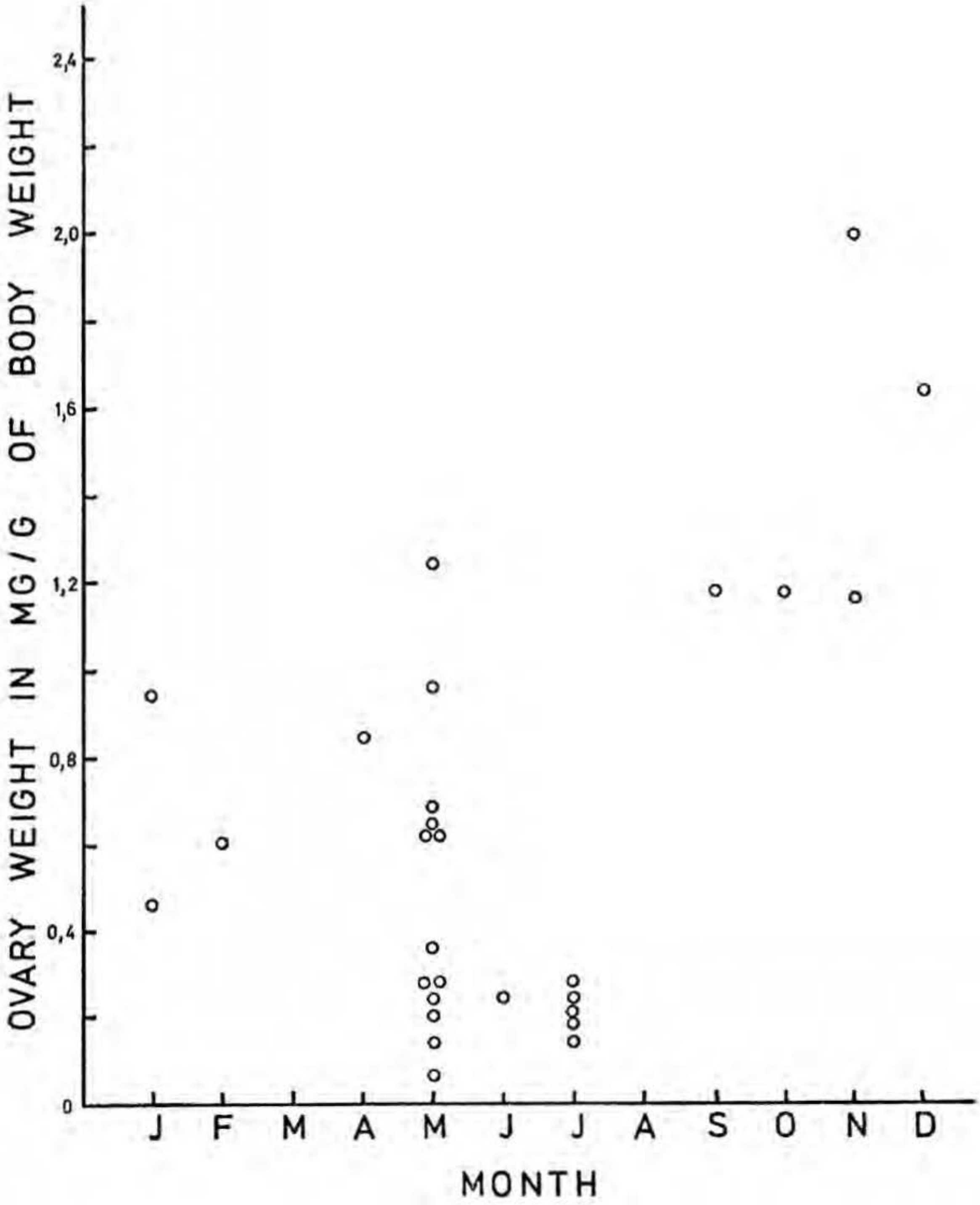


Fig. 22. Fluctuation of the weight of the paired ovaries of adult O. irroratus. Ovary weight is expressed in mg/g of clean body weight.

