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Otomys irroratus.

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Otomys Cuvier, 1824

The generic synonymy below follows Meester et al. (1986).

Otomys Cuvier, 1824:255. Based on two new species that were not named by Cuvier until 1829. Meanwhile, Brants (1827) described one of these as *Euryotis irrorata*, which Sclater (1899) subsequently designated as the type species.
Euryotis Brants, 1827:93. Type species *Euryotis irrorata* Brants, 1827, by original designation.
Oreomys Heuglin, 1877:76. Type species *Oreomys typus* Heuglin, 1877, by original designation.
Oreinomys Trouessart, 1881:111. Substitute for *Oreomys* Heuglin, 1877, thought to be preoccupied by *Orenomys* Aymard, 1855.
Myotomys Thomas, 1918:204, 206. Type species *Otomys unisulcatus* Brants, 1827 (=*Otomys unisulcatus* Cuvier, 1824, by original designation).
Anchotomys Thomas, 1918:208. As a subgenus of *Otomys* Cuvier, 1824. Type species *Otomys anchietae* (Bocage, 1882), by original designation.
Lamotomys Thomas, 1918:208. As a subgenus of *Otomys* Cuvier, 1824. Type species *Otomys laminatus* Thomas and Schwann, 1905, by original designation.
Metotomys Broom, 1937:765. Type species *Otomys turneri* Wroughton, 1907, by original designation.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciurognathi, Infraorder Myomorpha, Superfamily Muroidea, Family Muridae, Subfamily Otomyinae. The taxonomic affinities of this subfamily are not clear. Roberts (1951) created the Otomyidae for it, whereas Chaline et al. (1977) assigned it to the Nesomyidae. Due to the lamellate nature of the molars, and the possession of an enlarged third upper molar, the Otomyinae were included in the Cricetidae by Allen (1939), de Graaff (1981), Honacki et al. (1982) and Misonne (1974). The most recent trend, which essentially follows the classification of Tullberg (1899), is to include all muroid subfamilies in the Muridae, an approach adopted herein.

The genus *Otomys* includes 10 extant species. The status of some species must be accepted with reservation (de Graaff, 1981). On the basis of marked morphological similarities, *O. irroratus* and the East and Central African *O. tropicalis* Thomas, 1902, were regarded as conspecific by Bohmann (1952), Delany (1975), Kingdon (1974), and Rosevear (1969). Following Misonne (1974), the two species are here considered distinct, since their ranges are markedly disjunct.

A key to the 10 extant species follows (modified from Misonne, 1974):

1 Two deep grooves on each lower incisor .... *O. typus*
  Fewer than two deep grooves on each lower incisor 2
2 (1) One deep and one shallow inner groove on each lower incisor 3
  No more than one groove on each lower incisor 8
3 (2) Nine to 10 laminae on M3 .... *O. laminatus*
  Five to eight laminae on M3 4
4 (3) Five laminae on m1 .... *O. anchietae*
  Four laminae on m1 5
5 (4) Posterior petrotympanic foramen elongate .... *O. angoniensis*
  Posterior petrotympanic foramen round 6
6 (5) Molar series <8.8 mm long; length of hind foot <25 mm; fur buffy dorsally .... *O. saundersiae*
  Molar series >8.8 mm long; length of hind foot >25 mm; fur grayish dorsally 7
7 (6) Greatest width of nasals >8 mm .... *O. tropicalis*
  Greatest width of nasals <8 mm .... *O. irroratus*
8 (2) One deep groove only on each lower incisor .... *O. denti*
  One faint groove, or no groove, on each lower incisor 9
9 (8) Tail short (<50% of length of head and body); posterior petrotympanic foramen elongate .... *O. sloggetti*
  Tail usually >60% of length of head and body; posterior petrotympanic foramen round .... *O. unisulcatus*

Otomys irroratus (Brants, 1827)

Vlei Rat

Euryotis irrorata Brants, 1827:94. Type locality near Constantia, Cape Town District, South Africa (fide A. Smith, 1834, see below, *Euryotis typicus*); Uitenhage, eastern Cape, South Africa (fide Roberts, 1929).
Otomys bisulcatus Cuvier and Geoffroy, 1829:61. Type locality Namaqualand, South Africa.
Otomys capensis Cuvier, 1829:208. Type locality unknown.
Euryotis typicus A. Smith, 1834:149. Type locality near Constantia, Cape Town District, South Africa. Renaming of *E. irrorata*.
Euryotis obscura Lichtenstein, 1842:10. Type locality "Kaffirland," South Africa.

