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# Rattus lutreolus.

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## *Rattus lutreolus* (Gray, 1841)

### Swamp Rat

*Mus lutreola* Gray, 1841:409. Lectotype locality Mosquito Island, Hunter River, New South Wales.

*Mus vellerosus* Gray, 1847:5. Type locality between Glenelg and Murray rivers, South Australia.

*Mus velutinus* Thomas, 1882:415. Lectotype locality Tasmania.

*Rattus lacus* Tate, 1951:347. Type locality Lake Barrine, Atherton Tableland, Queensland.

**CONTEXT AND CONTENT.** Order Rodentia, Family Muridae, Subfamily Murinae, Genus *Rattus*, Subgenus *Rattus* (Carleton and Musser, 1984; Taylor and Horner, 1973*a*). Australian species assigned to *Rattus* may not be congeneric with Asian *Rattus* for the genus lacks adequate definition (Musser, 1981). *R. lutreolus* occurs only in Australia and three subspecies are recognized and described in detail by Taylor and Horner (1973*a*):

*R. l. lutreolus* (Gray, 1841:409), see above (*vellerosus* Gray, *cambricus* Troughton and *imbil* Troughton are synonyms; Taylor and Horner, 1973*a*).

*R. l. velutinus* (Thomas, 1882:415), see above.

*R. l. lacus* (Tate, 1951:347), see above.

**DIAGNOSIS.** *Rattus lutreolus* has the shortest tail, darkest hind feet, narrowest incisive foramina, and broadest incisors and molars of all Australian *Rattus* (Taylor and Horner, 1973*a*). Relative to occipitonasal length, the palatal length is the longest among Australian *Rattus* and M3 is relatively shorter in its contribution to molar-row length.

**GENERAL CHARACTERS.** The swamp rat is stocky and robust with short hind feet and tail (Fig. 1). The dark dorsal pelage varies from dark gray to reddish brown or blackish, blending to a somewhat paler hue ventrally. Individual hairs are translucent basally, and the overall coloration is produced by the distal portions of the hairs that may be banded terminally or tipped with rust, bronze, or yellow. The pelage is soft and loose, and is longer in rats from cooler southern regions and upland localities than in populations from hotter regions. The soft pelage mostly conceals the rounded short ears covered by fine hairs. The plantigrade feet have clawed digits, except for the reduced pollex that bears a flattened nail, and possess five palmar and six plantar tubercles. The ventral surface of all four feet is naked, but the dorsal surface bears short dark brown hairs. The hind feet average less than 20% of the head and body length. The tail is blackish or dark brown and is covered by overlapping scales with three short bristlelike hairs emerging from the edge of each scale. Tail length is about 75% of the head and body length. There are two pairs of mammary glands pectorally, and two (*velutinus*), three (*lutreolus*), or as yet undetermined (*lacus*) pairs abdominally.

The skull is robust, slightly convex dorsally, and bears wide incisors and molars (Fig. 2). The supraorbital-temporal ridges are conspicuous and continue posteriorly from half to the full length of the parietals. The rostrum is stout, closely flanked by the broad zygomatic plates, and the nasal bones end about in line with the anterior faces of the upper incisors. The long narrow incisive foramina become slitlike as they approach and end near the first loph of M1. The molars are broad, the intermolar width correspondingly narrow, and the molar rows terminate near the posterior end of the hard palate. The tympanic bullae usually are shorter than the alveolar length of M1-M3 and average 18 to 20% of the basal length of the skull. The posterior cingulum of m1 and m2 is lacking on mainland subspecies, *R. l. lutreolus* and *R. l. lacus* (Taylor and Horner, 1973*a*).

**DISTRIBUTION.** *Rattus lutreolus* occurs in the eastern coastal and subcoastal mainland, primarily in the southeastern portion, and in Tasmania, including insular distribution in Bass Strait (Fig. 3). The westernmost extension of the range is on Kangaroo Island and nearby mainland of South Australia; it extends eastward and northward to southeastern Queensland at Imbil. Farther north, the species occurs on the highlands of north coastal Queensland at Mt. Spec, Kirrama, and Lake Barrine (Taylor, 1975; Taylor and Horner, 1973*a*). This species is primarily lowland in distribution, except the north Queensland sites, ranging from sea level to about 1,525 m (Taylor and Horner, 1973*a*). Its distribution hugs the coast and rarely extends more than 200 km inland. Only in the Darling Downs of southeastern Queensland is it recorded west of the Great Dividing Range.

**FOSSIL RECORD.** Western Victoria and southwestern New South Wales harbor a few fossil sites of *R. lutreolus*. The latter records indicate its former distribution in the Murray-Darling basin extended at least 400 km from the coast (Watts and Aslin, 1981). These fossil remains are Holocene, 4,000 years old or less (Archer and Hand, 1984; Wakefield, 1963, 1964, 1967).

