

*Rattus fuscipes*. By J. Mary Taylor and John H. Calaby

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*Rattus fuscipes* (Waterhouse, 1839)

Bush Rat

*Mus fuscipes* Waterhouse, 1839:66. Neotype locality 4 mi. S. Mt. Melville, Albany, Western Australia.

*Mus greyii* Gray, 1841:410. Lectotype locality South Australia.

*Mus assimilis* Gould, 1858:241. Lectotype locality Clarence River, New South Wales.

*Rattus mondraïnese* Thomas, 1921:428. Type locality Mondraïn Island, Archipelago of the Recherche, Western Australia.

*Rattus murrayi* Thomas, 1923a:601. Type locality Pearson's Island, Investigator Group, South Australia.

*Rattus glauerti* Thomas, 1926:308. Type locality East Wallaby Island, Houtman's Abrolhos, Western Australia.

**CONTEXT AND CONTENT.** Order Rodentia, Family Muridae, Subfamily Murinae, Genus *Rattus*, Subgenus *Rattus* (Carleton and Musser, 1984; Taylor and Horner, 1973a). Australian *Rattus* may not be true *Rattus* as the genus is inadequately defined (Musser, 1981). Four subspecies are recognized (Taylor and Horner, 1973a):

*R. f. fuscipes* (Waterhouse, 1839:66), see above.

*R. f. greyii* (Gray, 1841:410), see above (*ravus* Brazenor, *peccatus* Troughton, and *pelori* Finlayson are synonyms; Taylor and Horner, 1973a).

*R. f. assimilis* (Gould, 1858:241), see above.

*R. f. coracius* (Thomas, 1923b:173). Type locality Dinner Creek, Ravenshoe, 2,900 ft, Queensland.

**DIAGNOSIS.** *Rattus fuscipes* is highly variable in range of adult body size and in general coloration; the tail usually is slightly shorter than head and body. However, there are few external characters that serve to distinguish it from some other soft-furred native *Rattus*. *R. fuscipes* is distinguished most clearly from all other native Australian *Rattus* by combined features of small tympanic bullae (17.5 to 19.6% of basal length of skull and relatively straight-sided incisive foramina (Taylor and Horner, 1973a).

**GENERAL CHARACTERS.** The bush rat ranges in body length and in hind foot length from among smallest to among largest of *Rattus* native to the mainland (Fig. 1). Body coloration varies from gray-brown to a warm reddish brown, and blends to light gray to buffy cream ventrally (Taylor and Horner, 1973a). In certain insular localities in South Australia, the pelage is lighter in color and the dorsum is redder (on Eyre Peninsula; Goat Island, the Investigator Group) than on the mainland. Foot color is dusky, rather than light, on rats from Kangaroo Island and Western Australia (Taylor and Horner, 1973a). The dorsal coat color tends to be darker in humid regions in areas receiving 75 cm or less annual rainfall (Taylor and Horner, 1973a). The pelage is dense, soft, and without spines, and tends to be longer in cooler southern areas. Individual hairs gray and translucent basally; surface body coloration produced by distal banding of the hairs; coarser, dark guard hairs interspersed dorsally with banded hairs. The short rounded ears are sparsely haired and approximate dorsal pelage in color. Feet pentadactyl and all digits clawed except pollex that is reduced and has flattened nail instead. Feet plantigrade, having five palmar tubercles and six plantar tubercles. Walking surface of foot devoid of hair, but upper surface sparsely covered by short hairs that range from white to brown. Tail is brown, gray, or occasionally blackish, and is covered with overlapping scales; three short bristlelike hairs occur at edge of each scale. There are 10 mammae, two pectoral pairs and three abdominal pairs, except in specimens from north of northern New South Wales in which there is only one pectoral pair (Taylor and Horner, 1973a).

Skull elongate and relatively flat; ridges in supraorbital-temporal region poorly developed or inconspicuous (Fig. 2). Incisive foramina terminate immediately posterior to anterior faces of first molars.

Nasals overhang anterior faces of incisors and premaxillae on the relatively narrow rostrum. Tympanic bullae equal in length, or slightly smaller than, alveolar length of M1-M3. A posterior cusp present on m1 and m2 (Taylor and Horner, 1973a).

**DISTRIBUTION.** *Rattus fuscipes* is a mainland species; it is primarily coastal in distribution and also occupies offshore islands (Fig. 3). It occurs in southwestern Australia, from near Jurien Bay to Israelite Bay and on the Abrolhos Islands farther north; discontinuously along southern and eastern regions from Eyre Peninsula, South Australia, including offshore islands, to near Portland, Victoria; from Terang, Victoria, to near Rockhampton, Queensland; and from Townsville to Cooktown in northern Queensland (Taylor and Horner, 1973a; Watts and Aslin, 1981). Although mainly a lowland species, *R. fuscipes* occurs in Australian Alps to 2,210 m.

**FOSSIL RECORD.** Subfossils known from Grampians Mountains in Victoria about 100 km inland from coast (Wakefield, 1963), from Mammoth Cave, southwestern Western Australia, dating to 37,000 B. P. (Archer and Hand, 1984), and from Fromm's Landing, South Australia, dating to about 4,000 B. P. (Archer and Hand, 1984). Also, subfossils are recorded within the present range (Watts and Aslin, 1981).