CONTEXT AND CONTENT. Context as noted above for genus. Meester et al. (1986) recognized eight subspecies provisionally, but stated that this number probably is too high.

O. i. irroratus (Brants, 1827:94), see *Euryotis irrorata* above (*capensis* Cuvier, *typicus* Smith, *bisulcatus* Cuvier and Geoffroy, and *obscura* Lichtenstein are synonyms).
O. i. auratus Wroughton, 1906:272. Type locality Vredefort, northern Orange Free State, South Africa.
O. i. cupreus Wroughton, 1906:273. Type locality Woodbush Hills, 48 km N Pietersburg, northern Transvaal, South Africa.
O. i. coenosus Thomas, 1918:208. Type locality Kuruman, northern Cape Province, South Africa.
O. i. natalensis Roberts, 1929:111. Type locality Kilgobbin Farm, Dargle Rail Station, central Natal, South Africa.
O. i. randensis Roberts, 1929:112. Type locality Fonteinebleu, Johannesburg, Transvaal, South Africa.
O. i. cupreoides Roberts, 1946:318. Type locality Newgate Farm, above Wylie's Poort, Soutpansberg, northern Transvaal, South Africa.
O. i. orientalis Roberts, 1946:318. Type locality Umzimkulu, Griqualand East, Natal, South Africa.

DIAGNOSIS. Skull sturdily built, with a narrow interorbital constriction (Fig. 1). Supraoccipital ridges prominent. Nasals expanded anteriorly, resulting in a broad, spoon-shaped rostrum deflected downward. Bullae small to medium-sized; posterior petrotympanic foramina large and rounded (Fig. 2). Palate narrow, with deep pterygoid fossae; palatal foramina long, nearly reaching M1. Basioccipital less narrowed than in *Parotomys*. Mandibles short, powerfully built, with deep, heavy ridges (Ellerman, 1941).

Length of maxillary toothrow exceeds 8.8 mm (Davis, 1973). Upper incisors each have a deep external groove; lower incisors usually with one deep outer and one shallow inner groove. First upper molar has three laminae, M2 two, and M3 usually six, sometimes seven. First lower molar is the largest tooth in the mandible, with four laminae; m2 and m3 each have two laminae.

Baculum is U-shaped, obovate basally, and grooved for part of its length (Fig. 3). Proximal portion comprises bone, the distal cartilage. Mean measurements (in mm) of the proximal portion are: total length, 5.44 (4.3 to 6.5); greatest width of base, 1.71 (0.9 to 2.3). Baculum size increases with age, and morphology changes, numerous processes developing laterally (Davis, 1973).

Otomys irroratus often is confused with its sibling species *O. angoniensis* (Davis, 1962; Misonne, 1974). Body color, size, and