**FORM AND FUNCTION.** Ranges in external measurements (in mm) of 194 adult *R. lutreolus* (Taylor and Horner, 1973*a*) are: length of head and body, 122 to 197; tail length, 82 to 147; length of hindfoot, 26 to 37. Ear length (in mm from notch) of 173 adults is 12 to 25, and body mass (in g) of 131 adults (excluding *lacus*) is 56 to 167. Ranges in measurements (in mm) for adult skulls (Taylor and Horner, 1973*a*) are as follows (*n* in parentheses): occipitonasal length, 35.0 to 43.3 (211); palatal length, 18.4 to 24.0 (263); length of incisive foramen, 5.5 to 7.9 (269); width of incisive foramina, 1.2 to 2.3 (270); width inside M1-M1, 1.8 to 3.8 (271); width outside M1-M1, 7.0 to 9.2 (271); bulla length, 5.6 to 7.6 (263); length of M1-M3 alveolus, 7.3 to 7.8 (273). Those rats with evidence of present or former breeding activity were placed in the adult category (Taylor and Horner, 1973*a*).

*Rattus lutreolus* has been confused with another rodent, *Mastacomys fuscus* (Higgins and Petterd, 1883, as *Mus castaneus*), also a darkly colored rat of similar body size possessing a relatively short tail; the two are sympatric and syntopic in the southern range of *R. lutreolus* (Green, 1967) and on Mt. Royal in northeastern New South Wales (Dickman and McKechnie, 1985). *R. lutreolus* has narrower incisors, a uniformly colored tail (bicolored in *M.*

FIG. 1. Photograph of *Rattus lutreolus lutreolus* from Port Stephens, New South Wales (provided by Ederic Slater).

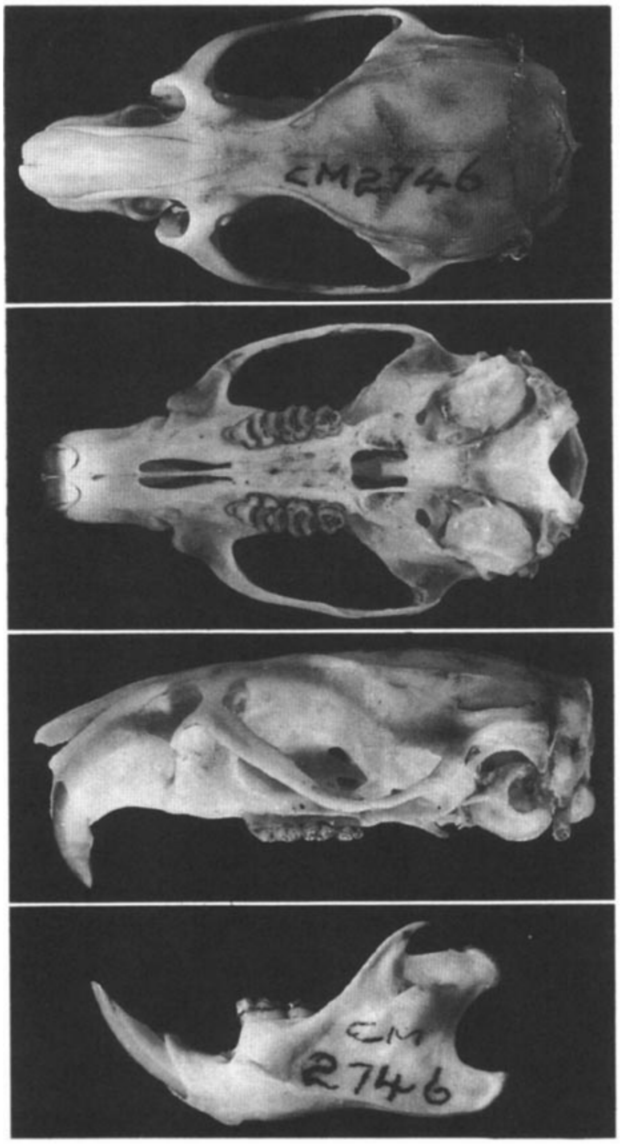

FIG. 2. Dorsal, ventral, and lateral views of cranium, and lateral view of mandible of *Rattus lutreolus lutreolus* (CM2746 from Salamander Bay, Port Stephens, New South Wales). Occipitonasal length of skull is 39.5 mm.

*fuscus*), and eight or 10 instead of four teats. The dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16.

The external structure of the glans penis has been photographed and described (Morrissey and Breed, 1982, figs. 12 and 13). The adult glans penis is about 5.8 mm long, 3.1 mm in maximum width, and 1.7 mm wide near its outer rim; its morphology is similar to that of other Australian *Rattus* examined (Morrissey and Breed, 1982). The spermatozoa are 162 to 164 μm in total length, 13 to 15 μm in head length, 54 μm for midpiece, and 95 μm for principal and end piece. They are similar to those of all other *Rattus* species examined and distinct from those of all other Australian genera of murid rodents (Breed and Sarafis, 1979).

Under experimental conditions, *R. lutreolus* was able to tolerate long periods of water deprivation, during which it lost 2.8 to 3.2% of body mass per day for 9 days (Baverstock, 1976). Intake of solid food and urine output declined during this period. This species is unique among four *Rattus* species examined in its ability to tolerate water deprivation by retaining metabolic products, rather than by excreting them and incurring further water loss, and by partly abandoning homeostasis. The ecological significance of its extraordinary tolerance for water imbalance requires study.

