Onychomys leucogaster. By Richard McCarty

Onychomys Baird, 1857

Onychomys Baird, 1857:480. Type species *Hypudaeus leucogaster* Wied.

CONTEXT AND CONTENT. Order Rodentia, Suborder Myomorpha, Superfamily Muroidea, Family Cricetidae, Subfamily Cricetinae, Tribe Hesperomyini. The genus *Onychomys* includes two recent species, *O. leucogaster* and *O. torridus.*

Onychomys leucogaster Wied, 1841

Northern Grasshopper Mouse

Hypudaeus leucogaster Wied, 1841:99. Type locality Mandan Indian village, near Fort Clark, Oliver Co., North Dakota.

Mus missouriensis Audubon and Bachman, 1851:327. Type locality Fort Union, near present town of Buford, Williams Co., North Dakota.

Onychomys pallidus Herrick, 1885:184. Type locality Lake Traverse, near sources of Minnesota and Boix de Siouz rivers, South Dakota.

Onychomys longipes Merriam, 1889:1. Type locality Concho County, Texas.

Onychomys fuliginosus Merriam, 1890:59. Type locality Black Tank Lava Beds, northeast of San Francisco Mountain, Coconino Co., Arizona.

Onychomys articeps Rhoades, 1898:194. Type locality Clapham, Union Co., New Mexico.

Onychomys ruidosae Stone and Rehn, 1903:22. Type locality Hales Ranch, Ruidoso, Lincoln Co., New Mexico.

CONTEXT AND CONTENT. Context presented in generic summary. The genus has been monographed by Hollister (1914), and a partial revision was provided by Van Cura and Hoffmeister (1966). The 13 recognized subspecies are:

O. l. albescens Merriam, 1904:124. Type locality Samalayuca, Chihuahua.

O. l. articeps Rhoades, 1898:194, see above.

O. l. breviauritus Hollister, 1913:216. Type locality Fort Reno, Canadian Co., Oklahoma.

O. l. brevicaudus Merriam, 1891:52. Type locality Blackfoot, Bingham Co., Idaho.

O. l. fuliginosus Merriam, 1890:59, see above (*capitulatus* Hollister is a synonym).

O. l. fuscogriseus Anthony, 1913:11. Type locality Ironside, Malheur Co., Oregon.

O. l. leucogaster Wied, 1841:99, see above (*pallidus* Herrick is a synonym).

O. l. longipes Merriam, 1889:1, see above.

O. l. melanophrys Merriam, 1889:2. Type locality Kanab County, Utah.

O. l. missouriensis Audubon and Bachman, 1851:327, see above.

O. l. pallescens Merriam, 1890:61. Type locality Moki Pueblos, Navajo Co., Arizona.

O. l. ruidosae Stone and Rehn, 1903:22, see above.

O. l. utahensis Goldman, 1939:354. Type locality south end of Stansbury Island, Great Salt Lake, Tooele Co., Utah (*aldousi* Goldman is a synonym).

DIAGNOSIS. *Onychomys* is a short-tailed, relatively stocky mouse with a distinctly bicolored pelage (figure 1). The head, back, and upper sides are pale brown to grayish or pinkish cinnamon and the underparts are white. *Onychomys* is most easily distinguished from species of *Peromyscus* by its shorter tail, larger forefeet, and more hypsodont molars. *O. leucogaster* averages somewhat larger than does *O. torridus* in the following specific characters: maxillary toothrow longer (3.8 to 4.8 mm and 3.3 to 4.0 mm, respectively), mandible longer (13.7 to 17.3 mm and 12.5 to 14.6 mm), broader zygomatic plate (12.6 to 17.3 mm and 11.9 to 13.7 mm), and a larger braincase (11.9 to 13.7 mm and 11.0 to 12.3 mm). The tail of *O. leucogaster* is usually less than half the body length, whereas the tail of *O. torridus* is usually more than half of the body length.