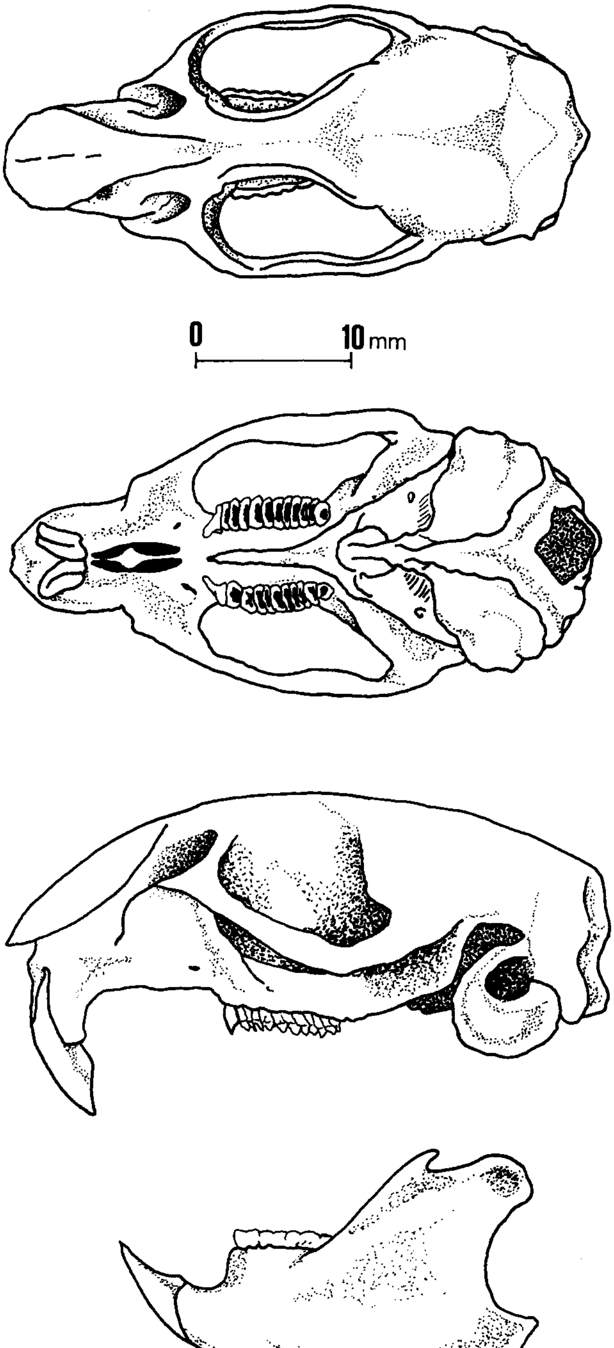

FIG. 1. Dorsal, ventral, and lateral view of skull, and lateral view of mandible of *Otomys irroratus*.

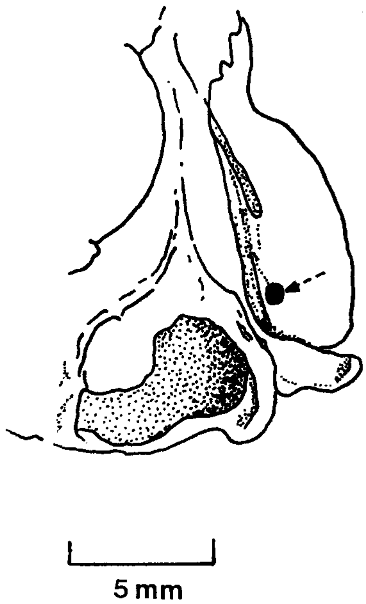

FIG. 2. Basicranial region of *Otomys irroratus* showing the round petrotympanic foramen (from Meester et al., 1986; used with permission of Transvaal Museum Press).

length of hind foot have been used to differentiate between these taxa (Davis, 1973), but these characters are not constant, and vary geographically. Relative size and shape of the petrotympanic foramen remains the only firm distinguishing character, being large and rounded in *O. irroratus*, and small and slitlike in *O. angoniensis* (Misonne, 1974).

Otomys sloggetti, *O. denti*, and *O. unisulcatus* differ in lacking lingual grooves on lower incisors. *O. typus* has two deep labial grooves on each lower incisor, as opposed to one deep and one shallow groove in *O. irroratus*. *O. laminatus* has nine to 10 laminae on M3, whereas *O. irroratus* has only six. *O. anchietae* has five laminae on m1, compared to only four in *O. irroratus*. The nasals of *O. tropicalis* are wider (>8 mm) than in *O. irroratus* (<8 mm).

GENERAL CHARACTERS. Body size is medium to large. Appearance is vole-like, with a stocky physique, medium-sized eyes, and large, well-haired pinnae (Fig. 4). Means and ranges (in parentheses) for body measurements (in mm) of 79 adult *O. irroratus* were: total length, 259 (229 to 303); length of tail, 98 (82 to 117); length of hind foot, 32 (29 to 34); length of ear, 21 (19 to 23). Mean mass was 143.7 g (102 to 206); mass varied seasonally, and declined in late winter when vegetation quality was poorest (Davis, 1973). Body measurements of males and females do not differ significantly at $P = 0.05$.

Dorsal color is dark slaty-gray, suffused with buffy and brown. Pelage composed of hairs that are slate-colored for basal four-fifths, subterminally buffy, with dark tips, and an admixture of long, wholly black hairs (de Graaff, 1981). Sides of body paler due to scarcity of black-tipped hairs. Ventral hair tips whitish to buffy. Head color resembles that of back, except for muzzle and cheeks that are lighter and rust-colored. Tail buffy ventrally and laterally, dorsally dark brown (Roberts, 1951). Feet dull grayish, palmar and plantar surfaces naked. All digits clawed, but hind claws longer; pollex and outermost digits of hind feet reduced in size. Body color varies geographically. *O. i. natalensis* and *O. i. randensis* generally darkest; *O. i. auratus* lightest, with body a dull golden color, because of preponderance of buff speckling.