**FORM AND FUNCTION.** External measurements (in mm) of 530 adult specimens of *R. fuscipes* (Taylor and Horner, 1973a) are: head and body length, 111 to 214; tail length, 105 to 195; hindfoot length, 25 to 40. Ear length (from notch) of 406 adults is 15 to 27, and body mass (in g) of 184 adults is 40 to 225 (Taylor and Horner, 1973a). Among the most diagnostic measurements (in mm) of adult skulls (Taylor and Horner, 1973a) are (*n* in parentheses): occipitonasal length, 34.1 to 46.9 (623); zygomatic width, 16.7 to 23.2 (599); interorbital width, 4.3 to 6.7 (750); palatal length, 16.9 to 25.4 (740); length of incisive foramen, 5.7 to 9.2 (750); bulla length, 5.4 to 8.3 (693). The adult category (Taylor and Horner, 1973a) contains those showing evidence of current or past breeding activity.

Body mass and hindfoot length in combination (Taylor, 1961, fig. 6), incisor width and molar wear (Warneke, 1971), and wet and dry mass of the eye lens (Myers et al., 1977) have been used to estimate age in *R. fuscipes*. The technique based on body mass and hindfoot length was derived from a small sample of males, thus, is useful only to 6 weeks of age when sexual differences in growth are evident (Taylor, 1961). The technique based on incisor width is more reliable than that based on molar wear after 6 months of



FIG. 1. Photograph of *Rattus fuscipes assimilis* from Tidbinbilla, Australian Capital Territory (provided by Ederic Slater).

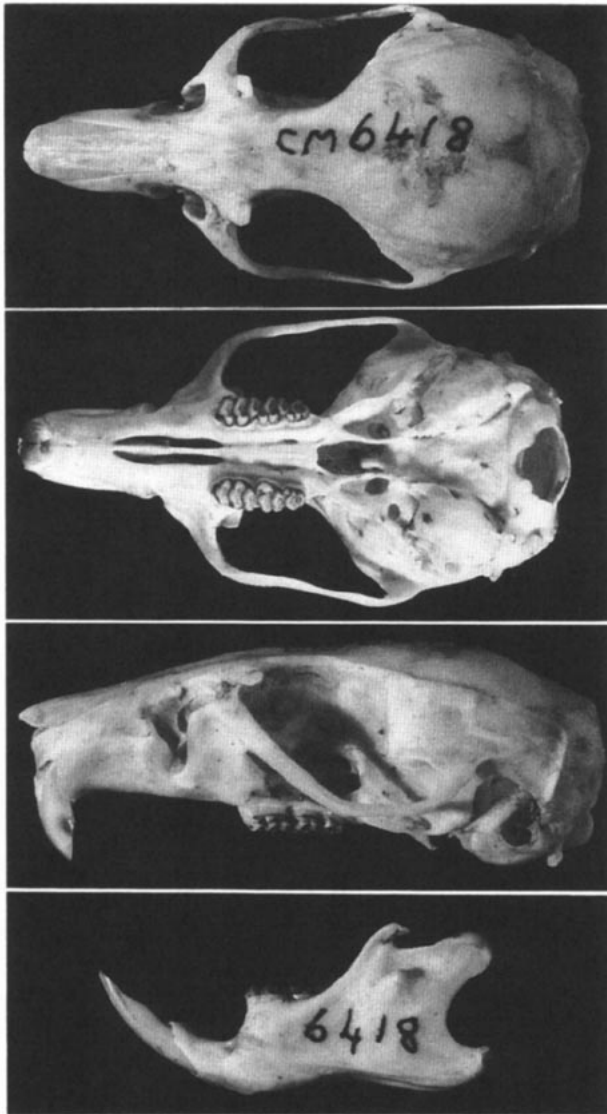


FIG. 2. Dorsal, ventral, and lateral views of cranium, and lateral view of the mandible of *Rattus fuscipes assimilis* (CM6418 from Granite Flat, via Mitta Mitta, Victoria). Occipitonasal length of skull is 40.0 mm.

age; no sexual differences were reported (Warneke, 1971). Wet mass of the lens was nearly as reliable as dry mass, but both were more reliable to 5 months than in older rats (Myers et al., 1977).

The geographically correlated transition in number of mammae was noted initially by Calaby (1966). At Clouds Creek in northeastern New South Wales, where overlap in numbers occurs, females with the higher count are significantly heavier and predominate in exotic pine forest (*Pinus taeda*), whereas those with the lower formula are in greater numbers in native wet sclerophyll and rain forest (Barnett et al., 1977). Because population movement between the two types of habitat is limited, the investigators suggested a measure of separation between populations.

Inconspicuous supraorbital-temporal ridging of the skull of *R. fuscipes* is a character shared with adult *Rattus leucopus* and most subadults of all other native species of *Rattus*. The dental formula is  $i\ 1/1$ ,  $c\ 0/0$ ,  $p\ 0/0$ ,  $m\ 3/3$ , total 16.