GENERAL CHARACTERS. *Onychomys leucogaster* has a bicolored pelage (see figure 1). The short, thick tail tapers to an obtuse point and the tip is often white. Total length is 119 to 190 mm; tail length 29 to 62 mm; length of hind foot 17 to 25 mm; length of ear 12.4 to 16.9 mm; length of baculum 4.8 to 6.6 mm, width at base 0.5 to 1.2 mm. The nasals are wedge-shaped. The length of braincase is 11.9 to 13.7 mm. The zygomatic plate is narrow (12.6 to 17.3 mm) and straight anteriorly. The length of maxillary toothrow is 3.8 to 4.8 mm. There are six mammae, two pectoral and four inguinal. Forefeet have five plantar tubercles, hind feet four; soles of feet are covered with fur from heel to beginning of tubercles. Dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16; M1 and M2 are well developed and M3 is reduced in size; M1 has two internal and three external cusps and its length is usually half that of upper molar toothrow; M2 has two external and two internal cusps and a narrow antero-external fold; M3 is longer than wide; m1 is higher than long and has one anterior, two internal, and two external cusps, and a postero-internal loop; m2 has two internal cusps, two external cusps, an antero-external fold, and a postero-internal fold; m3 is large, having up to half the crown surface of m2. The skull is illustrated in figure 2. More detailed descriptions and data on intraspecific variability are available in Hollister (1914), Hooper (1959), and Van Cura and Hoffmeister (1966).

DISTRIBUTION. The range of *O. leucogaster* extends from Saskatchewan, Alberta, and Manitoba south to extreme northern Mexico, west into northeastern California and central Oregon and east to western Minnesota and Iowa (figure 3). Populations of *O. torridus* and *O. leucogaster* occur together in Nevada, New Mexico, and Arizona but may remain ecologically separated due to differing habitat preferences. *O. torridus* prefers relatively xeric areas at lower elevations whereas *O. leucogaster* tends to occur in more mesic areas at higher elevations (Gennaro, 1968; Pinter, 1971).

Northern grasshopper mice have been trapped in the following habitats: short grass prairies of northeastern Colorado (Flake, 1973), semi-stabilized dunes of windblown sand in Utah (Egoscue, 1960), a sagebrush desert in west-central Nevada (O'Farrell, 1974), areas with sandy soil and little mulch in north-central Kansas (Kaufman and Fleharty, 1974), and short grass prairies, semi-stabilized dunes, and grasslands of Oklahoma (Ruffer, 1964). Egoscue (1960) suggested that *O. leucogaster* may require edaphic characteristics that allow for frequent dustbathing. This behavior aids in maintaining the pelage in a clean, non-oily condition.

FIGURE 1. An adult *Onychomys leucogaster*, female, courtesy of Dr. Thomas P. O'Farrell. Photograph by Mr. Scotty Getchell, Battelle Laboratories.
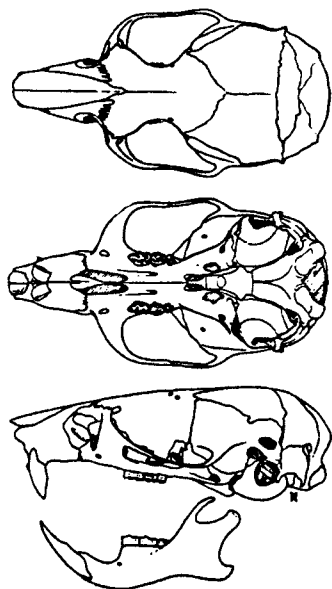
FIGURE 2. Skull and jaw of *Onychomys leucogaster*; from top down, dorsal, ventral, and lateral views of skull and lateral view of lower jaw (from Hall, 1955:122).