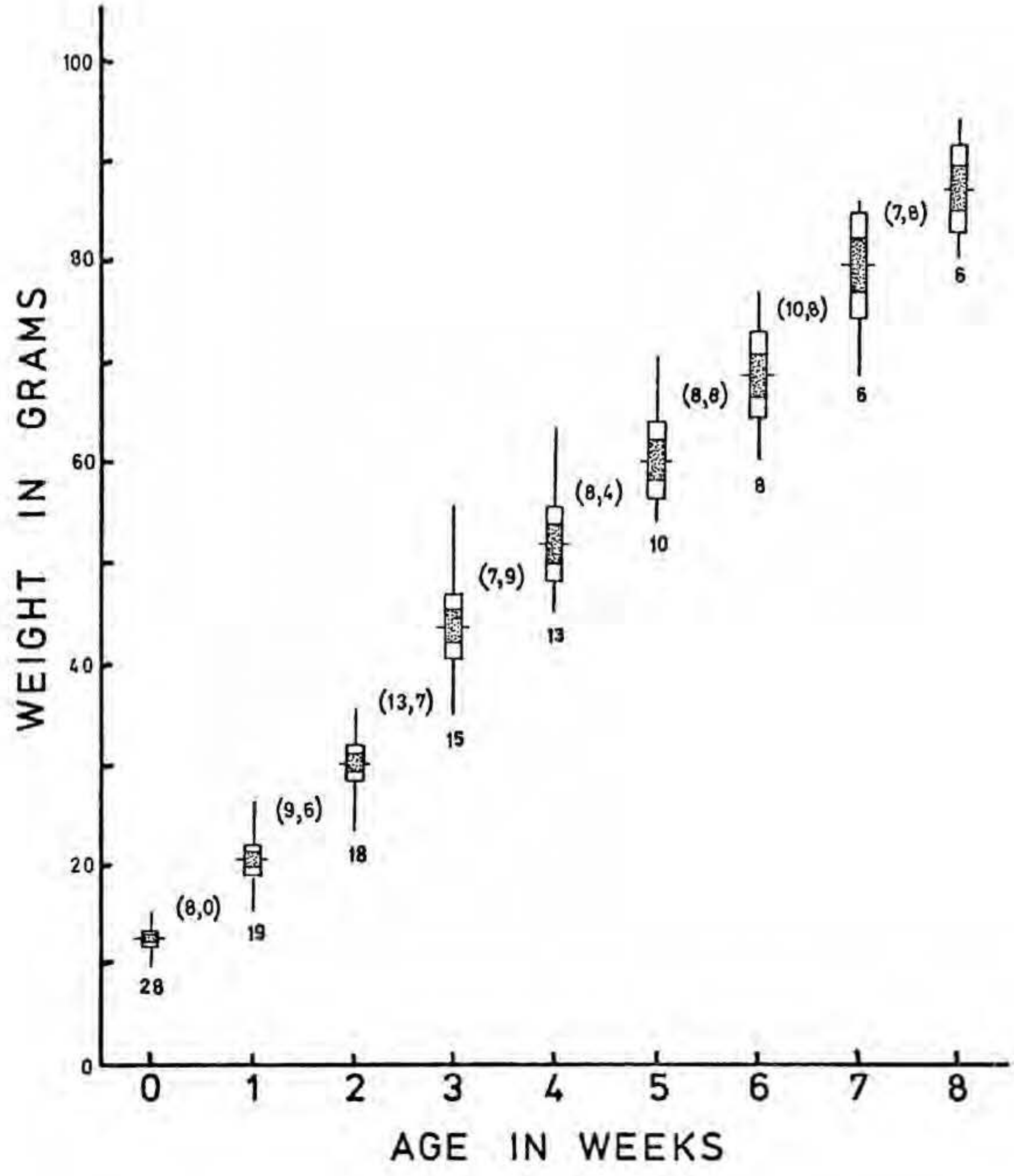


Fig. 23. Weight increase of O. irroratus from birth to eight weeks of age. The vertical line indicates the total variation of the sample; the crossbar, the mean; the shaded bar, one standard error on either side of the mean; the open bar, two standard errors on either side of the mean; the number in parentheses, the mean weight increase per week; and the number below each sample, the sample size.

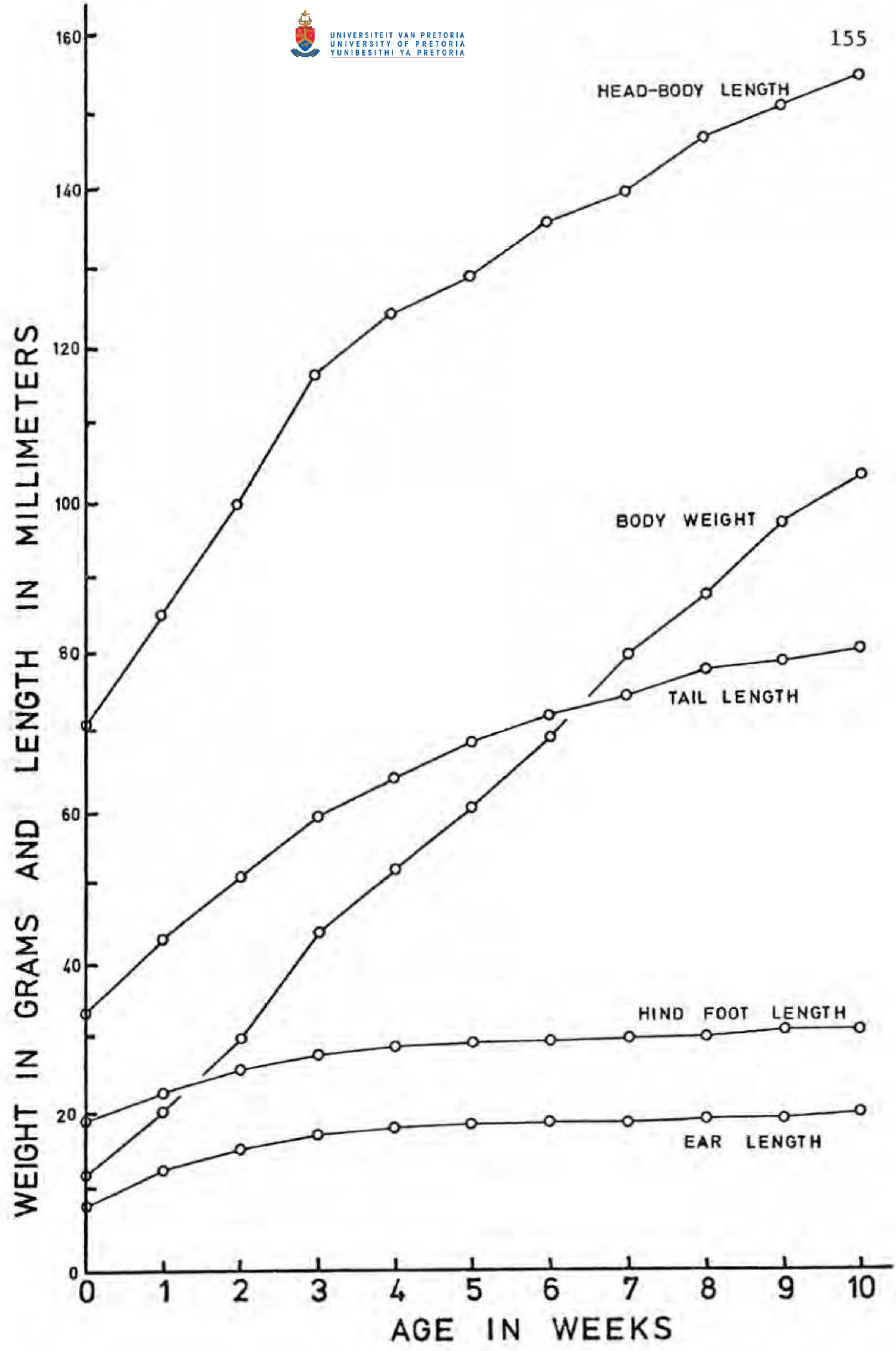


Fig. 24. Rate of increase in five external measurements of captive O. irroratus from birth to 10 weeks of age. Weight was recorded in grams and other measurements in millimeters.