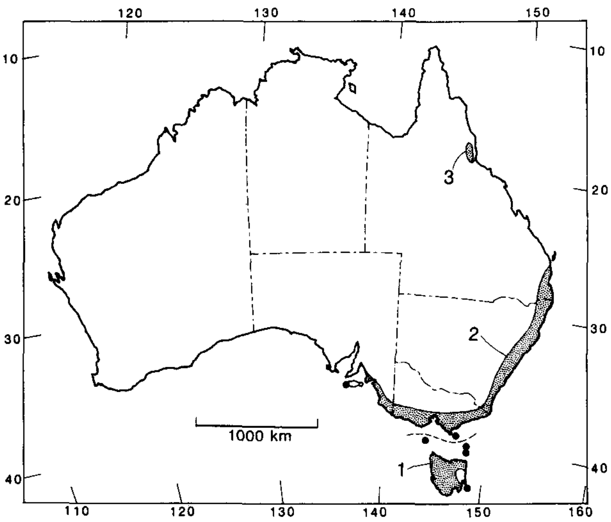

FIG. 3. Geographical distribution of the three subspecies of *Rattus lutreolus*: 1, *R. l. velutinus*; 2, *R. l. lutreolus*; 3, *R. l. lacus*. Island occurrences are shown as closed circles.

Between 10 and 31°C, approximately the spectrum of ambient temperatures within its geographic range, *R. lutreolus* regulates its body temperature effectively (Collins, 1973). A significant increase in the rate of evaporative water loss occurs above 31°C in conjunction with controlled hyperthermia up to 41.5°C, at which point ambient and body temperatures are about equal. Effective dissipation of metabolic body heat under stress of high ambient temperatures is brought about by insensible water loss through the skin, salivation, licking, and hyperventilation. This response may be elicited by an increase in cholinergic activity at ambient temperatures above 31°C, but is perhaps seldom exercised in this species; heat stress usually is avoided by retreating to a burrow (Collins, 1973).

**ONTOGENY AND REPRODUCTION.** The estrous cycle is estimated as 4 (3 to 5), 4.7, or 5.2 days (Braithwaite, 1979*a*; Breed, 1978; Fox, 1985), and the number of corpora lutea formed per cycle ranges from four to nine (Taylor and Horner, 1973*b*). The diameter of fresh corpora lutea in adults is 1,000 to 1,250 μm and largest diameter of follicles is 550 to 1,125 μm (Taylor and Horner, 1973*b*). Largest diameter of follicles in juveniles is to 250 μm (Taylor and Horner, 1973*b*). *R. lutreolus* experiences a postpartum estrus (Taylor and Horner, 1973*b*), and gestation length is 23 to 25 days, but may be extended to 28 to 33 days when the female is nursing a litter (Braithwaite, 1979*a*; Fox, 1985). Litter size ranges from one to 11 (Braithwaite, 1979*a*) with means ranging from four in Tasmania and a small island (Braithwaite, 1979*a*; Green, 1967) to 5.8 on the mainland (Braithwaite, 1979*a*).

Reproductive rate appears to be correlated with habitat types (Braithwaite, 1979*a*). In study sites from Victoria, *R. lutreolus* occupying a riparian habitat were least productive, those in heathlands were more so, and those in a commensal relationship were the most productive. Mean number of litters was 1.5, 2.4, and 3.7, respectively, the duration of the breeding season was 4, 5, and 7 to 8 months, respectively, and the relative number of young breeding in their season of birth also increased in this order (Braithwaite, 1979*a*) according to the text, but not Table 2. Litter size, however, was not significantly different among populations in the three habitats examined. Length of breeding season seems to contribute most to the correlation between reproductive productivity and habitat type (Braithwaite, 1979*a*).

Testes of breeding males are 17 to 25 mm long by 10 to 15 mm wide, those of nonbreeding adults 6 to 15 mm long by 4 to 9 mm wide, and those of juveniles 6 to 7 mm long by 4 to 5 mm wide (Green, 1967; Taylor and Horner, 1973*b*). Among breeding males, diameter of seminiferous tubules is about 230 μm, and of Cowper's glands 2.3 to 3.4 mm; length of seminal vesicles is about 13.3 to 16.1 mm. Among adult nonbreeders, the diameter of seminiferous tubules is about 74 μm (Taylor and Horner, 1973*b*). The histology of these reproductive tissues is essentially the same in all native Australian *Rattus* (Taylor and Horner, 1973*b*).