FOSSIL RECORD. A summary of the six fossil species of *Onychomys* has been presented (McCarty, 1975). Additional fossil *Onychomys* specimens, including some *O. leucogaster*, have been reported. Most specimens identified only to genus resemble present day *O. leucogaster* more closely than they resemble *O. torridus*. Fossil remains of *Onychomys* sp. have been reported for the following locations: Red Light local fauna, Hudspeth Co., Texas (Akerston, 1970); Sandahl local fauna, McPherson Co., Kansas (Semken, 1966); Butler Spring local fauna, Meade Co., Kansas (Schultz, 1965); and the Seymour Formation, Knox and Baylor counties, Texas (Hibbard and Dalquest, 1966). Fossil specimens of *O. leucogaster* have been reported by Skinner (1942) for the Papago Springs Cave local fauna, Santa Cruz Co., Arizona; by Dalquest and Roth (1970) from a limestone cave in extreme southern Tamaulipas; and by Hibbard (1949) for the Jones Ranch fauna, Meade Co., Kansas.

Hoffmeister (1944) suggested that the grasshopper mouse group probably diverged from *Peromyscus* during or prior to the late Miocene as the genus *Miochomys*. *Symmetrodontomys* and *Onychomys* were thought to have evolved from *Miochomys* in the middle Pliocene. Both *Miochomys* and *Symmetrodontomys* are now extinct.

FORM. Egoscue (1963) presented a detailed study of the pelage characteristics of *O. l. utahensis* in western Utah. Dichromatism was noted, with adults occurring as a pale normal phase or a dark melanistic phase. Pale phase juveniles had upper parts a uniform pale gray, whereas dark phase juveniles had upper parts a blackish gray.

The pattern of juvenile molt in nine males and six females of *O. l. breviauritus*, housed in the laboratory, was presented by Ruffer (1965a). At days 57 to 62 of age, a vertical cinnamon bar appeared immediately posterior to the forelegs. The pelage change then proceeded in a posterior direction until, 10 days later, the area between the forelegs and hind legs was covered by the adult pelage. On day 12 of the molt, cinnamon spots appeared on the rump and the ventral portion of the neck. These spots then spread anteriorly and posteriorly until the molt to adult pelage was complete by the twentieth day (80 days of age). There were no significant sexual variations to this pattern and three individuals of the dark phase molted in the same fashion.

Ruffer (1964) reported that adults had no lateral or ventral sebaceous glands, although there was a concentration of glandular material at the anal region that produced a characteric, musky odor. More recently, however, Pinter (personal communication) studied changes in the morphology and activity of the ventral gland of *Onychomys* with respect to sex, age, and reproductive status. The significance of ventral gland secretions in the chemical communication of this species remains an interesting area of study.

The morphology of the glans penis of two *O. leucogaster* males trapped in Las Animas County, Colorado, was described by Hooper (1959). The surface of the glans is covered with
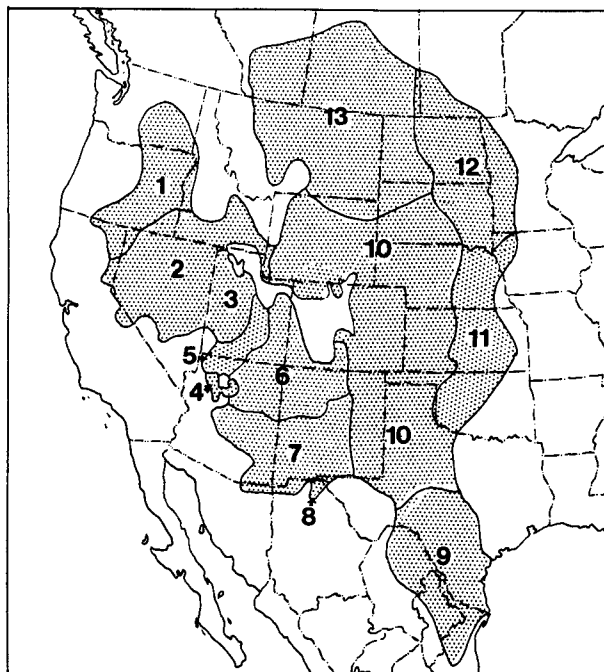

