**Mammalian Species** No. 298, pp. 1–8, 3 figs.

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

Published 15 January 1988 by The American Society of Mammalogists

---

**Rattus fuscipes (Waterhouse, 1839)**

Bush Rat


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


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

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

*Rattus glauceri* 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). Australian *Rattus* may not be true *Rattus* as the genus is inadequately defined (Musser, 1981). Four subspecies are recognized (Taylor and Horner, 1973a):

2. *R. f. greyii* (Gray, 1841:410), see above (raurus Brazenor, peccatus Troughton, and pelori Finlayson are synonyms; Taylor and Horner, 1973a).
4. *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 characteristics that serve to distinguish it from some other suit-and-tanned native *Rattus*. *R. fuscipes* is distinguished most clearly from all other native Australian *Rattus* by combined features of small tympanic bulla (17.5 to 19.6% of body length of skull and relatively straight-sided incisors or incisor (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 touffy 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; 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 with 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 abdominals 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 maxillaries on the relatively narrow rostrum. Tympanic bulla is 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 Terrang, 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.** Subfossil 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): occipitoanassal 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 age.

---

**Fig. 1.** Photograph of *Rattus fuscipes assimilis* from Tidbinbilla, Australian Capital Territory (provided by Eleri Slater).
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 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 subspecies 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* (Morrissy and Breed, 1982) and 9 to 10 mm long in *R. norvegicus*; otherwise, the two are similar in configuration (Argyropulo, 1929; Morrissy 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. fuscipes* is almost twice the length (7 to 9 mm) of that of *R. norvegicus*; neither contains an os clitidis (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 climates (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; McIvor, 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 corticosterone 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, 1985). 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).
ONTOTYPY AND REPRODUCTION. The estrous cycle of R. f. assimilis is 4.5 days (Taylor, 1961) and of R. f. coracioides is 5.3 days (Boyd, 1976). In the former, proestrus lasts 10 to 14 h, estrus is typified by well-correlated 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 14 days 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 ovum or conceptus occurs about 40% (Taylor, 1971). 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. coracioides 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. greyi 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 males being from 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 correlated with laboratory conditions, where fed rat chow ad libitum, and even in those in which lighting is reduced to 61:18D (Iry 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 crystallloid inclusions (Iry 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 (Iry 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 fed a low-protein diet, testis length and mass decline only moderately (Iry et al., 1984). Prolactin ('gonadotropin') 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 (Iry et al., 1984). This staggering of events may result from a negative feedback on LH secretion caused by the low-protein diet. Young adult males increase testosterone levels (Iry 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 within 15 min after birth and are masticated and gutted by the mother 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 meatus open, and are young aware of heights. By the next day, the young run about and climb objects, becoming increasingly active in eating 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 the R. fuscipes and R. greyi growth curves are steeper 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 2 months and plateaux 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 spermatogonial when testis length is over 20 mm and the diameter of the seminiferous tubules is 200 μm (Taylor and Horner, 1973b). Spermatogonia of R. fuscipes differ from those of all other Australian genera, but are similar to those of other Australian Rattus, R. norvegicus, and R. rana (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 ± 0.2 g), seminal vesicles and coagulating gland (1.3 ± 0.2 g), and ventral prostate (0.2 ± 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 weeks (at 14L:10D). 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 pyorrea can develop (Warneke, 1971). Parasitic infestation appears to increase with age, and fatty degeneration of the cortical parenchyma and cystic follicles in the oxalized body occur.

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). Rattus fuscipes have a more complex life cycle than bush rat lives in dry and wet sclerophyll forests with dense ground cover (Taylor and Horner, 1973a), dense scrub (Brazenor, 1936), heathland (Taylor and Horner, 1973a), stream borders (Jones, 1925), edges of swamps (Taylor and Horner, 1973b), mangroves (Fladbyay, 3
(1960), beach sandplains (Storr, 1965), and sandhills (Jones, 1925). In the north, R. fuscipes is confined to tropical rain forests where ground litter is low (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 (Braunoser, 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 viremposium, juveniles are present in all months and adults are in abundance in February (Barnett et al., 1977; Wood, 1971). Mortality might 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 range per year for males 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 buses 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. Initial 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 Kosciusko 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 in 2 years in Victoria; Warneke, 1971). Warneke (1971) noted that densities on lowland ranges (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 25 by 9 by 8 cm was 5.5%, with a large wooden trap measuring 9 by 8 by 6 cm was 17%, and with wire snares (44 by 22 by 18 cm wire mesh) and smallest (20 by 6 by 6 cm wooden) traps 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 plastic strips soaked in raw linseed oil (Warneke, 1971). Ear-catching (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 vegetation cover reaches its maximum several years later, especially in forest habitat, density of R. fuscipes may exceed preferable levels (Catling et al., 1982). As forests mature and their vegetation diminishes, density probably declines to prefer 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 (Dennis, 1956; McDougall, 1946; McNally, 1965; 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., 1977), and nonmammalian predators of this rat include avian raptors and reptiles (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).