*Rattus lutreolus* is a seasonal breeder; its major breeding efforts occur between September and March (Barritt, 1976; Taylor and Horner, 1973*b*). In its southernmost insular distribution, breeding may begin a few weeks later and extend into April (Green, 1967; Taylor and Horner, 1973*b*); onset of breeding also may vary with habitat (Braithwaite, 1979*a*). In southern Queensland, there are breeding records in May and midJuly, suggesting that seasonality of breeding may be reduced in subtropical latitudes (Taylor and Horner, 1973*b*). There is no information on breeding for the isolated tropical subspecies, *R. l. lacus.*

Like all other *Rattus* studied, neonatal *R. lutreolus* is naked except for vibrissae; pinnae are folded; umbilicus is evident; eyes are closed; and for the first several days milk in the stomach shows through the translucent skin. The young can right themselves when overturned. Although some earlier authors (for example, Le Souef and Burrell, 1926; Troughton, 1941, 1967) described newborn young of *R. lutreolus* as precociously furred, they confused *R. lutreolus* with the similar rat, *Mastacomys fuscus*, that produces precocious young. By 2 days of age, the dorsal skin of *R. lutreolus* develops some pigmentation, and the young can crawl; by 3 days, the pinnae are unfolded and fine body hair is evident. Teats are visible on females by 8 days, and by 13 days the young are fully furred. Incisors erupt by 14 days. By 15 days, young can crawl actively; eyes open by 17 days. By 19 days young can eat solid food. Young are independent between 22 (Green, 1967) and 25 days (Fox, 1979). Although there are minor differences in timing of certain events, *R. lutreolus* reaches independence at the same time as *R. fuscipes*, another Australian *Rattus* (Taylor, 1961).

At birth, body mass (in g) for males and females averages 5.2 and 5.0, respectively; average lengths (in mm) of head and body are 45.6 and 43.8, and of hindfoot 8.5 and 8.3 for the two sexes. By 25 days, the same dimensions for both sexes are about 25 g, 22 mm, and 92 mm, respectively. Mensural differences between sexes at birth are significant only for head and body length and do not continue as young develop, but become significant in all three dimensions at adulthood (Fox, 1979). Both sexes approach puberty at about 4 weeks of age and attempt to copulate at about 9 weeks, with earliest conception at 73 days (Fox, 1979). Growth continues for 3 years in the laboratory and presumably continues throughout life. In nature, however, *R. lutreolus* seldom lives beyond 1 year (Lunney, 1978), although there is a longevity record of 29 months (Watts, 1982).

Juveniles can be distinguished from adults, the latter showing past or current indications of breeding activity, on the basis of occipitonasal length, 35.0 mm or less in juvenile *R. l. lutreolus* and 34.9 mm or less in *R. l. velutinus* (Taylor and Horner, 1973*a*). No juveniles of *R. l. lacus* are known. Fox (1979) found head and body length the most reliable dimension for determining age to about 4 months for *lutreolus* in the field.

**ECOLOGY.** *Rattus lutreolus* inhabits coastal and subcoastal habitats in the southeastern temperate region of Australia, including Tasmania, and a few sites in the highland subcoastal tropics of northern Queensland. This species occurs primarily in wetlands harboring tall grasses or sedges, along the banks of streams, in coastal sand dunes, peaty ridges, heaths, and wet shelves of hillsides (Calaby, 1966; Keith and Calaby, 1968, fig. 5; Taylor and Horner, 1973*a*; Waite, 1900). In Tasmania, where it is the only species of *Rattus*, it occupies a wide range of habitats, including temperate rain forest, sedgelands, and coastal swamps (Green, 1967; Taylor and Horner, 1973*a*). Unlike its southern mainland conspecifics, the Tasmanian form selects well-drained habitats that are moist only seasonally (Green, 1967). Although the mainland form is not known to occur in subalpine habitats, the Tasmanian subspecies occupies high elevations that are snowcovered seasonally (Finlayson, 1933; Green, 1967). In warm to hot moist environments, *R. lutreolus* inhabits dense stands of bladey grass (*Imperata cylindrica*; Fox and Fox, 1984) that grows on poorly drained soils. The tropical form also is associated with bladey grass, in this instance near a lake, as well as with open forest that has a ground cover of grass. In all habitats, *R. lutreolus* is associated closely with dense vegetative cover and a source of green vegetation (Watts and Aslin, 1981). *R. lutreolus* has become an invader of exotic (*Pinus radiata, P. taeda*) and native (*Araucaria cunninghamii*) pine plantations (Barnett et al., 1977; Davis, 1956; McNally, 1955; Troughton, 1937), where it is a pest of economic importance. The rats damage bark and roots, and undermine trees by constructing burrows among interstices of their root systems. The damage occurs during winter months in *Araucaria* plantations (Davis, 1956).

The deep burrow systems and runways of *R. lutreolus* often are conspicuous (Waite, 1900). Where their habitats are flooded seasonally, they move to elevated ground as their burrows fill with water (Brazenor, 1936). Fresh runways can occur in sodden soil and even that covered by shallow water, indicating extensive activity in wet substrates and free navigation through water (Taylor and Horner, 1973*a*). Runways through swamps often are fully concealed from above by vegetation and permit activity under cover. In coastal dunes with low beach vegetation nearby, runways and other signs of activities of the rats generally are absent (Taylor and Horner, 1973*a*). Runways of Tasmanian *R. lutreolus* are about 4 cm wide, and are constructed and maintained by gnawing; burrows beneath the surface substrate are well branched and shallow (Green, 1967). Natural hollows, rotting logs, and fallen vegetation also are used for cover. Calaby (1966) came upon a *R. lutreolus* sharing the cover of a fallen elkhorn fern (*Platycerium bifurcatum*) with a spiny anteater (*Tachyglossus aculeatus*). Nesting materials within burrows generally are composed of dried vegetation. Braithwaite (1982) suggested that isolated small groups of *R. lutreolus* in good habitat maintain stable breeding populations, whereas those in marginal habitats do not breed and lack social structure. Such poor habitats may serve as temporary refuges for dispersing individuals.