FIGURE 3. Geographic distribution of *Onychomys leucogaster* and subspecies in western North America (modified from Hall and Kelson, 1959). Subspecies are: 1, *O. l. fuscogriseus*; 2, *O. l. brevicaudus*; 3, *O. l. utahensis*; 4, *O. l. fuliginosus*; 5, *O. l. melanophys*; 6, *O. l. pallescens*; 7, *O. l. ruidosae*; 8, *O. l. albiscens*; 9, *O. l. longipes*; 10, *O. l. articeps*; 11, *O. l. breviauritus*; 12, *O. l. leucogaster*; 13, *O. l. missouriensis*.

curved, sharp, overlapping spines, except at the base and extreme tip. These spines become progressively larger toward the base of the glans, where they are as much as 0.6 mm long. The glans of *O. leucogaster* is slimmer in appearance than that of *O. torridus* and nearly circular in cross-section. The oval tip terminates in four flaps of soft tissue, a larger lateral pair and a smaller pair placed dorsally and ventrally. The baculum is an osseus blade, approximately one-fourth the length of the hind foot and less than three-fourths the length of the glans. The basal part of the bone is inflated, and the remainder is thin and tapered. The obtuse tip is covered with a thin layer of cartilage.

FUNCTION. Few detailed studies have been reported on the physiological responses of *O. leucogaster*. Pinter (personal communication) studied the morphology and activity of the ventral gland of *Onychomys* following ovariectomy or orchiectomy. Subjects were administered either testosterone propionate or estradiol benzoate. Testosterone maintained a functional ventral gland in both sexes.

Clark (1962a) reported that *Onychomys* has the largest adrenal gland weight proportional to body weight (as high as 2000 mg/kg body weight) of any species in a comparative study of adrenal function.

Scudder et al. (1966) examined the levels of brain biogenic amines in *O. leucogaster*. The following values are expressed as $\mu g/g$ wet weight: dopamine, 1.36; norepinephrine, 0.68; epinephrine, 0.07; and serotonin, 0.93. The relatively high levels of brain biogenic amines for *O. leucogaster* are interesting in view of the behavioral response of this species to tranquilizing drugs. Clark (1962a) and Cole and Wolfe (1970) observed that high does of chlorpromazine had no effect on attack latency, attack time, or time to kill in tests with laboratory mouse opponents. In additional studies, Cole and Wolfe (1970) reported that sodium pentobarbital had no effect and chlordiazepoxide increased time spent fighting a laboratory mouse opponent. These results suggest the need for additional studies on the relationship between brain neurochemistry and behavior in *O. leucogaster*.

ONTOGENY AND REPRODUCTION. Considerable variation is evident in laboratory records for length of gestation in *O. leucogaster*. Egoscue (1960) reported a gestation of 29 to 32 days for nonlactating females and 32 to 38 days for lactating females of *O. l. utahensis*. Pinter (1970) calculated a gestation of 26 to 37 days for nonlactating females of *O. l. articeps*, and

Horner (1968) reported gestation of no more than 27 days for nonlactating females of *O. l. brevicaudus*. Finally, Svihla (1936) observed 33 to 47 days of gestation for lactating *O. l. fuscogriseus* females.

A detailed description of parturition of *O. leucogaster* is not available. Postpartum estrous does occur from several hours to two days following birth of the young (Egoscue, 1960). Pinter (1970) recorded a mean litter size of 3.7 from a sample of 153 litters born in her laboratory, whereas Egoscue (1960) calculated an average of 3.54 (range 1 to 6) from 197 laboratory-born litters. Other values for mean litter size include 3.2 (Scudder et al., 1967) and 3.8 (Ruffer, 1964). Most litters are born from February through August (Egoscue, 1960), with peak production during June, July, and August (Pinter, 1970). The onset of reproductive activity may be timed by the increasing photoperiod and cessation would be influenced by shortening of day length (Pinter, 1970).