Internal reproductive anatomy strongly resembles that of the laboratory rat, *Rattus norvegicus* (Greene, 1935), however, the external genitalia are less similar. The glans penis is 6 mm long in *R. f. assimilis* (Morrisey and Breed, 1982) and 9 to 10 mm long in *R. norvegicus*; otherwise, the two are similar in configuration (Argyropulo, 1929; Morrisey and Breed, 1982; Taylor, 1961). The basal portion of the baculum is smaller in *R. fuscipes*, and the distal portion differs in shape (Taylor, 1961, fig. 8). The clitoris of *R.*

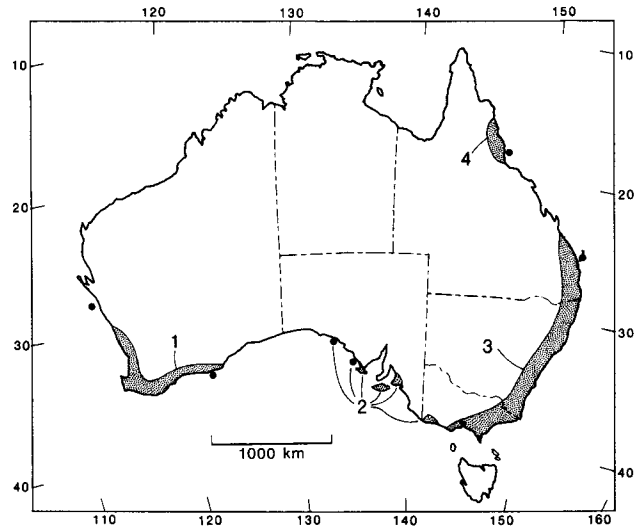


FIG. 3. Geographical distribution of the four subspecies of *Rattus fuscipes*: 1, *R. f. fuscipes*; 2, *R. f. greyii*; 3, *R. f. assimilis*; 4, *R. f. coracius*. Island occurrences are shown as closed circles.

*fuscipes* is almost twice the length (7 to 9 mm) of that of *R. norvegicus*; neither contains an os clitoridis (Taylor, 1961).

The thermoregulatory capacity of *R. fuscipes* in a hot, northern locality in Western Australia is slightly greater than that of conspecifics from a cooler, southern locality. However, animals from both regions are less able to use evaporative cooling as a mechanism to retard lethal hyperthermia than two species of native *Rattus* from even hotter northern climes (Collins, 1973). The inability of *R. fuscipes* to thermoregulate adequately in hot climates may limit extension of its range farther northward (Collins, 1973). Although once considered to be poorly endowed with a mechanism for water economy (Baverstock, 1976), a more recent study has shown that *R. fuscipes* falls within the range of other Australian congeners studied (Magnusson, 1985).

A serendipitous discovery relating to dietary intake of fluoroacetate by *R. fuscipes* of Western Australia followed the observation that the vertebrate pesticide compound 1080 (sodium monofluoroacetate) was relatively ineffective in controlling this species in Western Australia (King et al., 1978). The tolerance to ingested fluoroacetate also appears to have evolved independently in several marsupials, and possibly other vertebrates as well, in areas where certain plants contain the toxin naturally. However, the same vertebrate species in areas of toxin-free vegetation are as susceptible to 1080 as other species (King et al., 1978; McIlroy, 1982). Proposal that the recent evolutionary history of *R. fuscipes* involved movement westward to Western Australia from an earlier eastern distribution is supported by use of fluoroacetate tolerance as a genetic marker in the western rats (Oliver et al., 1979).

Insular *R. fuscipes*, with higher population densities and larger body size than mainland counterparts, show less adrenal response based on corticosteroid levels than the latter animals after being subjected experimentally to the same stress levels (Barnett, 1977). This mechanism is interpreted as an adaptive response to an island situation where emigration and dispersal are restricted severely and high densities result in greater frequency of social encounters (Barnett, 1977).

Montane *R. fuscipes* exhibited seasonal changes in body mass and composition, associated with adaptation to winter, over 3 years that the population was monitored (Stewart and Barnett, 1983). In winter, weights of heart, spleen, adrenals, and testes declined, whereas carcass lipid and brown adipose tissue, and pelage weight, increased. Liver, lean carcass, and body weight were lowest as winter approached (May), peaked slightly in June, and declined in July and August. Body masses of captive rats exposed to natural light and temperature declined in winter, even though food and water were provided ad libitum. *R. fuscipes* undergoes these weight changes as an adaptive mechanism to winter conditions rather than to a direct effect of changes in diet or food supply (Stewart and Barnett, 1983).

**ONTOGENY AND REPRODUCTION.** The estrous cycle of *R. f. assimilis* is 4.5 days (Taylor, 1961) and of *R. f. coraciis* is 5.3 (Breed, 1976). In the former, proestrus lasts 10 to 14 h, estrus is typified by well-cornified vaginal epithelium and lasts 24 h, metestrus usually lasts less than 10 h, and diestrus, 50 to 60 h. Mating generally occurs in early estrus well before cornification fully develops (Taylor, 1961). Uterine diameter, greatest during estrus, diminishes by half or more during a cycle. Postpartum estrus occurs about 41 h after birth and lasts less than 24 h. Lactational anestrus of 20 to 24 days follows postpartum estrus whether or not copulation occurs. Females enter anestrus at the end of a breeding season.

Pseudopregnancy can be induced by electrical stimulation of the cervix and vaginal wall during estrus, and lasts 15 to 17 days (Taylor, 1961). It is not known whether infertile copulations induce pseudopregnancy in field populations, nor is there evidence from laboratory stock that this occurs.