Skull arched, with a narrow palate, and a high median keel. Mandible short and deep, with heavy ridges; mandibular ramus deep; coronoid process small. Mastoid bulla moderately enlarged compared to other muroids. Tympanic bulla small to moderate, of globose form (Carleton and Musser, 1984; de Graaff, 1981; Ellerman, 1941; Roberts, 1951). Means and ranges (in parentheses) for cranial measurements (in mm) of 79 *O. i. randensis* are: greatest length, 40.6 (38.3 to 44.8); condylobasal length, 39.5 (36.8 to 43.5); basilar length, 33.1 (30.8 to 36.9); zygomatic breadth, 16.8 (15.6 to 18.7); rostral breadth, 7.5 (7.0 to 8.3); length of nasal, 18.5 (16.7 to 20.8); length of bulla, 7.3 (6.7 to 8.4); length of incisive foramen, 7.2 (6.5 to 8.2); length of maxillary toothrow, 10.1 (9.5 to 11.0; Davis, 1973). *O. i. orientalis*, *O. i. coenosus*, and *O. i. randensis* usually have larger skulls than other subspecies (Roberts, 1951).

DISTRIBUTION. Confined to southern Africa at elevations from 0 to 2,400 m (Fig. 5), unlike *O. tropicalis* which occurs in East and Central Africa (Zaire, Cameroun, through Uganda and Kenya). Range markedly disjunct, mainly because of need for mesic habitats. Found mainly in montane and submontane grasslands of the Southern Savanna Biotic zone (Davis, 1973), but also in the Forest and South West Cape zones (de Graaff, 1981). Occurs from southern Cape Province through Natal, Lesotho, and the Orange Free State to the southern and central parts of the Transvaal (Davis, 1962, 1974; Davis, 1973; de Graaff, 1981; Meester et al., 1986; Misonne, 1974; Rautenbach, 1982; Smithers, 1983). Four relict

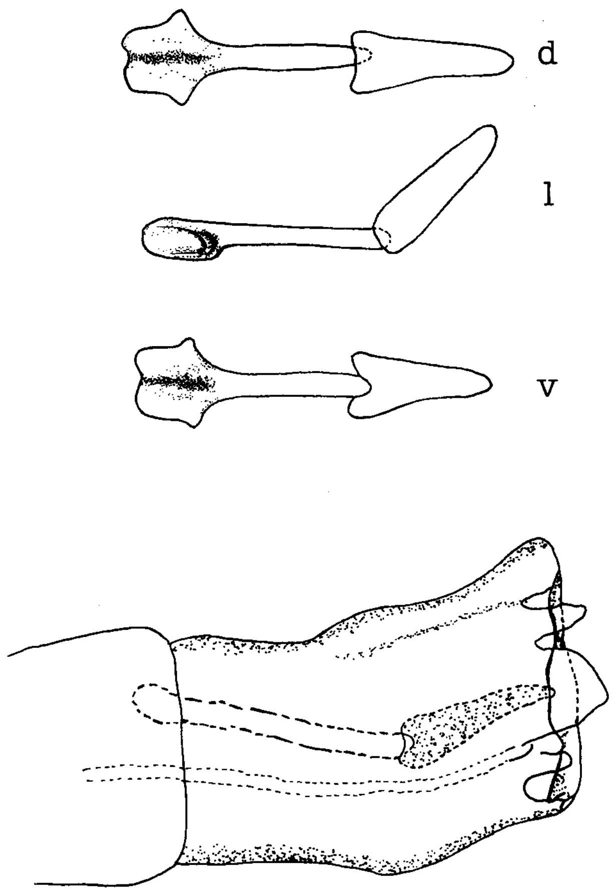

FIG. 3. Dorsal, lateral, and ventral views of baculum, and lateral view of phallus, of *Otomys irroratus* (from Davis, 1973). See text for measurements.

populations are known: three in the South West Arid zone (Cape: Kamiesberg; Upper Karoo; Kuruman), and one in the forest patches of eastern Zimbabwe-western Mozambique (Davis, 1973; Smithers and Lobao Tello, 1976; Smithers and Wilson, 1979).

FOSSIL RECORD. *Otomys* predominates among rodents in southern African Pleistocene deposits, and *O. irroratus* was recorded at Florisbad, Orange Free State (Dreyer and Lyle, 1931). Broom (1937) described *Palaeotomys* from fossil beds in South Africa (late Pliocene) and East Africa (late Pleistocene), and *Prototomys* was recorded in late Pliocene beds in the Transvaal (Broom and Schepers, 1946; Lavocat, 1978). *Euryotomys* was found in early Pliocene deposits of the Cape (Pocock, 1976).

FORM AND FUNCTION. Fur shaggy, individual hairs long and soft. Seasonal molt sequences in adults not known; Davis (1973) suggested that *O. irroratus* replaces hairs continuously. Injury to skin often results in the development of patches of white fur.