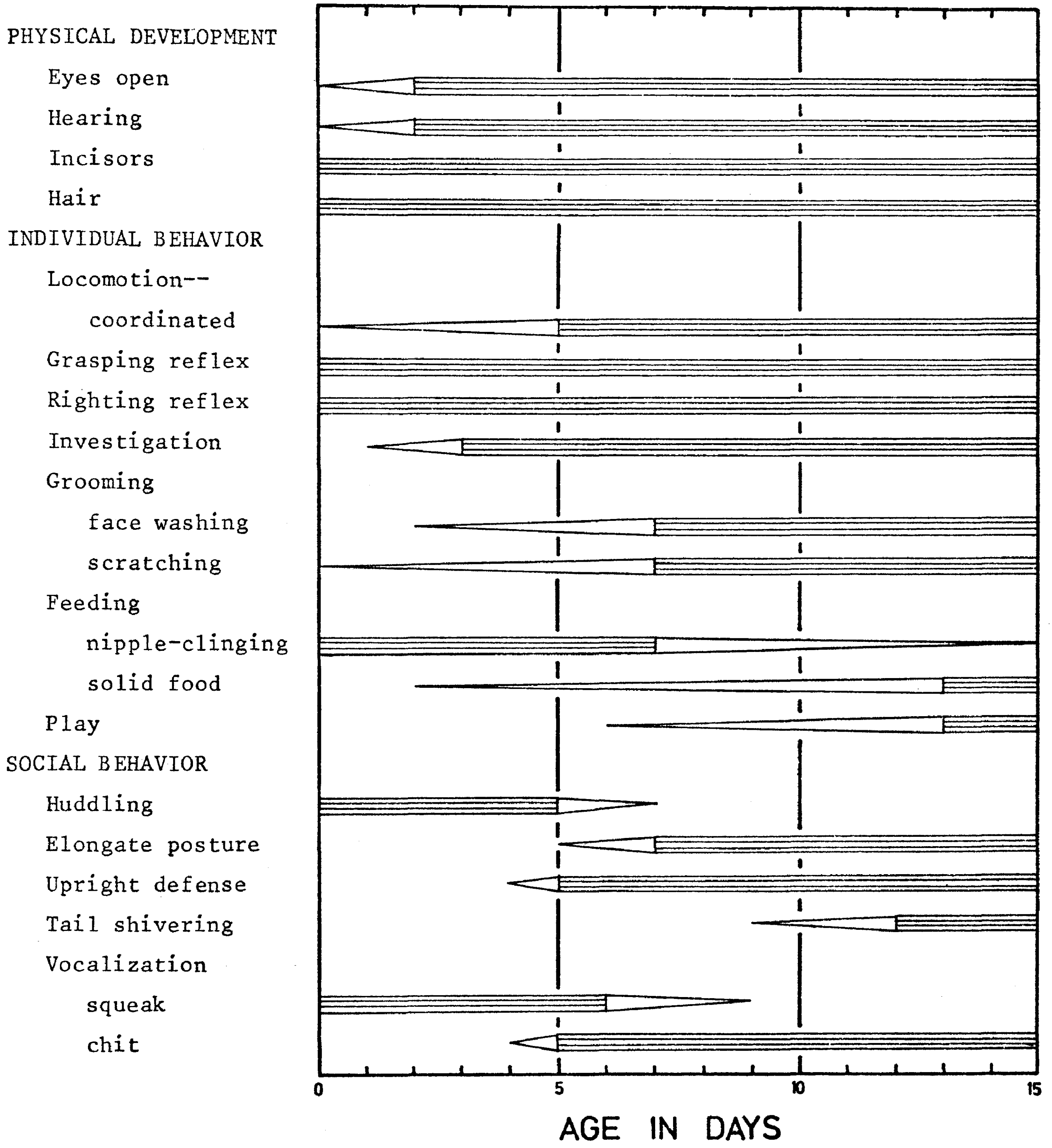


Fig. 25. Summary of physical and behavioral maturation rates of _O. irroratus_ from birth to 15 days of age. The shaded bar indicates the time of mean appearance or disappearance of a character or activity and its duration; the open wedge, the difference between the time when a character or activity was first or last seen in any individual to or from the time of mean appearance or disappearance.

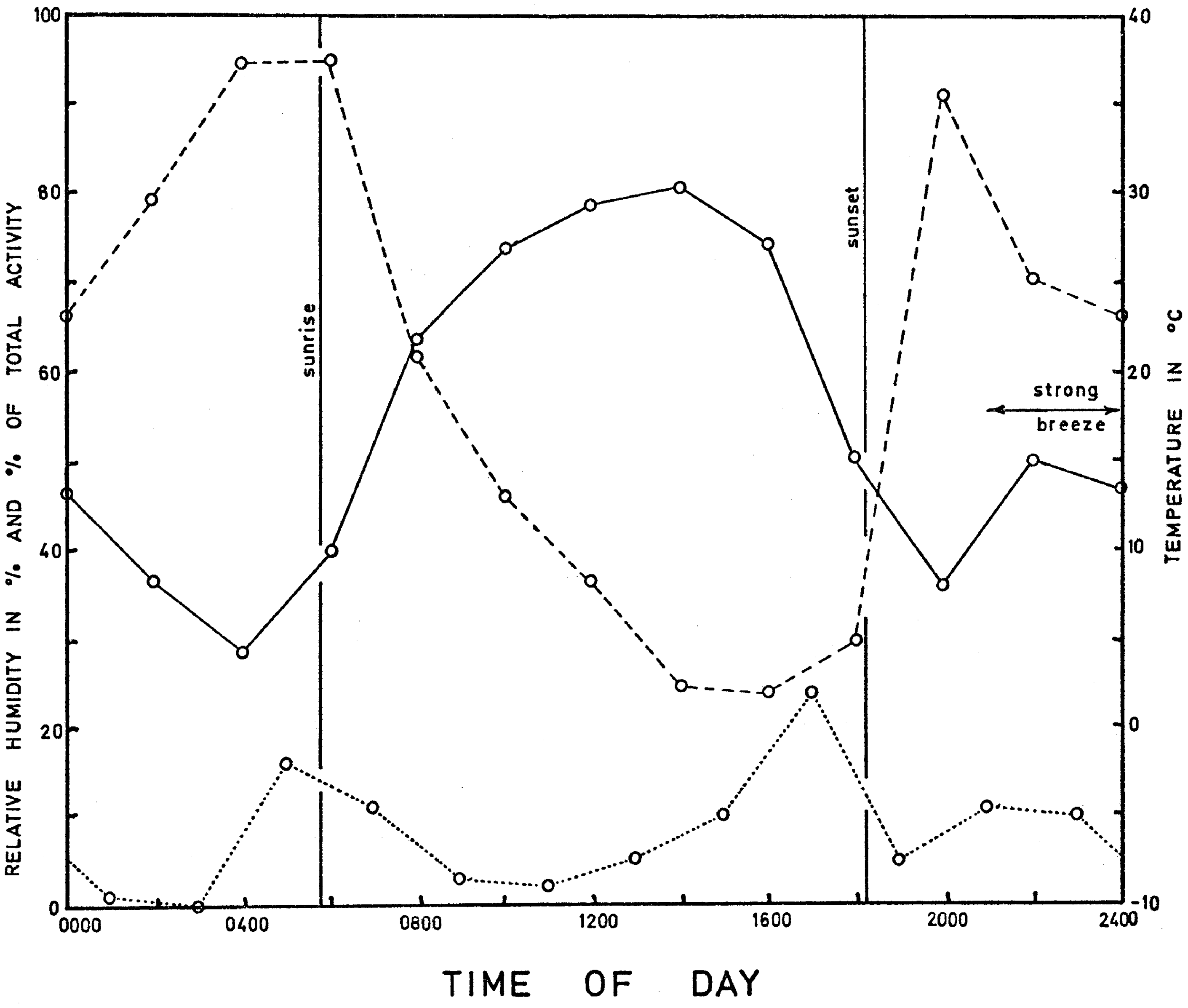


Fig. 26. Activity cycle of O. irroratus recorded on the study grid during a 24-hour period in October 1970. Activity during each two-hour interval is indicated as a percentage of the total recorded activity during the 24 hours. The dotted line indicates activity; the solid line, temperature; the broken line, humidity; and the vertical solid lines, official sunrise and sunset.