Gestation period, defined as the interval between retrieval of vaginal sperm and parturition, is 22 to 24 days, averaging 22.8 days (Taylor, 1961); defined as the length between the last estrus and parturition, it is 20 to 21 days, averaging 20.4 days (Warneke, 1971). Embryos implant on the 6th day following fertilization (Taylor, 1961). Gestation length may be extended to 28 to 32 days by delay in implantation during lactation, the longer delays being associated with larger nursing litters (Taylor, 1961). Prenatal loss of ova or embryos is about 40% (Taylor, 1961). In captivity, birth is usually between 1400 and 2000 h, and the sex ratio is 50:50, similar to that obtained from advanced pregnancies in the field (Taylor, 1961; Warneke, 1971). Litter size in captivity is one to seven, averaging four (Taylor, 1961), and in the field is one to eight, averaging about five (Warneke, 1971). *R. f. assimilis* and *R. f. coraciis* appear to have lower average ovulation rates (4.9 to 5.4; Breed, 1978; Taylor and Horner, 1972, 1973b) and litter size (3.8 to 4.6; Taylor and Horner, 1972, 1973b), whereas *R. f. fuscipes* and *R. f. greyii* have higher ovulation rates (6.4 to 8.4) and litter size (5.0 to 6.7; Breed, 1978; Taylor and Horner, 1972, 1973b). Females from Victoria usually produce three litters in a breeding season (Warneke, 1971). Mean number of litters born to a laboratory female is 3.6; as many as 14 litters in 15 months are recorded (Taylor, 1961). In captive colonies, breeding dwindles rapidly in the third generation (Taylor, 1961; Watts, 1982).

Populations at lower latitudes, such as those from Queensland, have a long breeding season with a short winter respite (Wood, 1971). In the higher latitudes of Victoria the same subspecies has a much shorter breeding period (Warneke, 1971), and 50% or more of the males are infertile for the 6 months centered on winter solstice, the time when all males are nonbreeding (Warneke, 1971). *R. fuscipes* breeds year-around under normal laboratory conditions (Taylor and Horner, 1972).

In a field population from Victoria, testis length increased after winter solstice and decreased after summer solstice. Large testis size can be maintained in laboratory controls kept at 14L:10D, 20°C, and fed rat chow ad libitum, and even in those in which lighting is reduced to 6L:18D (Irby et al., 1984). Testis size declines only moderately in those for which temperature also is reduced (from 20°C to 12°C). Only when food quality is diminished (from 20% protein to 3.2% protein) do testes regress to match those of nonbreeders in the wild; spermatogenesis ceases, Sertoli cells accumulate lipid droplets (Hodgson et al., 1979), and Leydig cells atrophy and accumulate crystalloid inclusions (Irby et al., 1984) called 'Reinke-type' crystals, thought to signal a reduction in luteinizing hormone, LH (Kerr et al., 1981). LH and testosterone levels, and weights of the prostate and seminal vesicles, all decline during sexual regression (Irby et al., 1984). When LH, follicle-stimulating hormone, and androgen rise upon sexual recrudescence, the lipid inclusions and crystalloids disappear (Kerr et al., 1980). When males kept at 14L:10D and 20°C are fed a low-protein diet, testis length and mass decline only moderately (Irby et al., 1984). Gonadotrophin concentrations peak in September to October and are minimal in February to July, whereas testosterone levels peak in December to January, then decline through October (Irby et al., 1984). This staggering of events may result from a negative feedback on LH secretion caused by increasing testosterone levels (Irby et al., 1984).

Young are pink and hairless by 1 day of age (24 to 48 h after birth), except for unpigmented mystacial vibrissae, weigh approximately 4 g, and are about 56 mm long. Pigmented eyes show through closed, slightly pigmented lids. Pinnae are folded over the auditory

openings, and the ingested milk in the stomach and the umbilicus are conspicuous. Distance between anus and urogenital aperture averages 2.6 mm in males and 1.7 mm in females. Young can right themselves when overturned. The skin is more wrinkled and pigmented by 3 days, and the pinnae unfold. By 4 days, fine fur covers the body, and for each of the next several days the dorsal skin increases in pigmentation and the unpigmented ventral skin becomes more opaque. Crawling behavior begins by 8 days and teats appear on females the following day. By 12 days, the young are well furred and the upper incisors have erupted. By 14 days, young retain body heat when isolated, and the lower incisors erupt. Washing and scratching movements and unsteady walking occur by 15 days, but not until 20 days do eyes and auditory meati open, and are young aware of heights. By the next day, the young run about and climb objects, becoming increasingly active in ensuing days, and by 25 days they weigh approximately 14 g and are about 82 mm long. Following slow and steady increments for the first 20 days, the average absolute growth rate accelerates 200 to 300% from days 20 to 25, at which time the young are sampling solid food. In the field, young of this age forage and enter traps, and presumably are weaned (Taylor, 1961).

These growth data (Taylor, 1961) are similar to those obtained by Warneke (1971), except bush rats in his sample from Victoria grew more quickly during the first 20 days. Watts (1979) suggested that *R. fuscipes* and other Australian *Rattus* have a more complex growth curve than other Australian rodent genera he measured.

Males begin to exceed females in size at 6 weeks of age (Taylor, 1961), a disparity that increases with age, as Warneke (1971, figs. 21 and 22) established in nomographs to estimate age of animals in the field. Growth decreases in rate at 3 months and pauses at 5 months (Taylor, 1961; Warneke, 1971). The borderline to adulthood coincides with loss of steely-gray juvenile pelage and acquisition of browner adult pelage.