For most of the year, the diet of *R. lutreolus* in Victoria is mainly basal stems, young rhizomes, and basal shoots of sedges and other monocotyledonous plants (Watts and Braithwaite, 1978). During summer, they may eat 25% or more (by volume) insects, fungi, and a variety of dicotyledonous plants (Watts, 1977). In heathlands, *R. lutreolus* ingests seeds as they become available in spring and early summer, a time coincident with breeding, thus possibly related to intake of high caloric and protein foods (Watts and Braithwaite, 1978). *R. lutreolus* in temperate climates seems to have a more specialized diet than other temperate rodents in Australia (Watts and Braithwaite, 1978). The diet of Tasmanian *R. lutreolus* is primarily vegetarian (Green, 1967) and includes sporangia of mosses (Mollison, 1960); in some instances, however, stomachs are filled with insect larvae (Green, 1967). Braithwaite (1979*b*) interpreted the long molar row of *R. lutreolus*, averaging longest of most Australian species (Ellerman, 1941; Taylor and Horner, 1973*a*), as an adaptation to herbivory.

Differential toothwear among *R. lutreolus* from Victoria is associated with differences in habitat; heathland populations that eat primarily sedge rhizomes have greater molar wear than riparian populations that feed on grass stems, and leaves and seeds (Braithwaite, 1979*b*). The greater abrasion by the sedges is thought to be related to an expected higher concentration of phytoliths associated with soils of low productivity. The higher incidence of a posterior cingulum on m3 among *R. lutreolus* occupying other than heathland habitats was interpreted by Braithwaite (1979*b*) as selection for its retention. This selective shift has occurred over the relatively short period of 100 years of human settlement during which these rats have exploited introduced grasses and other plants in riparian habitats.

Two free-living populations of *R. lutreolus* in Victoria, one in a heathland habitat and the other in a commensal situation in the grounds of a zoo, showed strong differences in their reproductive profiles (Braithwaite, 1980). In the latter situation, the breeding season was 2 to 3 months longer, body size was greater, juvenile growth and attainment of sexual maturity were accelerated, and the minimum survival rate was lower. Furthermore, the heathland population remained close to good vegetational cover in its daily activities, but the commensal rats were not restricted by lack of cover in zoo enclosures and, unlike the heathland rats, freely occupied adjacent grassland and bracken habitats (Braithwaite, 1980). The differences between the two populations seemed related primarily to differences in diet; the zoo habitat provided high caloric and protein foods year-round, whereas heathland habitat was subjected to strong seasonal changes in food quality. The life-history flexibility of *R. lutreolus* in adapting to a commensal relationship within a period of less than 30 years is remarkable. Braithwaite (1980) suggested that, when commensal opportunities for a species are juxtaposed with marginal habitat, the evolutionary pathway to commensalism is augmented.

Following a major fire at Nadgee Nature Reserve, New South Wales, that burned between 60,000 and 70,000 ha of heathland and forest, *R. lutreolus* survived by escaping to underground burrows (Recher et al., 1975). The following month, rats were present in peripheral situations, but even in the 2nd year were uncommon in the burned heathlands. In the 2nd year, however, *R. lutreolus*, normally not a forest dweller, became common in previously burned forests at this stage of regeneration when ground cover and vegetation could support its activities both day and night (Catling et al., 1982; Newsome and Catling, 1983; Recher et al., 1975). A nocturnal and more omnivorous rat, *Rattus fuscipes*, occupied forests within the first month of the burn (Recher et al., 1975). *R. lutreolus* was the first native rodent to recolonize heathland following the fire; it occupied and bred in both wet and dry prime habitats during the first 2 years, and wet and dry marginal habitats by the 6th year (Catling, 1986). It also became reproductively active at lower body masses on marginal heathland than on prime heathland habitats (Catling, 1986). In contrast, at another coastal site, *R. lutreolus* had poor dispersal and colonizing ability, and was unable to breed for the first 5 years after a fire (Fox, 1982). At Nadgee, prime habitat of *R. lutreolus* was on maturing heaths and the least favorable was in forests in which rats were restricted to cover of low vegetation and ground litter, sources of refuge that diminish with increase in forest height (Catling et al., 1982).

Over 28 months of declining annual rainfall and related food resources, *R. lutreolus* from Victoria declined in numbers in each of three winters and commenced its seasonal breeding progressively earlier following each winter (Braithwaite and Lee, 1979). The authors concluded that lower winter density may have promoted earlier breeding. The lowest survival of *R. lutreolus* was in summer coincident with the peak in breeding, but it was relatively high in winter; the period of low survival possibly was related to heightened stress associated with breeding. Individuals in habitats yielding better food supplies had smaller ranges, tended to be older, heavier, and less transient (Braithwaite and Lee, 1979). The habit of *R. lutreolus* to remain near a predictable food supply limits its opportunities to encounter conspecifics of the opposite sex. This habit may result in a less promiscuous mating system than its close relative, *R. fuscipes*, a more transient dietary opportunist (Braithwaite and Lee, 1979).