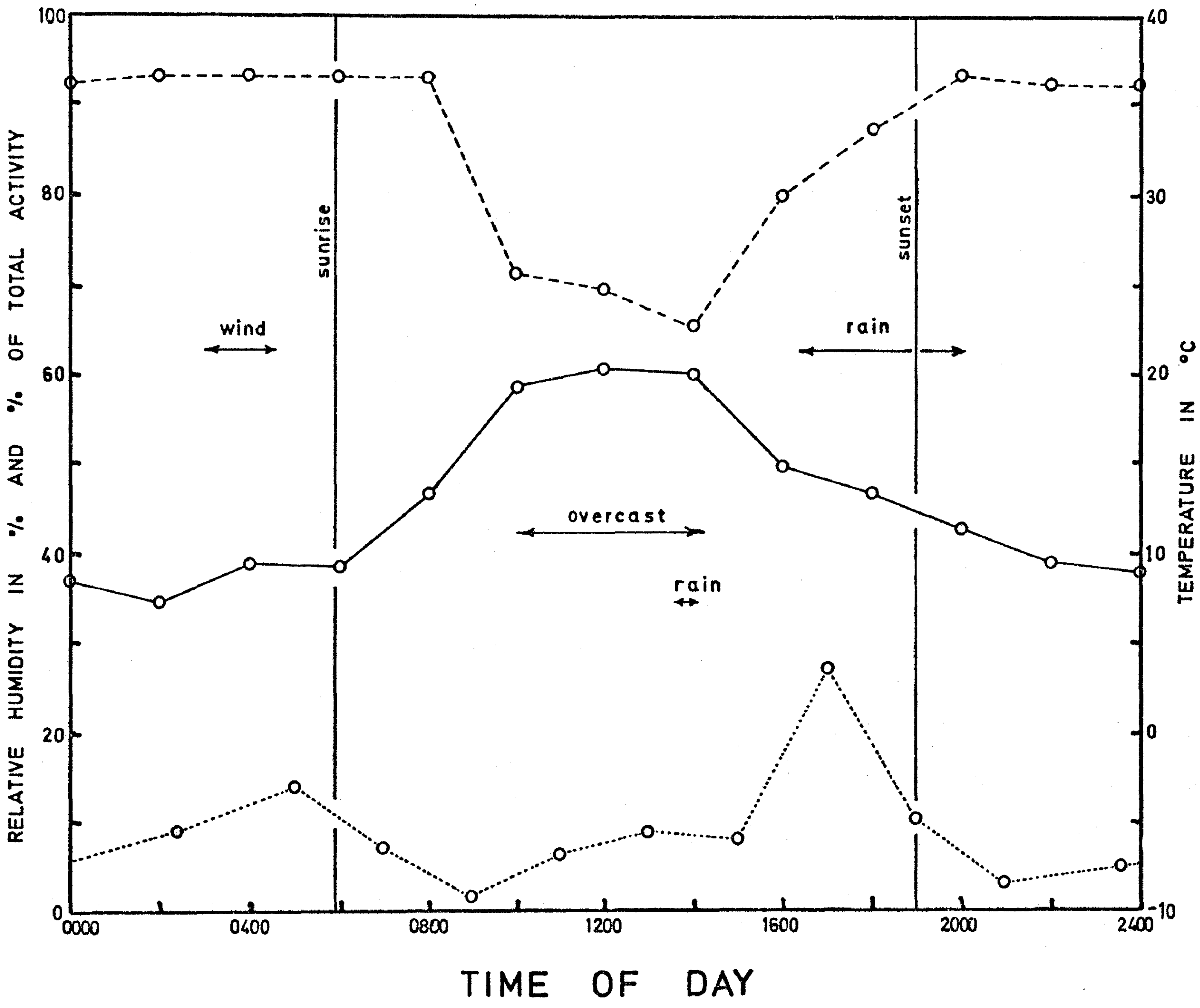


Fig. 27. Activity cycle of O. irroratus recorded on the study grid during a 24-hour period in February 1971. See Fig. 26 for further explanation.