*Rattus fuscipes* becomes sexually mature in captivity between 6 and 9 weeks of age, a month to 6 weeks earlier than in the field (Breed, 1976; Taylor and Horner, 1971). Males are spermatogenic when testis length is over 20 mm and the diameter of the seminiferous tubules is 200  $\mu\text{m}$  (Taylor and Horner, 1973b). Spermatozoa of *R. fuscipes* differ from those of all other Australian genera, but are similar to those of other Australian *Rattus*, *R. norvegicus*, and *R. rattus* (Breed and Sarafis, 1979, Fig. 2). The preputial gland of *R. fuscipes* achieves full secretory state in both sexes before sexual maturity and, unlike that of *R. norvegicus*, is not sexually dimorphic (Taylor and Horner, 1971). The other accessory glands are similar histologically to those described elsewhere for laboratory *R. norvegicus*. Adult mean weights of testes ( $4.4 \pm 0.2$  g), seminal vesicles and coagulating gland ( $1.3 \pm 0.2$  g), and ventral prostate ( $0.2 \pm 0.4$  g) of *R. fuscipes* are recorded (Breed and Sarafis, 1979). In the laboratory, the earliest record of vaginal perforation is at 21 days of age (usually 35 to 57 days), yet estrous cycles and ovulation do not occur for several more weeks (Taylor, 1961).

Average life expectancy of weaned *R. fuscipes* in the field is 12 months (Taylor, 1961; Warneke, 1971), and in the laboratory is 16 months (Taylor, 1961). There is a field record of 3.8 years (Watts, 1982) and a laboratory record of 5.3 years (Warneke, 1971). The pelage loses its sleek appearance and looks bleached in old individuals, and external scars, particularly on the tail and feet, are numerous (Warneke, 1971). Occasionally, malocclusion of the incisors, bone resorption around the molars, or even pyorrhea can develop (Warneke, 1971). Parasitic infestation appears to increase with age, and fatty degeneration of the cortical parenchyma and cystic follicles in the ovaries have been noted (Warneke, 1971).

With minor exception, the population turns over each year. In regions where the breeding season is distinct and restricted, the age structure of the population shifts seasonally, with juveniles and subadults unrepresented in the late winter nonbreeding period (Warneke, 1971). Predation, parasitism, and disease contribute to the annual mortality of adults.

**ECOLOGY.** *Rattus fuscipes* occupies a wide variety of habitats that afford cover and friable soil in which to burrow, or hollow logs or rock crevices for refuge (Taylor and Horner, 1973a). The bush rat lives in dry and wet sclerophyll forests with dense ground cover (Taylor and Horner, 1973a), dense scrub (Brazenor, 1936), heaths (Taylor and Horner, 1973a), stream borders (Jones, 1925), edges of swamps (Taylor and Horner, 1973b), mangroves (Finlayson,

1960), beach sandplains (Storr, 1965), and sandhills (Jones, 1925). In the north, *R. fuscipes* is confined to tropical rain forests where ground litter, or cover of low-growing vegetation, is dense (Taylor and Horner, 1973a). The two southern subspecies, *R. f. fuscipes* and *R. f. greyii*, can live in drier habitats than *R. f. assimilis* and *R. f. coracius* (Watts and Aslin, 1981).

Although once considered solely a vegetarian (Brazenor, 1936; McNally, 1955; Troughton, 1967), *R. fuscipes* now is known to be omnivorous with a seasonally variable diet, at least in its southern distribution. During spring and summer, at the peak of breeding effort and juvenile growth, this rat feeds on arthropods, seeds, and fibrous plant tissues, and by autumn has accumulated heavy reserves of fat (Warneke, 1971). Rat populations are at their nadir during late winter and individuals are lean and under nutritional stress following their winter diet of fibrous plant tissues and fungi low in nutritive value (Warneke, 1971; Watts and Braithwaite, 1978). Given the opportunity, overwintering rats penetrate bark of young introduced pines (*Pinus radiata*) to cambial tissue, apparently in quest of carbohydrates in the sap (Warneke, 1971). In subtropical southeastern Queensland, the diet of *R. fuscipes* is less cyclical and plant materials predominate year-around (Freeland, 1972).

The population structure of southern *R. fuscipes* is regulated seasonally by its 1-year lifespan and restricted breeding season. Juveniles, then subadults, join the population in late spring, and subadults predominate in summer, the time of peak population density. As the rats enter adulthood in autumn, the juvenile category declines precipitously, and by winter the entire population is adult (Warneke, 1971). However, in northern populations that breed virtually year-around, juveniles are present in all months and peak in abundance in February (Barnett et al., 1977; Wood, 1971). Mortality may be high at times, but seasonal patterns are not defined sharply, even with a winter decline in breeding (Wood, 1971).

At one site in southeastern Queensland, averages of individual ranges of movement were to 127 m for females and to 183 m for males (Wood, 1971). At another northern site, males again moved significantly greater distances than females in October and February, but not in other months (Barnett et al., 1977). Movements of adult males were significantly greater in the major breeding season than in winter and movements of breeding adults were significantly greater than those of juveniles and subadults (Wood, 1971). A high proportion of transients occurred in the population year-around and, although it was random for females, the proportion peaked for males just as they entered the major breeding period (Wood, 1971).

In southern Victoria, 90% of the bush rats were residents in winter, whereas the residents dropped to 53.5% in the breeding season from mid-October to late May (Warneke, 1971). The shift in proportion of transients probably was correlated with breeding and subsequent dispersal of subadults.

Maximum dispersal records in a population from Victoria are 213 m for a female and 762 m for a male (Warneke, 1971), and in southeastern Queensland records of at least 365 m are noted for both sexes (Wood, 1971). A track of 500 m in length on the snow surface at Kosciuszko National Park, New South Wales, was attributed to *R. fuscipes* (Osborne, 1980). Near a forest reserve in South Australia, an individual traveled 550 m in 2.5 days (Thomas and Cockington, 1980).