Excellent descriptions of the developing young have been provided by Horner (1968) and Ruffer (1964, 1965c) to supplement the earlier work of Bailey and Sperry (1929) and Svihla (1936). At birth, the neonates are pink and quite vocal; the dark irides are visible through the sealed lids and the pinnae are folded and sealed; the mystacial vibrissae are white and silky; and the digits are fused. Within 24 hours, the dorsal surface is faintly pigmented and the average weight is 2.8 g. Young animals move about the nest in an uncoordinated fashion on day 2, with marked improvement on succeeding days. By day 3, the pinnae are unfolded in a majority of animals and weights average 3.8 g. Movement out of the nest occurs on day 4. On day 8, the incisors begin to erupt, the dorsal fur is dark, fine white hairs appear on the ventral surface, and the weight averages 6.5 g. The lower incisors erupt in all mice by day 10 and the teats are visible for the first time. The young can maintain their body temperature for periods up to 10 minutes away from the nest at day 10. Ruffer (1964) observed that at this age they eat seeds or insect remains left by the parents. From day 10 onward, the mice become extremely active and defecate freely when handled. Grooming, digging, and fighting (between litter mates) occurred on day 13. On day 14, the auditory meatus is open in all mice, chirping vocalizations are frequently heard, and weights average 9.2 g. Significant variation exists for the time of eye opening; values include day 9 for *O. l. breviauritus* (Ruffer, 1964), day 15 for *O. l. ruidosae* (Scudder, et al., 1967), day 18 for *O. l. brevicaudus* (Horner, 1968), and day 19 for *O. l. fuscogriseus* (Svihla, 1936). Ruffer (1964) first observed burrowing by young animals away from the nest burrow on day 20 and weaning occurred by day 23.

Sexual activity in *O. l. articeps* occurs no earlier than day 90 for females and day 120 for males. An analysis of body weight changes suggests that the onset of sexual maturity occurs between weeks 7 and 8 (Pinter, 1970). The youngest *O. l. utahensis* female to give birth was six months old, and Egoscue (1960) reported that most laboratory-reared females produced their first litters in the breeding season following the year of birth. Detailed studies of the estrous cycle of *O. leucogaster* have not been reported. However, Dewsbury (personal communication) suggests that laboratory-housed adult *O. leucogaster* cycle every five to seven days.

In the laboratory, females produced an average of three to six litters per year and remained reproductively active for up to three years. Egoscue et al. (1970) reported a maximum of 12 litters and 52 young per female per year, and 20 litters and 83 young per female per lifetime. Pinter (1970) described one wild-trapped female that bore 11 litters over a 27-month period in captivity.

Under controlled conditions, northern grasshopper mice have lived more than four years (Egoscue, 1960; Pinter, 1970). It is doubtful, however, that subjects would survive for this long in a natural setting.

ECOLOGY. Local populations of *Onychomys leucogaster* are probably not regulated to any measurable degree by avian or mammalian predators. Egoscue (1960) cited several studies that demonstrated a scarcity of grasshopper mouse remains in the nests of great horned owls and red-tailed hawks. Later, Egoscue (1962) reported a low incidence of *Onychomys* remains near the den entrances or in the fecal passages of the kit fox. Sperry (1941), in an exhaustive study of the food habits of the coyote, found only 11 *Onychomys* specimens in examinations of 8339 coyote stomachs. Additional reports of predation on *Onychomys* include: swift fox (Cutter, 1958), barn owl (Glass, 1953), and great-horned owl (Finley, 1954; Long and Kerfoot, 1963).