The well-defined breeding season, a lifespan of about 1 year, and the limited opportunity for young to breed in their season of birth impose marked seasonal changes in age classes. Late winter and early spring populations usually are entirely adults, whereas immatures enter the population in late spring through autumn. *R. lutreolus* can breed year-around in the laboratory, however (Watts and Aslin, 1981).

Except in commensal circumstances, *R. lutreolus* occurs in low densities. Taylor and Horner (1973*b*) had a 1.3% trap success for *R. l. lutreolus*, and a return of 5.8% for *R. l. velutinus*. Green (1967) expected a 10% return from populations of *R. l. velutinus* of relatively high density. At a forest site in northwestern New South Wales, mean distance between successive captures of individuals was 20.5 m (Barnett et al., 1977). In a heathland population from Victoria, the average adjusted distance between successive captures ranged from 23 to 97 m; the distance for adult males was significantly greater than for other groups during the breeding season (Braithwaite and Lee, 1979). The average adjusted distance between successive captures for mature females was similar year-around to that of immaures of both sexes. For all age-sex groups, the distance decreased with increase in density (Braithwaite and Lee, 1979). The average density of males examined across several habitats measured 2.8/ha and in wet habitats measured 5.4/ha (Fox, 1981). Breeding pairs of *R. lutreolus* in Tasmania have a home range of about 45 m in radius, and their litters tend to remain in the vicinity of this range for several months before dispersing (Green, 1967). The proportion of transients is thought to be lower in *R. lutreolus* than in *R. fuscipes*, and was calculated at 7.6% in a Victorian population of *R. lutreolus* over a 27-month period and 17.7% for *R. fuscipes* over 24 months (Braithwaite and Lee, 1979). In a population south of Sydney, New South Wales, adjusted home range length was the smallest in winter populations (primarily young of the previous breeding season), 93 m for males, 77 m for females (lower density) or 64 m for males, 54 m for females (higher density); it was largest after the onset of breeding while the trappable population was still entirely adult, 262 m for males and 105 m for females (Lunney, 1978). At the end of the breeding season, lengths were 168 m for adult males, 107 m for adult females and between 38 and 49 m for young of the season (Lunney, 1978). In a population recovering from effects of a fire in December 1972, density increased from 4.0 males/ha and 5.0 females/ha in June 1974, to 7.9 and 10.1, respectively, 12 months later (Lunney, 1978). Home ranges overlap in all seasons, reaching a peak in early summer when reproductive effort is at its height (Lunney, 1978).

*Rattus lutreolus* can be caught in any type of small box trap or break-back trap. Compared to *R. fuscipes* captures, those of *R. lutreolus* tend to be delayed initially, a factor probably related to the time taken to locate the traps rather than to trap shyness (Braithwaite and Lee, 1979). Swamp rats are attracted to a variety of baits including rolled oats, sunflower seeds, peanut butter, fruits, bacon, cheese, raw meat, honey, and bread (Green, 1967; Taylor and Horner, 1973*a*). Capture success usually is greatest when traps are set in runways or beneath logs and overhanging vegetation (Green, 1967). Individuals have been marked permanently by a system of toe-clipping (Barnett et al., 1977) or ear-tagging with fingerling fish tags (Green, 1967).

Although destruction of suitable habitat by fire, by grazing by domestic animals, and by the direct hand of man exercises a powerful influence on the abundance and distribution of *R. lutreolus*, undoubtedly some measure of natural control is exerted by predators. The masked owl (*Tyto novaehollandiae*) and other birds of prey, both nocturnal and diurnal, the marsupial native cat (*Dasyurus viverrinus*), the marsupial mouse (*Antechinus swainsonii*), and the feral cat (*Felis catus*) are viewed as likely predators of *R. lutreolus* in Tasmania (Green, 1967). About 2% of fecal passages of the introduced fox (*Vulpes vulpes*) in Victoria contain *R. lutreolus* (Brunner et al., 1975). Another study in Victoria, this of the fox and feral dog, or dingo (*Canis familiaris*), indicated an occurrence of *R. lutreolus* in 0.2% of the droppings in each of two areas (Brunner et al., 1976). In both studies, the sympatric rat, *R. fuscipes*, occurred in much greater frequency (7 to 27% of the droppings).

*Rattus lutreolus* exhibits strong sensitivity to sodium monofluoroacetate (1080), used as a poison in rodent and carnivore control. At a dosage of 1 mg/ml, swamp rats died 2.3 to 14.4 h later and were only slightly less susceptible to the poison than *R. fuscipes* in eastern Australia (McIlroy, 1982).