Laboratory experiments designed to examine seasonal locomotor activity (by simulating the light regime of each season, but holding the temperature at 22°C), revealed an increase in exploratory activity under the summer regime over that of winter (Stewart and Barnett, 1981). These results suggest that activity not related to nutrition is reduced in winter when energy conservation is at a premium.

Trap success with live traps ranged from about 2.3% (7,900 trap-nights during 1 year near Sydney; Taylor, 1961) to 2.6% (7,372 trap-nights in northeastern New South Wales; Barnett et al., 1977), and with break-back traps was about 2.3% also (61,000+ trap-nights during 2 years in Victoria; Warneke, 1971). Warneke (1971) estimated that densities on his study area were usually less than 11/ha, but fluctuated seasonally. Population densities are known to fluctuate between 2 and 30 individuals/ha (Lee et al., 1981).

In the study by Taylor (1961), trap success with solid metal traps measuring 23 by 9 by 8 cm was 5.5%, with a large wooden trap measuring 22 by 8 by 8 cm was 2.9%, and with the largest (44 by 22 by 18 cm wire mesh) and smallest (20 by 6 by 6 cm wooden) traps were less productive, the latter yielding mostly subadults. Subsequently, with solid metal traps only, trap yields of the

western subspecies ranged from 2.0 to 2.7% (Taylor and Horner, 1973a). Attractive baits are a mixture of rolled oats and peanut butter (Taylor and Horner, 1973a) or leather strips soaked in raw linseed oil (Warneke, 1971). Ear-notching (Taylor, 1961) or ear-tagging (Warneke, 1971; Wood, 1971) are satisfactory methods of marking for individual identification.

During major fires, *R. fuscipes* retreats into burrows; afterward it hides in deep accumulations of ash (Recher et al., 1975). A fire may reduce rat numbers substantially, probably because of acute shortages of food and cover (Newsome and Catling, 1983). When vegetational cover reaches its maximum several years later, especially in forest habitat, density of *R. fuscipes* may exceed prefire levels (Catling et al., 1982). As forests mature and shrub vegetation diminishes, density probably declines to prefire levels (Catling et al., 1982).

*Rattus fuscipes* is an economic pest, damaging cane fields (McDougall, 1944) and pine (*P. radiata*, *Araucaria cunninghamii*) plantations, the latter by gnawing and ringbarking young trees (Davis, 1956; McDougall, 1946; McNally, 1955; Warneke, 1971). Otherwise, *R. fuscipes* avoids man-modified habitats and seems unable to withstand clearing of its native habitat of dense cover (Taylor, 1961).

Dingoes (*Canis familiaris*) from northeastern New South Wales eat *R. fuscipes* at a relatively low daily intake, an average of 1.25 rats per dropping (Robertshaw and Harden, 1985). They tend to consume older rats (Robertshaw et al., 1985). Foxes (*Vulpes vulpes*) also eat *R. fuscipes* (Brunner et al., 1975), and nonmammalian predators of this rat include avian raptors and reptiles (Warneke, 1971).

*Rattus fuscipes* is the known host of more parasites than any other Australian rodent. Some are implicated in human diseases. They include protozoa: *Haemobartonella*, *Hepatozoon*, *Sarcocystis*, *Toxoplasma*, *Trypanosoma* (Mackerras, 1959; Rzepczyk and Scholtzsek, 1976); bacteria: *Brucella*, *Leptospira*, *Pseudomonas*, and *Streptobacillus* (Cook et al., 1967); rickettsia: *Coxiella*, *Eperythrozoon*, and *Rickettsia* (Cook et al., 1967; Glazebrook et al., 1978); a virus (Campbell et al., 1977); fungi (Rees, 1967; Ridley, 1961); cestodes: *Bertiella*, *Choanotaenia*, *Hepatotaenia*, *Hymenolepis*, *Raillietina*, and *Taenia* (Mackerras, 1958; Mawson, 1971); Obendorf, 1979); nematodes: *Angiostrongylus*, *Austroheligmonema*, *Capillaria*, *Contraecaeum*, *Dipetalonema*, *Ganguleterakis*, *Gongylonema*, *Hepatojarkus*, *Longistriata*, *Neoascaris*, *Nippostrongylus*, *Odilia*, *Ophidascaris*, *Paraustrostrongylus*, *Physaloptera*, *Protospirura*, *Rictularia*, *Stammerinema*, *Strongyloides*, *Subulura*, *Syphacia*, and *Trichosomoides* (Bhaibulaya, 1968; Durette-Desset, 1973; Hugot and Quentin, 1985; Mackerras, 1958; Mawson, 1961, 1971a, 1971b; Obendorf, 1979; Spratt, 1985; Sprent, 1963; Sprent and McKeown, 1979; Taylor et al., 1966); trematodes: *Brachylecithum*, *Fasciola*, and *Neodiplostomum* (Angel and Pearson, 1977; Pearson, 1959; Spratt and Presidente, 1981); unidentified acanthocephalan (Mackerras, 1959); chiggers: *Ascoschoengastia*, *Eutrombicula*, *Gahrlipeia*, *Guntheria*, *Leptrotrombidium*, *Neotrombicula*, *Schouedenichia*, and *Trombicula* (Domrow and Lester, 1985); other mites: *Andreacarus*, *Archaeopodella*, *Austrochirus*, *Gymnolaelaps*, *Haemolaelaps*, *Laelaps*, *Laelapsella*, *Listrophoroides*, *Mesolaelaps*, *Ornithonyssus*, *Paraspeleognathopsis*, *Peramelaelaps*, *Pneumonyssus*, *Proctolaelaps*, *Radfordia*, and *Speleognathopsis* (Athias-Henriot, 1977; Domrow, 1958, 1962, 1963, 1967, 1972, 1973, 1974; Fain and Lukoschus, 1981); ticks: *Ixodes* and *Haemaphysalis* (Roberts, 1970); a louse: *Hoplopleura* (Kuhn and Ludwig, 1966); fleas: *Acanthopsylla*, *Bibikovana*, *Choristopsylla*, *Leptopsylla*, *Macropsylla*, *Metastivalius*, *Nosopsyllus*, *Parapsyllus*, *Pulex*, *Pygiopsylla*, *Stephanocircus*, and *Xenopsylla* (Dunnet and Mardon, 1974; Traub, 1980); staphylinid beetle: *Myotyphlus* (Warneke, 1971).