Patriarchal behavior in captivity includes nest attendance, washing young, hoovering over young in nest, covering them upon parturition, and washing young 22 days after birth (Warneke and Taylor, 1969). On one occasion, a sire sat nearby while its mate gave birth, ate the placenta, and washed the young. A postpartum 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 piping, ultrasonic whistle, and coughing, the first three subdivide into two forms each. They are the basic repertoire of all native species of *Rattus* in Australia and for *R. rutilus* and *R. norvegicus* (Watts, 1980). Bush rats also emit two unvoiced sounds, hissing and tooth-chattering. Interspecific differences in sounds are more frequent 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 places the other’s flank against its 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 visible. In the event 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 as she chins on her mid dorsum. 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 females 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 not detectable except where vegetation 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 are large, and pairs 4 to 9 are telocentrics. Pairs 10 and 11 are large metacentrics replacing four pairs of telocentrics in *R. lutreola* 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. All supernumerary chromosomes occur, they are small metacentrics (Baverstock et al., 1977).

Comparison of karyotypes of *R. fuscipes* and other Australian species demonstrated that the karyotype of *R. fuscipes* could be derived from a karyotype similarity to that observed in *R. lutreola* by two fixed fusions (Baverstock et al., 1977). Four pairs of telocentrics of *R. lutreola* are replaced in *R. 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 *R. fuscipes* from an ancestral *lutreola* stock was postulated earlier on the basis of multivariate analysis of cranio-metric data (Taylor and Horner, 1973a).

Minor variation in chromosome number occurs in *R. fuscipes*, with additional small metacentric chromosomes (β chromosomes) raising the number from 38 to 39. 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 Dambula in northern Queensland (Taylor and Horner, 1973a). All others are occasionally (Watts, 1982). Phenotypic variation in test number associated with its north-south distribution was earlier described.

Conspecifity of the four subspecies of *R. fuscipes* was proposed by Taylor and Horner (1973a). They demonstrated genetic compatibility by cross-breeding among subspecies (*R. f. fuscipes*, *R. f. geyrei* and *R. f. assimilis*) that they were able to secure alive (Horner and Taylor, 1965). Fecundity in the F1 generation was comparable to that of the parents. Their attempts to cross-breed *R. fuscipes* with another native species, *R. lutreola*, failed; however, in a later study two *R. lutreola* females gave birth to this hybrid cross (Fox and Murray, 1979). One young survived beyond 50 days and later sired offspring when backcrossed to *R. lutreola*. These results are significant because no hybrids have been detected in wild populations. Rather, the two species are morphologically distinct and, although they may have some hybridization events, they are separate to a large extent. Also significant is that the diploid chromosome number of *R. fuscipes* is 38 but that of *R. lutreola* 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 nature are not always accompanied by chromosomal incompatibility (Taylor et al., 1983). In fact, chromosome numbers of Australian *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. lutreola* (Taylor and Horner, 1967, 1973a). Part of the confusion arose because the holotype of *R. fuscipes* was later followed by Gray (1843) placing *lutreola* 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 geyrei*) with a conflation rodent, *Mus gouldii* (then known as *Mus gouldii*). Gould (1858) described *Mus menziesii*, 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 unconstrained rodent, *Mus manicatus*, 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.

C. H. S. Watts provided thorough review and valuable commentary on the manuscript. We also thank J. K. Jones, Jr. and G. G. Musser for their comments. The animal was photographed by Erle Shwayder and the skull by Graeme Chapman; the map was drawn by Frank Knight. This is Technical Paper No. 8037, Oregon Agricultural Experiment Station.

**LITERATURE CITED**


HORNER, B. E. 1962. Trichobezoars (hair balls) in Rattus assi-


HUGOT, J.-P., AND J. C. QUENTIN. 1985. Etude morphologique de six especes nouvelles ou peu connues appartenant au genre Sypophilis (Oxyuridae, Nematomatida) parasites de rongeurs cricet-

IRBY, D. C., J. B. KERR, G. P. RIBBINDER, AND D. M. DE KRETSER. 1984. Seasonally and experimentally induced changes in tes-


KERR, J. B., D. C. IRBY, AND D. M. DE KRETSER. 1981. Formation of 'Renke-type' crystals during experimental testicular regress-


cuean Soc. New South Wales, 83:126-143.

———. 1959. The Haematozoa of Australian mammals. Aus-


MASON, P. M. 1961. Trichostrengyle from rodents in Queens-


——. 1946. An investigation of the rat pest problem in Queens-


ROBERTS, H. S. 1970. Australian ticks. CSIRO, Melbourne,


SPRANTJ, J. F. A., AND E. A. MCKEOWN. 1979. Studies on ascar-


Editors of this account were B. J. VERTS and J. K. JONES, JR. Managing editor was CARLETON J. PHILLIPS.