Parasites of *R. lutreolus* include cestodes: *Choanotaenia ratticola* (Obendorf, 1979) and *Taenia taeniaeformis* (Munday and Green, 1972); nematodes: *Capillaria gastrica*, *Dipetalonema lutreoli*, *Ganguleterakis spumosa*, *Odilia emanulae*, *O. mackerrasae*, and *Ophidascaris robertsi* (Durette-Desset, 1973; Mackerras, 1962; Obendorf, 1979); a fungus (Rees, 1967); mites: *Guntheria coorongensis*, *G. derricki*, *G. kallipygos*, *G. quatuor*, *G. queenslandica*, *Gymnolaelaps annectans*, *Laelaps assimilis*, *Laelapsella humi*, *Listrophoroides expansus*, *Mesolaelaps australiensis*, *M. bandicoota*, *Neotrombicula novaehollandiae*, *Ornithonyssus bacoti* (Domrow, 1961, 1963, 1973, 1977; Domrow and Lester, 1985; Green and Munday, 1971); lice: *Hoplopleura irritans* and the introduced *Polyplax spinulosa* (Green and Munday, 1971; Kuhn and Ludwig, 1966); ticks: *Ixodes cornuatus*, *I. fecialis*, *I. tasmani*, *I. trichosuri*, *I.* (*Sternalixodes*) sp. (Green and Munday, 1971; Roberts, 1970); fleas: *Acanthopsylla r. rothschildi*, *Bibikovana arcuata*, *B. colossa*, *B. rainbowi*, *Leptopsylla segnis* (introduced), *Macropsylla hercules*, *Metastivalius rectus*, *Nosopsyllus fasciatus* (introduced), *Pygiopsylla hoplia*, *P. zethi*, *Stephanocircus dasyuri*, *S. greeni tasmanica*, *S. pectinipes*, *S. simsoni* (Dunnet and Mardon, 1974; Traub, 1980); a staphylinid beetle, *Myotyphlus jansoni* (Calaby, 1962).

**BEHAVIOR.** Unlike most *Rattus* native to Australia, *R. lutreolus* is active both by day and by night (Green, 1967). Its well-developed system of covered runways permits diurnal activity with reduced chance of detection overhead. Activity of *R. lutreolus* at seven sites in Victoria was measured by times of trap captures. Of these populations, five were as active during the day as at night, and the other two were more active during the day (Braithwaite, 1979*a*). However, an insular population examined in another study was largely nocturnal, an activity pattern possibly imposed by the almost exclusive presence of diurnal avian predators (Braithwaite, 1977). The more usual day-night activity of *R. lutreolus* may be related to its bulky diet of vegetation and low intake of food parcels of high caloric value (Braithwaite, 1977).

Tail injuries, a measure of aggressive social encounters, appear to be inflicted largely on the vanquished member of a fight. The degree of tail scarring in free-living populations occurs with greatest incidence on adult males during the breeding season (Braithwaite, 1979*a*). Three native species of *Rattus* examined for social postures in the laboratory exhibit threat posture by piloerection, head turned toward its opponent, back arching and leg extension, but, of the three, *R. lutreolus* is the least inclined to attack a conspecific (Barnett et al. 1982).

The basic vocal repertoire of all *Rattus* native to Australia can be divided into four types: squeal, ultrasonic pipping, ultrasonic whistle, and coughing. Two nonvocal sounds, hissing and tooth-chattering, complete the array of sound emissions of these rats (Watts, 1980). Of all calls, the long whistle is the most distinctive between species. For *R. lutreolus*, the mode in fundamental frequency of this call is 35 kHz; that of other species ranges from 28 to 45 kHz (Watts, 1980). Analysis of these sound emissions points to evolutionary conservatism within *Rattus* and the inference that these emissions are a basic element in the behavioral repertoire of the genus (Watts, 1980).

Grooming behavior in captive *R. lutreolus* is regular and includes scratching the body with the claws of the hind feet followed by cleaning the claws with the teeth. Rubbing the face with the forepaws and licking also are frequent (Green, 1967). Swamp rats urinate and defecate at random over feeding areas and along runways in the field. The elongate oval fecal pellet of an adult is 12 to 15 mm long and 4 to 5 mm in diameter; that of subadults may be smaller. The pellet is coarse in texture and varies in color between gray and brown (Green, 1967).

Although described as a water-loving species (Jones, 1925), given the Latin name of *lutreolus*, and occasionally called the water rat by earlier investigators, the Tasmanian subspecies of *R. lutreolus* appears to avoid swimming and to keep its pelage dry whenever possible (Green, 1967).

**GENETICS.** In the karyotype of *R. lutreolus*, pair 1 is a large subacrocentric, pairs 2 to 12 are telocentric, pair 13 is subacrocentric, and pairs 14 to 20 are metacentric. The X-chromosome is a medium-sized telocentric and the Y-chromosome is a very small telocentric. The usual fundamental number is 60. In some individuals, pair 5 is heteromorphic for a subacrocentric and a telocentric element (Baverstock et al., 1977).