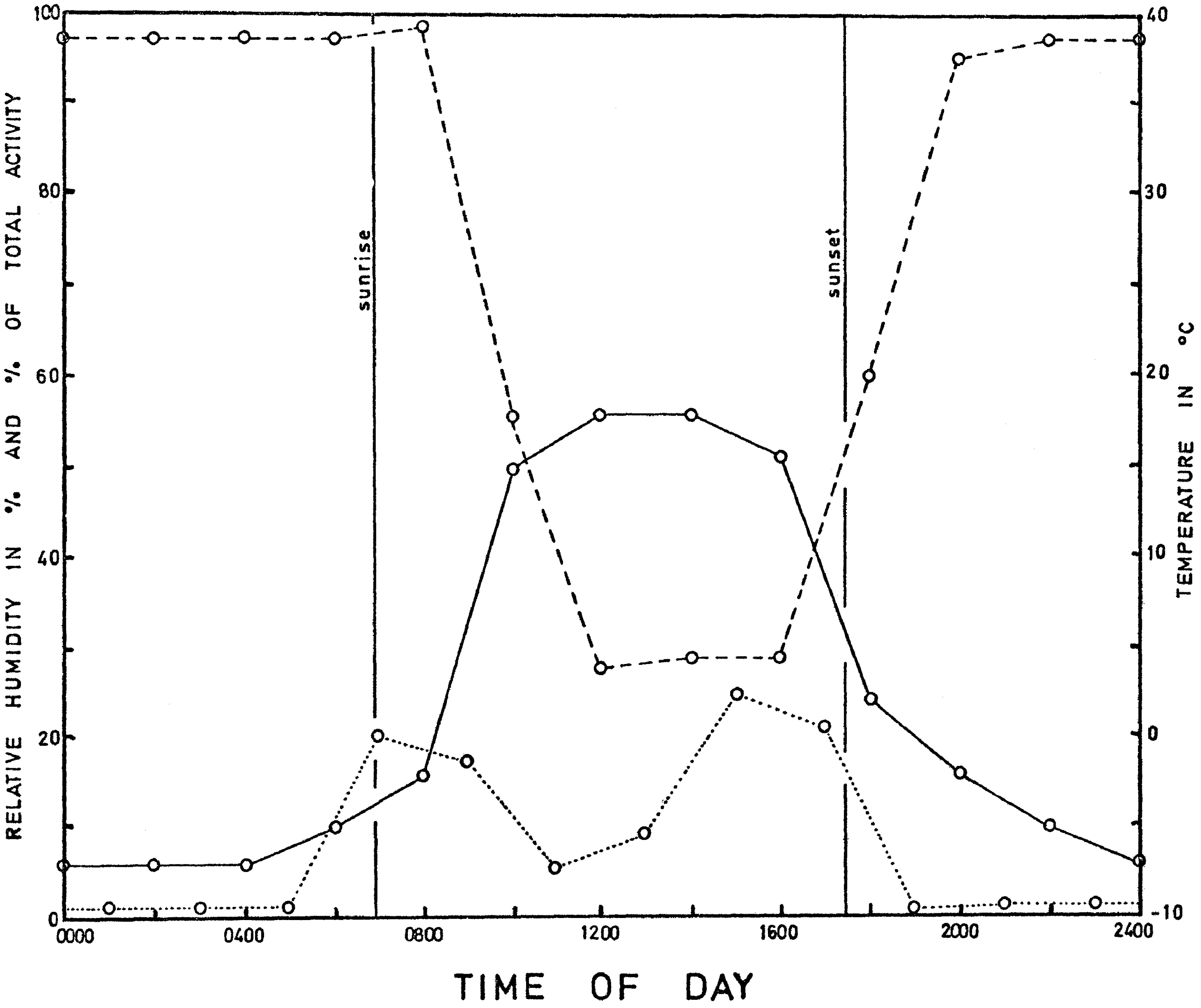


Fig. 28. Activity cycle of O. irroratus recorded on the study grid during a 24-hour period in July 1971. See Fig. 26 for further explanation.

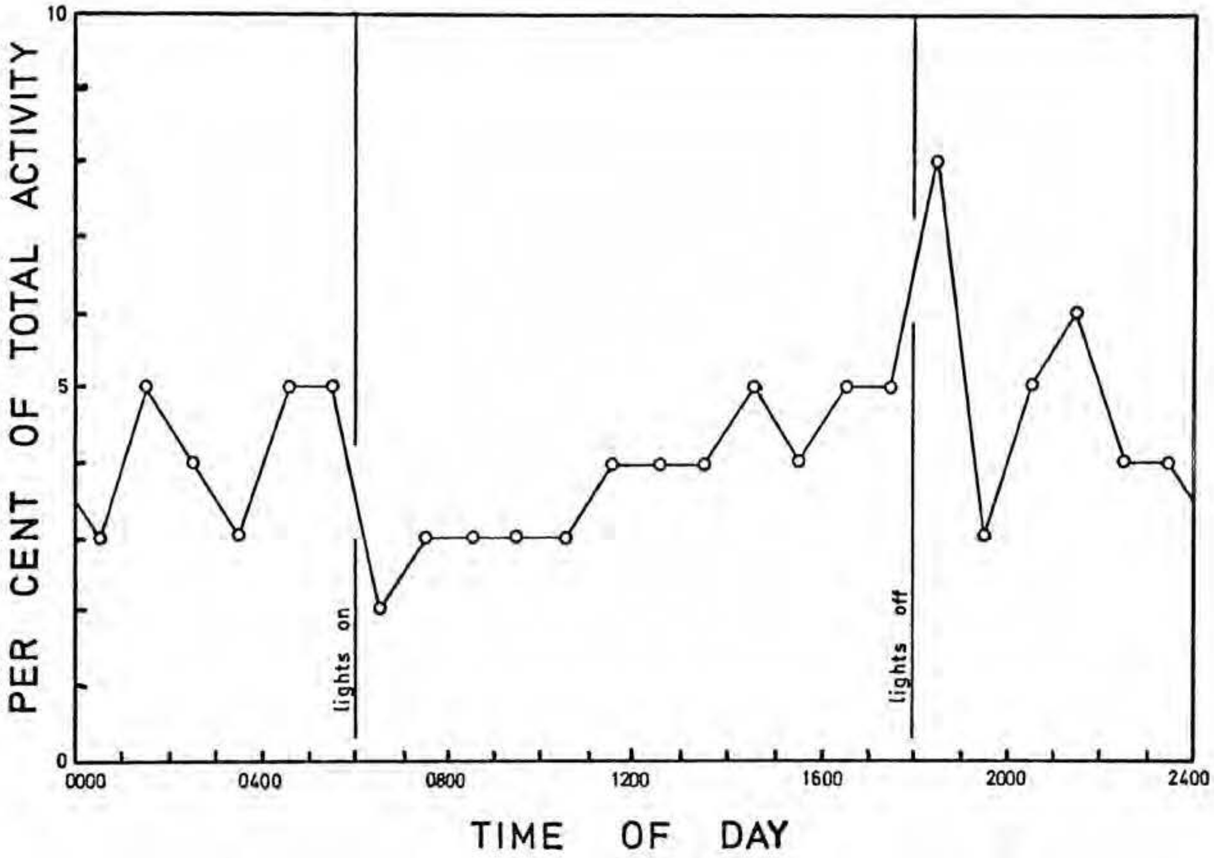


Fig. 29. Activity cycle of _O._ _irroratus_ recorded in the laboratory. Activity during each one-hour interval is indicated as a percentage of the total recorded activity during 24 hours. Vertical lines indicate when lights switched on or off.