**BEHAVIOR.** Regular sampling of *R. fuscipes* in southeastern Queensland indicates that it is active year-around, only at night (Wood, 1971), and its peak activity is bimodal, just after sunset and just before sunrise (Warneke, 1971). Strong winds and temperatures below freezing suppress this pattern (Warneke, 1971).

Paternal behavior in captivity includes nest attendance, washing young, hovering over young in the nest, covering them upon departing, and following weanling young as they explore (Horner and Taylor, 1969). On one occasion, a sire sat nearby while its mate gave birth, ate the placenta, and washed the young. A postparturient female tends to be aggressive, however, and may kill the male as it

attempts to mate during postpartum heat. Female aggression may even inhibit development of paternal behavior (Horner and Taylor, 1969).

*Rattus fuscipes* engages in stereotyped behavior, such as boxing (upright position and forelimbs extended), threat posture (arched back, limbs extended, hair upright, eyes partially closed, flank toward opponent), clash (biting, scratching), and approach (walks toward intruder that assumes defensive posture), upon encountering an intruder (Barnett and Stewart, 1975). Rising up on the hind legs is an alternative to stereotyped threat posture (Barnett et al., 1982). Sound emissions frequently accompany these postures. Four categories of vocalizations have been identified: squeal, ultrasonic pipping, ultrasonic whistle, and coughing, the first three subdivisible into two forms each. They are the basic repertoire of all native species of *Rattus* in Australia and for *R. rattus* and *R. norvegicus* (Watts, 1980). Bush rats also emit two unvoiced sounds, hissing and tooth-chattering. Interspecific differences in sounds are more in frequency than in their nature, the long whistle (24 kHz for *R. fuscipes*) being the most distinctive (Watts, 1980).

Some encounters are silent, including mutual approach in which two rats move toward each other and sniff, sometimes with body elongated; nosing whereby one pushes the other's flank with nose; genital exploration; and allogrooming in which one rat chews hair of the other or pulls it out (Barnett and Stewart, 1975). Allogrooming commonly accompanies precopulatory and postcopulatory activity. One rat allogrooms the interscapular area and nape of the neck while the recipient crouches and rarely defends itself, even when its skin is torn to the point of lethal wounding (Taylor, 1961). The development of trichobezoars in the stomach probably is a result of such vigorous grooming (Horner, 1962).

Captive *R. fuscipes* copulate at night, regardless of the time of pairing (Taylor, 1961). The male clasps the lower abdomen of the female and rests his chin on her middorsum. When she assumes lordosis, he may pick up her entire hindquarters while licking her genitalia. Sexual activity can last 30 min, the female emitting a squeal most of this time (Taylor, 1961). Copulation, but not ejaculation, may take place whether or not the female is in estrus.

While giving birth, the female sits with her hind legs tucked under her, tail to one side, and forelegs in front for support. She licks each young as it emerges rump first, eats the placenta and umbilical cord, then may cleanse the young thoroughly, a procedure that is repeated until all young are born in the nest (Taylor, 1961). She covers the young with nesting material when she departs temporarily, and for the first week transports them by holding their heads in her mouth (Taylor, 1961).

The diurnal refuge, sleeping chamber, and nursery of *R. fuscipes* is the burrow. Surface runways connect burrows, but usually are inconspicuous except where vegetational cover is thick (Taylor and Horner, 1973a). A typical burrow consists of a main tunnel that descends 30 to 45 cm below the surface to a nest chamber (Warneke, 1971). The tunnel may twist through root systems and be joined by ancillary burrows, some of which are blind. The nest is lined with grass and other fibrous vegetation, and is about 15 cm in diameter (Warneke, 1971).

Besides being a burrower, *R. fuscipes* is active on the surface of the ground. Occasionally, it ascends trees, usually for food, and may climb 3.5 to 4 m (Warneke, 1971). It hoards food and retrieves water-laden objects, particularly following a period of deprivation. The nature of oral stimuli received when licking or eating the food appears to determine which objects are retrieved (Wallace, 1982).

**GENETICS.** In the karyotype of *R. fuscipes*, pair 1 is a large subacrocentric, pairs 2 and 3 and pairs 5 to 9 are telocentric, pairs 4 and 10 are large metacentrics replacing four pairs of telocentrics in *R. lutreolus* by fusion with pair 8 and pair 12, respectively, and pairs 14 to 20 are smaller metacentrics (Baverstock et al., 1977, 1983). The X-chromosome is a medium-sized telocentric and the Y-chromosome is a small telocentric. The fundamental number is 60. When supernumerary chromosomes occur, they are small metacentrics (Baverstock et al., 1977).