A number of studies have focused on external parasites harbored by *O. leucogaster*. Rail et al. (1969) reported recovering the fleas *Meringis rectus*, *M. nidi*, and *M. dipodomys* from a sample of 18 mice collected at Red Bluff Ranch, New Mexico. Two species of sucking lice, *Hoplopleura hesperomydis* and *H. arboricola*, were collected from *Onychomys* and associated small mammals from the region of the Great Salt Lake Desert (Ignoffo, 1956). Thirteen different species of fleas were recovered from a sample of 405 *Onychomys* trapped in Santa Fe County, New Mexico, with an average of 1.9 fleas per specimen examined (Morlan, 1955). Egoscue (1960) suggested that grasshopper mice become infested with various ectoparasites through their direct (through predation, for example) or indirect (in burrows, for example) contact with other small mammals. Of 10 species of fleas collected from grasshopper mice trapped in western Utah, only one (*Monopsyllus exilis*) has the grasshopper mouse as its preferred host in the western United States (Hubbard, 1947).

An undescribed demodicid mite (*Demodex* sp.) has been recovered from the tongue, esophagus, and oral cavity of adult *O. leucogaster* captured near Richland, Washington (Nutting et al., 1973). No mites were found in the stomach. The incidence of infection was as follows: tongue tissue (nine of 11 animals), esophagus (four of 14 animals), and oral epithelium (one of 11 animals). In most cases, mite populations were small and caused only minor cell damage. Mites of this species may be transferred between host animals during the process of allogrooming.

Ruffer (1964) compiled a list of 34 mammalian species known to be associated with *Onychomys*. The relatively low densities of grasshopper mice in their natural habitat and their strong preference for insect prey may serve to minimize the potential for interspecific competition for food, space, and other limited resources.

Detailed studies of the structure and dynamics of natural populations of grasshopper mice are lacking. The absence of such studies may result from the relatively low densities of grasshopper mice in the wild (Bailey and Sperry, 1929; Ruffer, 1964). Egoscue (1960) suggested that adult *Onychomys* occur as isolated individuals or bisexual pairs. The predatory behavior of *Onychomys* is reflected in its unusually large home range, which averaged 2.3 hectares (5.8 acres) for four adult males studied by Blair (1953). Bailey and Sperry (1929) reported that grasshopper mice are hunters and wanderers that follow no definite pathways. In favorable habitats, however, *Onychomys* may become quite numerous and exert a controlling influence on the abundance of arthropods and other small mammals (Bailey and Sperry, 1929).

Bailey and Sperry (1929) provided the first detailed record of food preferences of *Onychomys* under natural and captive conditions. A laboratory examination of the stomach contents of 96 field-trapped grasshopper mice revealed the following percentages in the diet: Orthoptera, 38.8; Coleoptera, 20.7; Lepidoptera, 17.0; Mammalia, 3.1; miscellaneous arthropods and unidentified animal material, 9.3; Hymenoptera, 2.0; Diptera, 0.7; Arachnida, 0.5; Hemiptera, 0.1; and plant material, 11.1. Animal material thus contributed 88.9% of the total food consumed by *Onychomys*, whereas cultivated grains represented less than 5.0% of the total. The following species were eagerly eaten by captive grasshopper mice: grasshoppers of several genera, Mormon crickets (*Anabrus simplex*), sand crickets (*Stenopelmatus*), cockroaches, praying mantes, adult and immature cicadas, chrysalises of moths, smooth caterpillars, rose bugs (*Macrodactylus subspinosus*), cucumber beetles (*Diabrotica 12-punctata*), larval and pupal flies of several species, scorpions of several species, and several small mammal genera. Those species rejected as foods in the laboratory included millipeds of several species, fuzzy and spiny caterpillars, and blister beetles (*Epicauta* sp.). Several small rodents, including *Peromyscus maniculatus*, *Perognathus parvus*, and *Microtus montanus*, were killed and eaten by *O. leucogaster* (Bailey and Sperry, 1929).