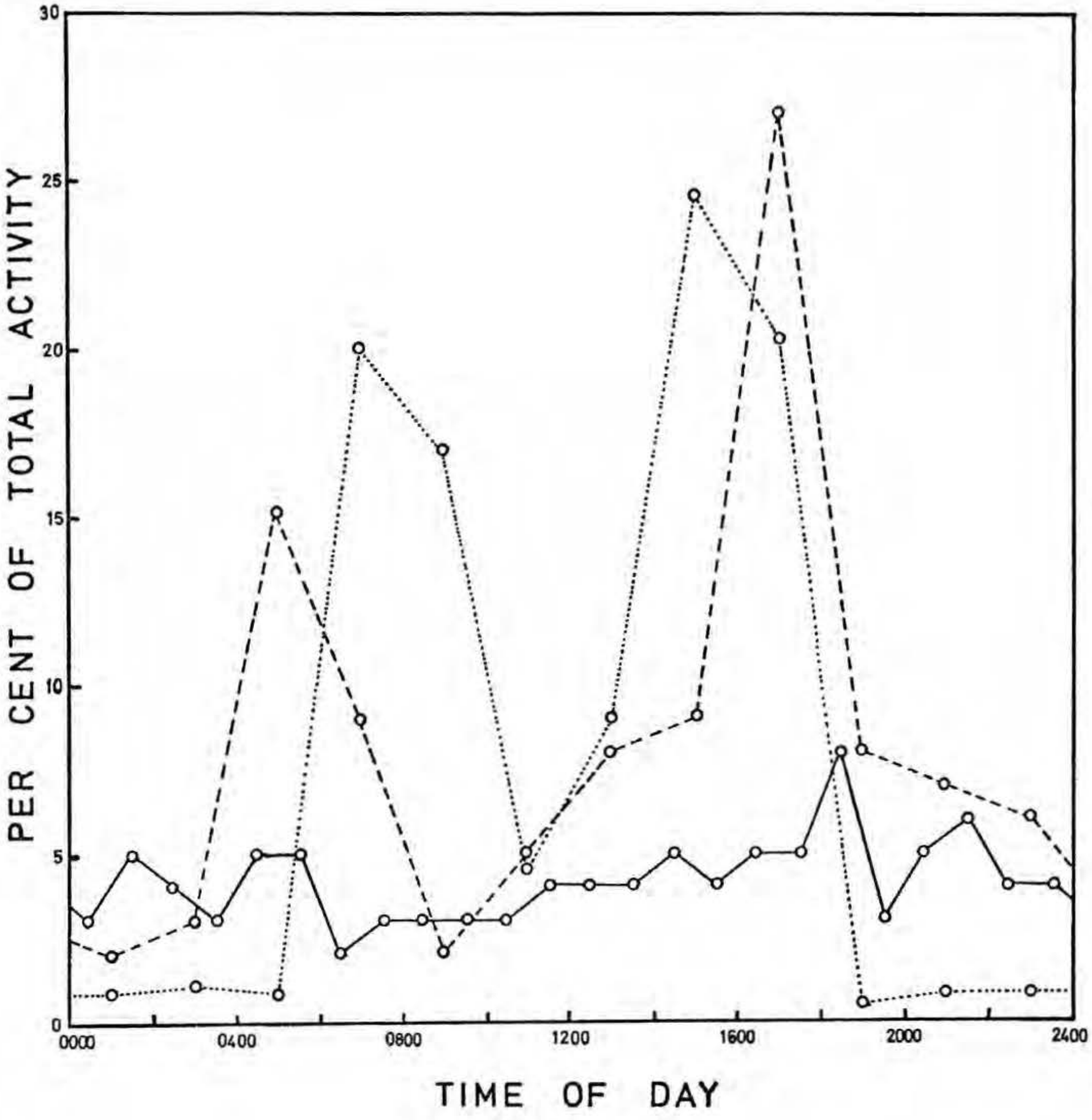


Fig. 30. Comparison of activity of O. irroratus recorded in two warm months (February and October), in winter (July), and in the laboratory. The broken line indicates the combined activity in February and October; the dotted line, winter activity; and the solid line, laboratory activity.

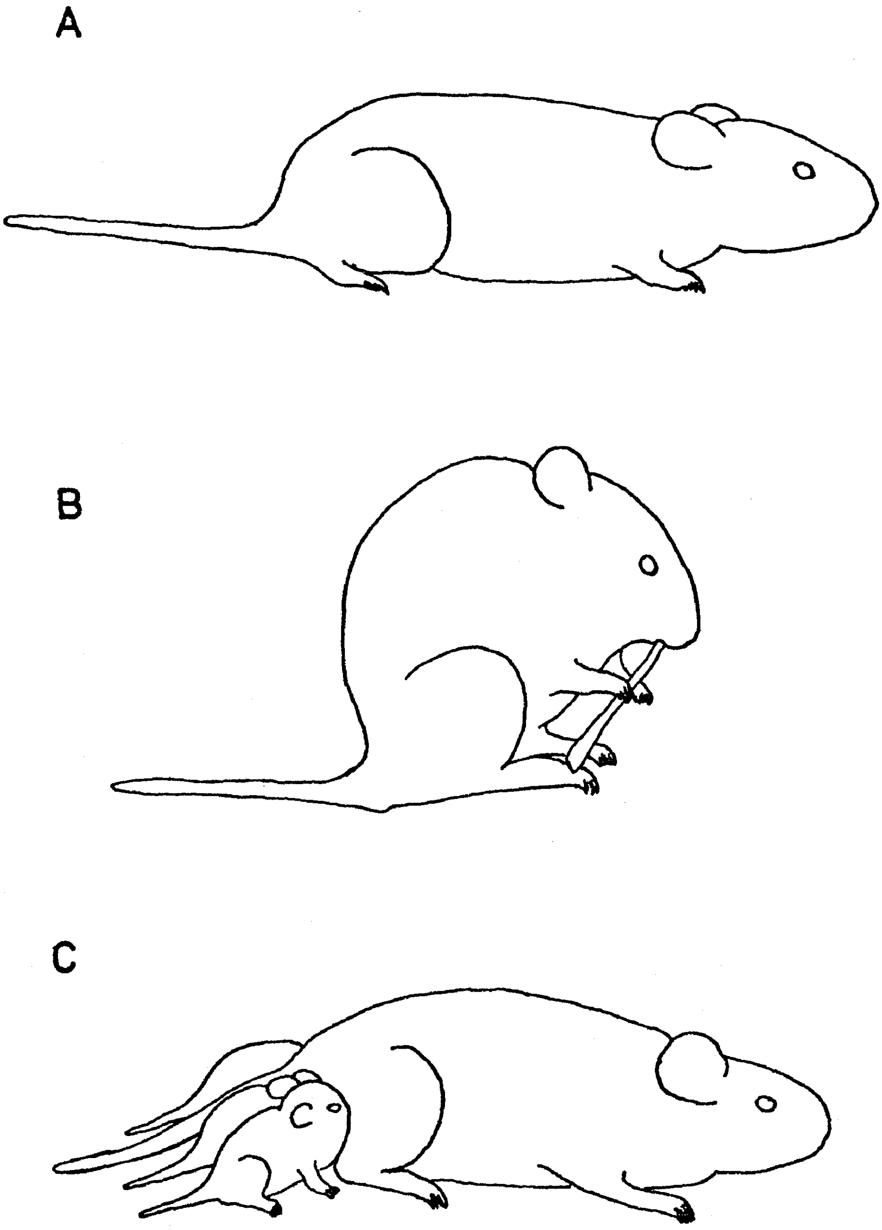


Fig. 31. Behavioral postures. A, elongate posture; B, feeding posture; and C, mother transporting nipple-clinging young.