Comparison of karyotypes of *R. fuscipes* and other Australian species demonstrated that the *fuscipes* karyotype could be derived from an ancestral karyotype similar to that of modern *R. lutreolus* by two fixed fusions (Baverstock et al., 1977). Four pairs of telocentrics of *lutreolus* are replaced in *fuscipes* by two pairs of large metacentrics. The fusions, once thought to occur in pairs 4 and 11, and 9 and 12 (Baverstock et al., 1977), have now been shown by

G-banding to involve pairs 5 and 9, and pairs 11 and 13 (Baverstock et al., 1983). The derivation of *fuscipes* from an ancestral *lutreolus* stock was postulated earlier on the basis of multivariate analysis of craniometric data (Taylor and Horner, 1973a).

Minor variation in chromosome number occurs in *R. fuscipes*, with additional small metacentric chromosomes ( $\beta$  chromosomes) raising the number from 38 to 39 or 40. All four subspecies have the same karyotype, evidence that Baverstock et al. (1977) used to support the revisionary interpretation made by Taylor and Horner (1973a). Serological and genetic analyses of *R. fuscipes* reveal partial RI-1b (=Igk-l; immunoglobulin kappa-1) cross-reactivity in all four subspecies, that indicates the presence of multiple specificities for RI-1b (Gutman and Baverstock, 1980).

The geographic distribution of the electrophoretic patterns of 13 proteins controlled by 16 genetic loci were examined in isolated mainland populations from South Australia plus those of one large island and a number of small islands off the coast, the latter separated from the mainland 6,000 to 14,000 years ago (Schmitt, 1975, 1977, 1978). These studies revealed a low level of genetic variability in the small island populations. The mean heterozygosity on the small islands was 0.0007 compared with 0.042 on the mainland and large island (Schmitt, 1978). Schmitt (1978) concluded that drift has been a powerful influence on the gene frequencies of the small isolated populations of *R. fuscipes*. Comparison between the protein variations and metric variations in 18 skull and body characters in each population revealed a broadly similar pattern of geographic variation (Schmitt and White, 1979).

In northern parts of the range of *R. fuscipes* (north of Jervis Bay, New South Wales), a white spot occurs on the chest of some individuals and sometimes extends posteriorly to the abdomen (Taylor and Horner, 1973a). A small white blaze between the ears marks some specimens at Danbulla in northern Queensland (Taylor and Horner, 1973a). Albinos occur occasionally (Watts, 1982). Phenotypic variation in teat number associated with its north-south distribution was described earlier.

Conspecificity of the four subspecies of *R. fuscipes* was proposed by Taylor and Horner (1973a). They demonstrated genetic compatibility by cross-breeding the three subspecies (*R. f. fuscipes*, *R. f. greyii* and *R. f. assimilis*) that they were able to secure alive (Horner and Taylor, 1965). Fecundity in the  $F_1$  generation was comparable to that of the parents. Their attempts to cross-breed *R. fuscipes* with another native species, *R. lutreolus*, failed; however, in a later study two *R. lutreolus* females gave birth to this hybrid cross (Fox and Murray, 1979). One young survived beyond 50 days and later sired offspring when backcrossed to *lutreolus*. These results are significant because no hybrids have been detected in wild populations. Rather, the two species are morphologically distinct and, although they may be captured in the same trapline, are ecologically separate to a large extent. Also significant is that the diploid chromosome number of *R. fuscipes* is 38 but that of *R. lutreolus* is 42. The hybrids had 40 chromosomes (Fox and Murray, 1979). These cross-breeding experiments suggest that natural barriers to breeding that maintain species integrity among sympatric species in the field are not always accompanied by chromosomal incompatibility (Taylor et al., 1983). In fact, chromosome numbers of Australasian *Rattus* may be of limited value as a taxonomic tool.

**REMARKS.** Taxonomic treatments of *R. fuscipes* have been complex for, not only have different subspecies been included within this species, and subspecies elevated to species status, the species name has been misapplied and confused with another native species, *R. lutreolus* (Taylor and Horner, 1967, 1973a). Part of the confusion arose because the holotype of *R. fuscipes* was lost, followed by Gray (1843) placing *lutreolus* in subjective synonymy with *fuscipes*. The taxonomic treatment remained clouded until Taylor and Horner (1967) clarified the distinction between the two species and designated a neotype for *R. fuscipes*. Gray (1843) included *fuscipes* (as *Mus greyii*) with a conilurine rodent, *Pseudomys gouldi* (then known as *Mus gouldii*). Gould (1858) described *Mus manicatus*, known only from a single specimen purportedly taken at Port Essington, Northern Territory, where no *R. fuscipes* have ever been recorded. Reasons to support the view that *manicatus* bears an erroneous locality label and recommendation that it be removed from future faunal lists of the Northern Territory were given by Calaby and Keith (1974). Most subsequent treatments retained *manicatus* as a full species until Ellerman (1949) included it under *R. fuscipes*, a designation supported by Tate (1951) and in a tentative fashion

by Taylor and Horner (1973a), all of whom have examined the sole damaged specimen. A full historical description of the intricate taxonomic treatments of *R. fuscipes* has been published elsewhere (Taylor and Horner, 1967, 1973a).

The species name, *fuscipes*, means "dusky foot" to describe that feature in the western subspecies, *R. f. fuscipes*, which has the darkest feet of any of the subspecies. The name is inappropriate, for the feet are light in color on most individuals of the other three subspecies.

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