Phallus of complex type, with a comparatively thin spongy layer (Fig. 3). Baculum a single bone (as in the simple type), but has an array of processes usually considered to characterize the complex type (Davis, 1973).

Dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16. Incisors broad and opisthodont, with the labial surfaces pigmented yellow. Cheekteeth lophodont, with no indication of cuspidation. Molar laminar formula is 3-2-(6 to 7)/4-2-2 (de Graaff, 1981).

Digestive tract specialized for herbivory, and resembles that of *O. tropicalis* (Dieterlen, 1968), and the meadow vole *Microtus pennsylvanicus* (Golley, 1960). Stomach U-shaped, and comprises an oesophageal sac capable of tremendous expansion, a fundic gland region, and a pyloric region, all lined extensively with glandular epithelia. Small intestine consists of duodenum (15.2 cm) and ileum (20.5 cm); length of large intestine averages 27.4 cm (Davis, 1973). Caecum is the dominant structure of the digestive tract, with a mean length of 14.9 cm, a complex form with many infoldings, and a papillose lining (Perrin and Curtis, 1980).

FIG. 4. *Otomys irroratus*, male, from Dargle Farm, near Pietermaritzburg, Natal.

ONTOGENY AND REPRODUCTION. *Otomys irroratus* is polyestrous, and breeds three to four times annually, mostly during the wet season. In the Transvaal, reproduction declined during the dry midwinter months (June and July) when nocturnal temperatures were low, days were short, and food scarce. Resumption of high levels of breeding activity in August followed an increase in photoperiod, but not in food availability, which was poorest then (Davis and Meester, 1981). In the eastern Cape, where rainfall is variable, but peaks in autumn and spring, *O. irroratus* bred throughout the year, but with a recession in midsummer. This decline in reproduction involved a reduced pregnancy rate, rather than testicular regression. Reproduction was not markedly influenced by rainfall, but seemingly relied on an abundant source of herbage on which to feed (Perrin, 1980*a*, 1980*b*).

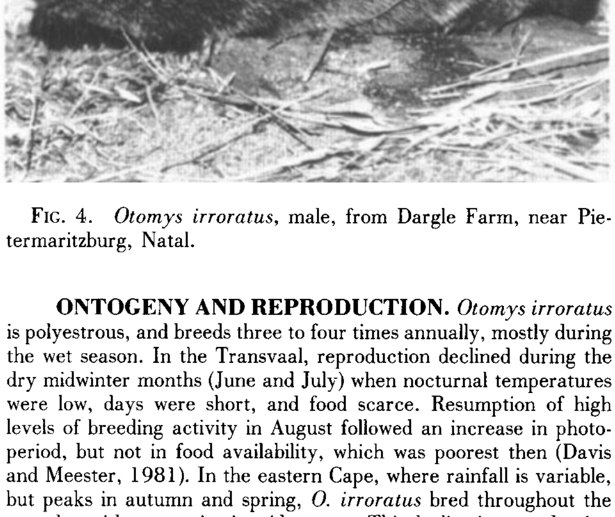

FIG. 5. Map of southern Africa showing the distribution of *Otomys irroratus*. Type localities of subspecies are indicated by triangles. Subspecies boundaries are provisional, awaiting a review of the species. Taxa are as follows: 1, *O. i. irroratus*; 2, *O. i. orientalis*; 3, *O. i. coenosus*; 4, *O. i. auratus*; 5, *O. i. natalensis*; 6, *O. i. randensis*; 7, *O. i. cupreus*; 8, *O. i. cupreoides*.

Gestation period is 35 to 40 days (Davis and Meester, 1981), sometimes as long as 42 days (Perrin, 1980*a*). This is long compared with that of similar-sized rodents, but is consistent with the large size and precociality of young at birth. FitzSimons (1920) stated that litter size ranges from five to 12, but this is unlikely, because females have only four (inguinal) mammae. In the Transvaal, mean litter size was 2.8 (1 to 4; Davis and Meester, 1981), whereas in the Cape it was 1.48 ± 0.61 ($n = 81$; Perrin, 1980*a*). Primiparous females bore litters (1.61 ± 0.61; $n = 18$) not significantly larger than those of multiparous females (1.43 ± 0.61; $n = 67$). Mean litter size was significantly ($P < 0.01$) higher in spring (1.81 ± 0.68; $n = 27$) than in other seasons, probably in response to the vegetation flush associated with high rainfall (Perrin, 1980*a*).