The standard karyotype of *R. lutreolus* is similar to that of *R. fuscipes*, but differs primarily from the latter in three additional pairs of chromosomes that are acrocentric and in one pair of submetacentric chromosomes instead of the two pairs of metacentric chromosomes characteristic of *R. fuscipes* (Kennedy, 1969). The chromosomes of *R. lutreolus* differ from those of *R. norvegicus* only in the morphology of the two pairs. Kennedy (1969) concluded that *R. fuscipes* was derived by two Robertsonian centric fusions from *R. lutreolus*, which in turn evolved from an ancestral form related to *R. norvegicus*. Subsequently, the karyotype of *R. lutreolus* also was shown to resemble closely that of *Rattus rattus* (Dartnall, 1970).

Based on multivariate morphometrics, Taylor and Horner (1973*a*) concluded that the progenitor of Australian *Rattus* may resemble an ancestral form of *R. lutreolus*. Discriminate function analysis, based on 20 cranial measurements of 1,274 specimens of all Australian species and subspecies, indicates two main clusters radiating from *R. lutreolus*. One consists of the *R. fuscipes* and *R. leucopus* representatives and the other, *R. sordidus* and *R. tunneyi* (Taylor and Horner, 1973*a*). When *Rattus* from both Australia and New Guinea were compared, either at the subspecies or species level, by use of a minimum spanning-tree projection, *R. lutreolus* again assumed a position between the *tunneyi-sordidus* group and the *fuscipes-leucopus* group (Taylor et al., 1983).

After examining karyotypes of all but one of the 13 species and subspecies of Australian *Rattus*, Baverstock et al. (1977) also concluded that *R. lutreolus* is most like an ancestral species for Australian *Rattus*. They judged this on the close resemblance of its karyotype to that of several Asian species of *Rattus*. They also concluded that karyotypic evolution of Australian *Rattus* occurred primarily by Robertsonian rearrangements. Based on electrophoretic screening at 20 loci, Australian species of *Rattus* group in a pattern similar to that demonstrated by Taylor and Horner (1973*a*) and reaffirms their conclusion that *R. lutreolus* is no closer to one main cluster than to the other (Baverstock et al., 1981).

Karyotype analysis, using G-banding and the karyotype of *R. lutreolus* as ancestral, permitted confirmation of the chromosomal rearrangements postulated in the earlier study and also led to the discovery of heteromorphism in pair 8 of the *R. lutreolus* karyotype (Baverstock et al., 1983*a*). G-banding analysis supports the view that karyotypes of Australian *Rattus* are substantially different from those of other genera of Australian rodents (Baverstock et al., 1983*b*). Australian *Rattus* show close affinity to Asian *Rattus* in their karyotype morphology (Baverstock et al., 1977; Yosida, 1973).

**REMARKS.** Long before similarity in karyotypes of *R. lutreolus* and *R. fuscipes* was demonstrated, the two species had been inappropriately linked taxonomically. A full historical review of the misapplication of the name *fuscipes* to include *lutreolus* is given by Taylor and Horner (1967). In summary, the taxonomic confusion resulted from the loss of the holotype of *fuscipes*, a species proposed by Waterhouse (1839), followed by Gray's (1843) decision to include *lutreolus* in subjective synonymy with *fuscipes*. Thomas (1906) corrected the error, but many later workers, including Tate (1951), continued to regard them as conspecific. Not until the entire historical development of the problem was addressed and described, followed by a major revisionary study of Australian *Rattus* (Taylor and Horner, 1967, 1973*a*), has the status of *R. lutreolus* as a full species been accepted universally. In addition to extensive morphometric analysis, the inability of *R. fuscipes* and *R. lutreolus* to hybridize in the laboratory was at one time presented as substantiating evidence of their biological distinctiveness (Horner and Taylor, 1965).

The proposals based on karyotypic and morphometric analyses, suggesting that *R. lutreolus* and *R. fuscipes* may be tied by close common ancestry (Baverstock et al., 1977; Dartnall, 1970; Kennedy, 1969; Taylor and Horner, 1973*a*), were followed by another laboratory attempt to hybridize the two species, and this time it was successful (Fox and Murray, 1979). The cross between *R. lutreolus* ($2n = 42$) and *R. fuscipes* ($2n = 38$) resulted in the survival of one offspring ($2n = 40$) that survived and sired a litter when backcrossed with *R. lutreolus*. The remaining five hybrids did not live to sexual maturity. The hybrid karyotype involved two chromosomal fusions (Fox and Murray, 1979). Although the relative success of this hybridization provides additional support for close ancestry of the two species, they are not known to hybridize under natural conditions despite their widespread sympatry on mainland Australia.

The least known of the *R. lutreolus* subspecies is *R. l. lacus*. It was described originally as a full species, *R. lacus*, on the basis of the only five specimens in existence, but it is significant that the describer, Tate (1951), regarded *R. lutreolus* and *R. fuscipes* as conspecific. Later, the original material was re-evaluated and judged to be a subspecies of *R. lutreolus* (Taylor and Horner, 1967, 1973*a*). Since then, one specimen has been collected at each of two other localities in the Atherton Tableland of Queensland (Taylor, 1975). This subspecies is of special interest for it is the only member of *R. lutreolus* to occur in tropical Australia, and, as presently known, is confined to highland sites. Until this subspecies is better understood, the biology of *R. lutreolus* at the species level remains only partially known.

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