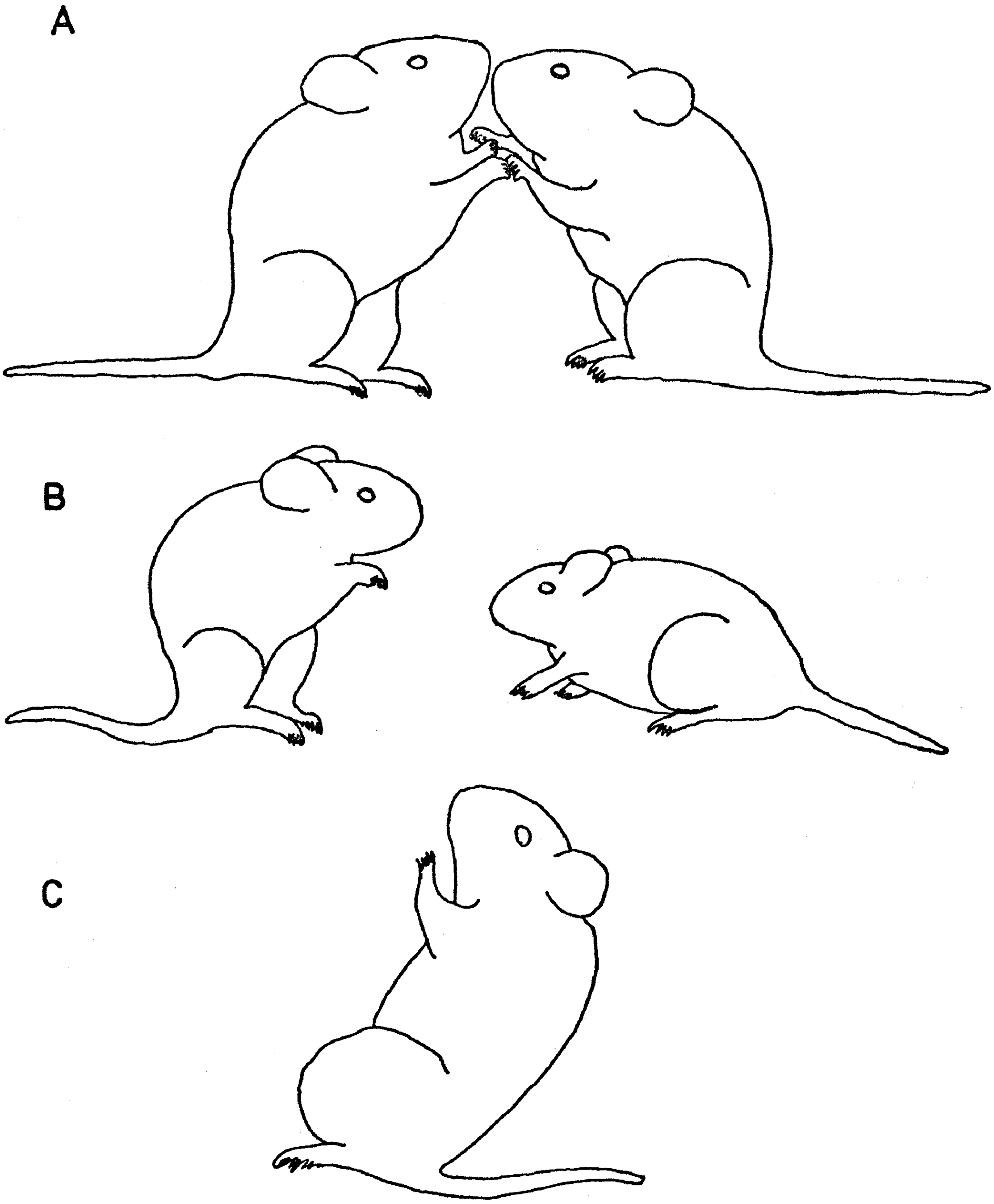


Fig. 32. Behavioral postures during encounters. A, mutual upright with sparring; B, upright defense posture by the animal on the left and lateral display (threat) by the animal on the right; and C, submissive appeasement.

Table 1. Mean monthly rainfall (in mm) recorded at the Rietvlei Waterworks, Van Riebeeck Nature Reserve. The mean is derived from the period 1935 to 1967.

Month	Mean	1969	1970	1971	1972
January	119	41	81	154	230
February	100	122	49	43	25
March	94	206	69	68	62
April	48	83	50	172	21
May	22	60	23	12	6
June	11	0	4	16	1
July	8	0	2	0	345
August	4	4	2	0	
September	19	7	58	42	
October	67	178	78	73	
November	107	81	75	152	
December	124	85	142	124	
Annual	723	867	633	856	
Per cent difference from annual mean		+19,9	-12,4	+18,4	-12,4

Table 2. Mean monthly temperatures (in °C) at Irene and Pretoria. The temperatures recorded at Irene, the nearest weather station to the Reserve (approximately 8 km W), are for the period 1904 to 1940. The temperatures for 1969 to mid-1972 are from Pretoria, the nearest weather station at that time.

Month	Irene	Pretoria	1969	1970	1971	1972
January	20,9	21,5	23,7	22,8	21,6	21,3
February	20,2	21,4	23,6	21,3	20,7	21,5
March	18,6	19,9	20,0	20,9	21,2	19,8
April	15,6	17,1	17,6	17,9	17,4	17,6
May	11,9	13,4	13,3	14,3	12,6	13,3
June	8,9	10,8	11,3	11,1	10,7	10,2
July	8,7	10,8	11,6	11,4	10,7	
August	11,5	13,7	13,7	14,8	13,0	
September	15,1	17,1	17,1	18,4	17,8	
October	18,8	19,7	18,6	19,2	18,4	
November	19,4	20,4	20,5	21,8	19,2	
December	20,5	21,3	21,0	21,5	20,9	
Annual mean	15,8	17,3	17,7	18,0	17,0	
Per cent difference from Pretoria annual mean			+2,3	+4,0	-1,7	-1,0

Table 3. Degree of significance of differences between age groups of *O. irroratus* for all external and cranial measurements based on Student's *t*-test. (o--$P>0,05$; +--$P=0,05-0,02$; ++--$P=0,02-0,01$; +++--$P<0,01$)

	0-I	I-II	II-III	III-IV	IV-V
External					
Total length	+++	+++	+++	o	++
Tail length	+++	+++	+++	o	o
Hind foot length	+++	+++	+++	o	o
Ear length	+++	o	+++	o	+++
Total body weight	+++	+++	+++	+++	+++
Cranial					
Greatest length	+++	+++	+++	+++	+++
Condylobasal length	+++	+++	+++	+++	+++
Basilar length	+++	+++	+++	+++	+++
Zygomatic breadth	+++	+++	+++	+++	+++
Interorbital breadth	o	o	+	+	o
Braincase breadth	+++	+	+++	o	+++
Rostral breadth	+++	+++	+++	o	+++
Nasal length	+++	+++	+++	+++	+
Bulla length	+++	+++	+++	++	+
Incisive foramen length	+++	+++	+++	+++	+++
Maxillary toothrow length	+++	+++	+++	+++	+++