Young are precocial at birth, with a fine fur (similar in color to that of adults) covering the head and body. Mean mass at birth is 12.5 g (9.6 to 15.5 g). The eyes are closed, but their positions are obvious as slight bulges beneath slits of black skin. Ear pinnae are erect and the auditory meati open. Neonates show a limited response to sound, but by the second day have an acute sense of hearing. Incisors are erupted at birth, enabling the pups to cling to the mother's nipples for the first 2 weeks (Davis, 1972; Davis and Meester, 1981).

Growth of young is rapid, and individual mass increases at a rate of 1.2 g/day for 5 weeks, to reach 71% of adult mass by 10 weeks of age. For the first few days after birth, young emit high-pitched squeaks when detached from the mother's nipples, these presumably aiding the mother to find them. Coordination for locomotion develops anteroposteriorly, and as the legs become coordinated, the pups run along behind the mother while attached to her inguinal mammae. The juvenile molt commences on the dorsal surface of the head on day 14, then proceeds posteriorly until day 42. The subadult molt starts between days 56 and 70, and is completed by day 84. Behavioral development of the young is rapid and most adult patterns are manifested by day 14 (Davis and Meester, 1981).

Davis and Meester (1981) found that females become sexually mature at 9 to 10 weeks old, when their mass is about 96 g, although some females matured at 45 g and 4 weeks of age. Males matured later, but at about the same mass (96 g and 13 weeks). Davis (1973) recorded the lifespan of a captive *O. irroratus* as 22 months, and commented that wild individuals probably do not live more than 2 years.

ECOLOGY. *Otomys irroratus* is terrestrial or semi-aquatic and occupies areas of lush grasses, sedges, and herbaceous vegetation associated with damp soils in vleis (marshes), or along the fringes of dams, rivers, and streams. In montane areas, it occurs on grass-covered hillsides, sometimes considerable distances from water (Davis, 1973). Open, bowl-shaped nests (15 cm in diameter) of shredded grass are made under heavy growths of vegetation and are connected to foraging areas by intricate, and well-defined, communal runway systems that often are also used by coexisting species, such as *O. angoniensis*, *Rhabdomys pumilio*, and *Crocidura flavescens*.

Davis (1973) found a highly significant association of *O. irroratus* with the following plant species on a grid near Pretoria, Transvaal: *Mariscus congestus*, *Eleocharis dregeana*, *Berula erecta*, *Agrostis lachnantha*, *Juncus punctorius*, *Pennisetum thunbergii*, and *Cirsium vulgare*. Schulz (1953), however, remarked that the density of vegetative cover probably contributes more than its floristic composition in determining the ecological distribution of vlei rats.

Vlei rats are specialized herbivores that use caecal-microbial symbionts to aid digestion of complex fibrous carbohydrates, and for the production of amino acids and vitamins. The diet is composed of only green plant material and has a fairly stable nutrient content with low lipid levels, and moderately high levels of soluble carbohydrates (Perrin, 1980*c*). Although young shoots and rhizomes of reeds (*Phragmites* sp.) and even exotic plants such as the thistle (*Cirsium vulgare*) may be consumed (Davis, 1973), the most frequently eaten items are succulent grass stems and leaves (Curtis and Perrin, 1979). *O. irroratus* also eats the softer bark and cambial layers of young conifers and causes substantial damage to pine plantations (MacKellar, 1952; Schulz, 1953, 1962). Damage to crops of lucerne (alfafa) by this species also has been reported (Shortridge, 1934). Captive *O. irroratus* will eat freshly picked grasses, lettuce, cabbage, carrots, and maize seeds.

Perrin (1980*c*) noted that *O. irroratus* modifies its diet in relation to precipitation to maintain an optimal energy intake for continued reproduction. When food is scarce, more abundant but poorer-quality vegetation is cropped. More leafy material is ingested after heavy rains when grass stems become coarser and more vascular.

Coprophagy is common in *O. irroratus*, and presumably facilitates caecal fermentation and vitamin metabolism. During weaning, young eat both their own feces and those of others, this habit insures that they obtain sufficient microbes for the digestion of solid food (Willan, 1982).

Otomys irroratus usually is plentiful where it occurs (de Graaff, 1981). Davis (1973) recorded population densities from 17 rats/ha in September following the winter decline in breeding, and when food availability was poorest, to 72 rats/ha at the end of the main breeding season (May). Mean density was 36 animals/ha. The main determinant of population size was rainfall and possibly temperature.

Population structure of *O. irroratus* varied seasonally. Juveniles were absent from July to September, and most abundant shortly after the onset of breeding (October to November), and again at the end of the main breeding season. Subadults were most numerous in June and July following maturation of the many juveniles recorded in May. Adults were least abundant in June and most numerous in September. Sex ratios fluctuated monthly, but showed no significant deviations from parity (Davis, 1973).

Mean home range size (calculated by the exclusive-boundary-strip method) of 40 *O. irroratus* was 1,443 m^2 (675 to 3,038 m^2). Males occupied significantly ($P < 0.01$) larger ranges (1,730 m^2) than females (1,252 m^2). Home range size decreased slightly, but not significantly, during winter (Davis, 1973).

Perrin (1980*b*) classified *O. irroratus* as a K-strategist. However, Davis and Meester (1981) remarked that this species occupies an intermediate position along the r-K continuum, citing several characteristics of K-selection (large body size; long lifespan; small litter size; prolonged breeding season; well-developed parental care; high survival of young), but also stressing the susceptibility of *O. irroratus* to climatic vagaries as indicative of r-selection. Willan (1982) pointed out that the habitats favored by *O. irroratus* usually are stable, and agreed with Perrin (1980*b*) that this species is a K-strategist.

Otomys irroratus disappeared from a study grid at a rate of 3.1%, with a peak in autumn and September (late winter to early spring; Davis, 1973). Inundation of available habitat by floodwaters (which probably resulted in drowning and starvation) and predation were the main mortality factors. Predators of *O. irroratus* include: Reptilia—python (*Python sebae*), mole snake (*Pseudaspis cana*), rinkals (*Hemachatus haemachatus*), Cape cobra (*Naja nivea*), and puffadder (*Bitis arietans*; FitzSimons, 1920); Aves—grey heron (*Ardea cinerea*; Geldenhuys, 1950), black-shouldered kite (*Elanus caeruleus*), long-crested eagle (*Lophaetus occipitalis*), barn owl (*Tyto alba*), grass owl (*Tyto capensis*), marsh owl (*Asio capensis*), spotted eagle owl (*Bubo africanus*; Benson, 1965; Dean, 1973, 1978; de Graaff, 1981); Mammalia, Carnivora—serval (*Felis serval*), wild cat (*Felis lybica*), genet (*Genetta* sp.), mongoose (species unrecorded), jackal (*Canis* sp.), African polecat (*Ictonyx striatus*), honey badger (*Mellivora capensis*), and possibly also Cape clawless otter (*Aonyx capensis*; Davis, 1973; FitzSimons, 1920); and humans (Smithers, 1983). The flesh of dead *O. irroratus* is readily scavenged by other rodents and shrews. The barn owl and grass owl, closely associated with the habitat of *O. irroratus*, are the main predators, and vlei rats compose 11% to 13%, and 42% respectively, of the prey in their pellets (Bateman, 1960; Skead, 1956, 1963). Data on predation rates by carnivores are scarce, but Davis (1973) stated that *O. irroratus* was by far the most prominent prey item in feces of the serval.

Geldenhuys (1950) found a dry maize meal-warfarin mixture an effective poison for reducing densities of populations of *O. irroratus*. Despite use of this rodenticide in pine plantations for the past 20 years, vlei rats continue to cause extensive damage to young trees.

Parasites of *O. irroratus* include: nematodes—*Physaloptera africana*, *Longistriata capensis*, *Paralibyostronglus* sp., *Capillaria hepatica* (Davis, 1973); trematodes—*Fasciola hepatica*; cestodes—*Paranoplocephala omphalodes*, *P. otomyos*, *Inermicapsifer congolensis*, *I. madagascariensis*, *Raillietina thryonomysi* (Collins, 1972); mites—*Laelaps giganteus*, *L. muricola*, *L. parvulus*, *L. transvaalensis*, *Heamolaelaps glasgowi*, *H. labuschagnei*, *H. murinus*, *H. taterae*, *Myobia otomyia*, *Trombicula panieri*, *Schoengastia gigantica*, *S. lavoipierrei*, *S. oubanguiana*, *S. rad-*

fordi, Euschoengastia africana, E. otomyia, Schoutedenichia andrei, S. panai, S. penetrans, S. schoutedeni, Gahrliepia longiscutullata, Listrophoroides womersleyi (Zumpt, 1961); fleas—*Echidnophaga gallinacea, Pulex irritans, Xenopsylla cheopis, X. eridos, X. brasiliensis, X. hirsuta, Ctenophthalmus calceatus, Dinopsyllus abaris, D. ellobius, D. lypusus, D. tenax, Listropsylla agrippinae, L. prominens, L. chelura, L. fouriei, Hypsophthalmus montivagans, H. temporis, Epirimia aganippes, Chiastopsylla roseinnesi, C. rossi, C. carus, Leptopsylla segnis* (Zumpt, 1966); ticks—*Ornithodoros zumpti, Ixodes alluaudi, Haemaphysalis leachii, Rhipicephalus appendiculatus, R. capensis, R. sanguineus, R. simus* (Theiler, 1962); and lice—*Polyplax otomydis* (Davis, 1973; Johnson, 1960).