Table 4. Results of Chi-square association test between the distributions of the 29 most common plant species and *O. irroratus* on the study grid. (*--significant, **--highly significant)

POSITIVE ASSOCIATION		NEGATIVE ASSOCIATION	
Plant species	Chi-square	Plant species	Chi-square
Mariscus congestus	61,19**	*Hyparrhenia dregeana*	35,28**
Eleocharis dregeana	58,28**	*Conyza podocephala*	33,68**
Berula erecta	57,55**	*Cynodon dactylon*	30,37**
Agrostis lachnantha	47,81**	*Melilotus alba*	27,78**
Juncus punctorius	31,54**	*Chironia palustris*	27,68**
Pennisetum thunbergii	26,58**	*Helictotrichon turgidulum*	23,95**
Cirsium vulgare	22,85**	*Berkheya radula*	15,42**
Paspalum dilatatum	21,30**	*Imperata cylindrica*	9,85**
Convolvulus ulosepalis	20,48**	*Juncus exsertus*	9,83**
Erigeron floribundus	18,00**	*Senecio erubescens*	9,64**
Mentha aquatica	15,90**		
Fuirena gracilis	14,60**		
Verbena bonariensis	14,29**		
Hemarthria altissima	12,87**		
Kniphofia porphyrantha	12,67**		
Plantago lanceolata	11,04**		
Arundinella nepalensis	5,48		
Agrimonia odorata	4,43		
Andropogon appendiculata	0,90		

Table 5. Results of Chi-square association test between the distributions of the 29 most common plant species and *O. angoniensis* on the study grid. (*--significant, **--highly significant)

POSITIVE ASSOCIATION		NEGATIVE ASSOCIATION	
Plant species	Chi-square	Plant species	Chi-square
Helictotrichon turgidulum	23,61**	*Mariscus congestus*	40,95**
Cynodon dactylon	23,37**	*Berula erecta*	36,21**
Melilotus alba	21,38**	*Eleocharis dregeana*	29,20**
Hyparrhenia dregeana	19,18**	*Agrostis lachnantha*	22,40**
Berkheya radula	17,96**	*Cirsium vulgare*	19,38**
Chironia palustris	17,20**	*Pennisetum thunbergii*	17,98**
Conyza podocephala	13,42**	*Juncus punctorius*	15,58**
Imperata cylindrica	6,29*	*Hemarthria altissima*	10,47**
Convolvulus ulosepalis	4,59*	*Kniphofia porphyrantha*	5,34*
Senecio erubescens	3,47	*Verbena bonariensis*	3,54
Paspalum dilatatum	2,80	*Agrimonia odorata*	2,97
Erigeron floribundus	2,38	*Mentha aquatica*	2,00
Plantago lanceolata	0,06	*Arundinella nepalensis*	0,36
Juncus exsertus	0,02	*Fuirena gracilis*	0,10
		Andropogon appendiculatus	0,00

Table 6. Rate of disappearance of *O. irroratus* from the study grid. The number of new animals captured during each period appears at the head and on the left of the appropriate vertical column. Disappearance in successive periods may be followed by reading down from the number of new captures during a particular month. Numbers in parentheses indicate animals dying in traps during that session. The number on the right of the column is the percentage of animals still remaining during that session, exclusive of those that died in traps.

	Mar.		Apr.		May		June		Aug.		Sep.		Oct.		Nov.		Dec.		Jan.		Feb.		May		July		Nov.		May	
M	27(2)	100																												
A	20(1)	80	22(1)	100																										
M	16(5)	67	15(1)	71	22(3)	100																								
J	13	69	10	50	13(1)	68	10(2)	100																						
J	-		-		-		-																							
A	8(1)	42	8(1)	40	12	67	4	50	12(1)	100																				
S	4	22	7	37	11	61	3	37	3	27	1	100																		
O	3	17	7(1)	37	9	50	4	50	3	27	1	100	9	100																
N	2	11	6	33	8	44	3	37	3	27	1	100	8	89	7	100														
D	2(1)	11	6	33	8	44	3	37	4	36	1	100	7	78	3	43	32(2)	100												
J	1	6	6(1)	33	7(2)	39	3	37	5	45	1	100	6	67	2	29	19	63	11	100										
F	0	0	3	18	5	31	3	37	4	36	1	100	5(1)	55	2	29	18	60	3	27	22(1)	100								
M	0	0	3(1)	18	4(1)	25	2	25	4(1)	36	1	100	3	37	2	29	17(3)	57	7(1)	64	12(1)	57	58(2)	100						
J	0	0	3	19	2	13	1	13	3	30	0	0	2	25	2	29	6	22	5	50	9	45	34	61	25	100				
N	0	0	1(1)	6	2(2)	13	1(1)	13	1	10	0	0	2	25	0	0	5	18	4(2)	40	8(2)	40	16(2)	29	8(1)	32	44	100		
M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	11	0	0	1	6	3	6	3	13	8	18	34	100

Table 7. Percentage composition of the prey species of the owls *Tyto alba* and *Tyto capensis* in the study area. Included is a comparison with the results of Vernon (1972).

Prey Species	*Tyto alba*		*Tyto capensis*	
	%*	%**	%*	%**
Reptilia	-	-	0,4	-
Aves	44,8	8,3	2,0	7,4
Myosorex sp.	1,7	4,4	7,9	11,1
Suncus sp.	6,9	2,2	8,7	1,9
Crocidura sp.	3,5	1,4	1,2	7,4
Chiroptera	-	0,7	-	-
Cryptomys hottentotus	-	-	1,6	5,6
Aethomys sp.	-	0,4	-	-
Praomys natalensis	12,1	47,1	14,7	18,5
Rhabdomys pumilio	-	2,5	36,9	7,4
Leggada minutoides	-	3,3	2,4	-
Steatomys sp.	-	2,9	-	-
Dendromus melanotis	3,5	2,9	2,8	-
Otomys angoniensis	1,7	?	0,8	?
Otomys irroratus	15,5	?	11,1	?
Otomys sp.(unidentifiable)	6,9	10,1	6,7	37,0
Mystromys albicaudatus	3,5	5,4	1,2	-
Tatera brantsi	-	8,3	0,8	3,7
Total no. of prey in sample	58	276	252	54

* Present study

** Vernon, 1972