Otomys irroratus is a probable reservoir of various zoonoses, including bluetongue virus (that affects sheep), bubonic plague (*Yersinia pestis*), tick-bite fever (*Rickettsia conorii*), and Q-fever (*Coxiella burnetii*; de Graaff, 1981; Powell, 1925). The pucilid fleas carried by *O. irroratus* are the principal vectors of plague endemic to southern Africa. However, due to their secretive nature and patchy distribution, vlei rats do not play a primary role in disease transmission to man (de Graaff, 1981).

BEHAVIOR. Activity essentially crepuscular, but with some diurnal and nocturnal activity (Davis, 1973). Perrin (1981) recorded a continual day-night activity profile and a definite short-term rhythm in the laboratory.

Otomys irroratus is quadrupedal, and uses the diagonal sequence of alternate limb movements during locomotion. Walking punctuated by brief hesitations is the main form of locomotion. Running is very quick, with the body held close to the ground in a flat posture, seemingly adapted for rapid movement along runways (Davis, 1972). *O. irroratus* is an able swimmer, but does not take to water readily (Smithers, 1983).

Feeding and grooming behavior of *O. irroratus* was studied by Davis (1972). The forepaws are used to manipulate food items, and to pass coarse portions back and forth through the mouth. Unpalatable pieces are often discarded as telltale piles which mark the feeding areas. Feeding is usually followed by grooming, which involves face-washing, and combing or scratching with the paws.

Otomys irroratus is a shy, aggressive species that exhibits complex threat and communication patterns indicative of an antisocial nature. Although individuals congregate in suitable mesic habitats, and often use the same runway systems, adults generally are solitary (Davis, 1972). Olfactory communication is well developed, and anal-gland marking, along with indiscriminate defecation and urination in runways, probably serve to minimize intraspecific conflict (Willan, 1982). Adults are at least partly territorial, and probably defend runways in the vicinity of their nests (Davis, 1973).

When individuals meet, nose-to-nose contact is made with the body held in an elongate, flat posture. Naso-anal contact sometimes occurs in intersexual encounters (Davis, 1973). A caste-specific hierarchy in aggression is displayed in the order—scrotal male > perforate female > non-scrotal male > imperforate female, and the heavier animal is usually more aggressive during intrasexual encounters. Initial contact between equal ranking individuals is followed by threat displays or outright attack. Fighting occurs after a short chase, is usually of short duration, and often results in the infliction of serious wounds. A renewed bout of combat then ensues, unless one animal flees, or shows submissive behavior. Submissive behavior is well developed in lower-ranking individuals and involves adopting an upright posture with the forelimbs extended (thereby exposing the vulnerable belly) accompanied by a soft chittering (Davis, 1973).

GENETICS. The karyotype of *O. irroratus* is composed of 9 pairs of biarmed and 4 pairs of acrocentric autosomes, a submetacentric X, and a small, acrocentric Y: thus, $2n = 28$ and fn = 47/48 (Robinson and Elder, 1987) although Matthey (1964) reported fn = 49/50. This contrasts with $2n = 28$ and fn = 50 in *O. unisulcatus* and $2n = 56$ and fn = 56 in *O. angoniensis*.

Extensive genomic reorganization, involving structural rearrangements, has resulted in changes to the karyotype of *O. irroratus* to the extent that no homologies with that of *O. unisulcatus*, or with the presumed ancestral rodent karyotype, are evident. Narrow ecological tolerance and susceptibility to climatic vagaries may, through the creation of isolated demes, have facilitated rapid chromosomal evolution in *O. irroratus*, perhaps as described by the population-flush model (Robinson and Elder, 1987).

REMARKS. The name *Otomys* is derived from the Greek *otos* meaning ear, and *mys* meaning mouse, with reference to the conspicuous ears. The species name comes from the Latin *irroro* meaning to sprinkle with dew, this referring to the speckling of buff in the pelage (de Graaff, 1981). A taxonomic review of *O. irroratus* is needed, not only to clarify subspecific relationships, but also to confirm its distinctness from *O. tropicalis*.

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