Egoscue (1960) repeated the laboratory tests of food preference reported by Bailey and Sperry (1929). Captive grasshopper mice readily consumed grasshoppers, tenebrionid beetles, and all species of sympatric cricetid and heteromyid rodents offered to them. Blood stains were observed on the throats and chests of several mice at the time of capture in the field, providing further evidence that small mammals are represented in the natural diet of *Onychomys*.

An analysis of the stomach contents of *O. leucogaster* from a short grass prairie in Colorado was reported by Flake (1973). Animal material contributed 73.9% of the volume in a sample of 291 specimens. Maximum animal material occurred in stomachs in late spring and early summer, the lowest levels in midwinter. Those forms most frequently found included larval and adult Coleoptera, grasshoppers, spiders, larval Lepidoptera, and small rodents. Several dead rodents were eaten from traps by grasshopper mice. Plant matter averaged 25.3% of volume over the 12-month study period, the highest values were in January and February. Forbs, grasses and sedges, and seeds were approximately equal in percentage of dry weight of the stomach contents (Flake, 1973). Hansen (1975) suggested that part of the

plant material in the stomach contents of *Onychomys* originates from plant material in the guts of ingested arthropods.

A distinct seasonal change in the food preferences of 27 adult *O. leucogaster* maintained in outdoor pens was noted by Jahoda (1970*b*). In the warmer summer months, mice subsisted on a diet of red meat supplemented with sunflower seeds. Following a week of cold weather in November, however, all mice shifted to a diet consisting almost entirely of beef fat. Seeds were never eaten and red meat was eaten only occasionally. This change in food preference following the onset of colder weather may reflect a requirement for high calorie food during winter months (Jahoda, 1970*b*).

Grasshopper mice are unique among North American rodents in having a diet composed primarily of animal material (Landry, 1970). It was previously suggested that *Onychomys* may function as a natural regulator of insect pest populations while consuming a minimal amount of commercially-produced grains (Bailey and Sperry, 1929).

BEHAVIOR. Intraspecific encounters between adult *O. leucogaster* have been observed by Clark (1962*a*, 1962*b*) and Ruffer (1968). In a typical encounter, the dominant animal rapidly chased the subordinate and pounced at its back repeatedly. If the subordinate animal reared on its hind legs in a defensive posture, the aggressor then bit at the tail and hind legs until the back of the subordinate was exposed to attack. The subordinate was then killed by a bite through the neck at the base of the skull. Of 90 like-sexed encounters (male-male and female-female) staged in a 5 m × 5 m seminatural enclosure, 70% ended in death of the subordinate within 24 hours after pairing. In all such encounters, the subordinate was killed within 72 hours after pairing. In groups of three to five adult grasshopper mice, a single animal quickly assumed dominance over a group of coequal subordinates (Ruffer, 1968). Several females were reported to kill their mates near the time of parturition, suggesting a possible hormonal basis for this type of aggression (Egoscue, 1960).

A similar pattern of rapid pursuit and attack has been observed for *O. leucogaster* adults during interspecific tests of aggression (Bailey and Sperry, 1929; Clark, 1962*a*, 1962*b*; Cole and Wolfe, 1970; Ruffer, 1964, 1968). The victim was rapidly chased, with attacks directed at the back and neck. Death of the opponent usually occurred within several hours after pairing, although coexistence and nesting together are not uncommon (Clark, 1962*a*, 1962*b*). If the opponent was not killed, the grasshopper mouse was always the more socially dominant. Rodent species attacked, killed, and eaten by *O. leucogaster* included *Peromyscus leucopus*, *P. maniculatus*, *Microtus montanus*, *Perognathus parvus*, *P. hispidus*, *Dipodomys ordii*, *Sigmodon hispidus*, *Reithrodontomys megalotis*, and laboratory strains of *Mus musculus* (Bailey and Sperry, 1929; Cole and Wolfe, 1970; Ruffer, 1968). Boice and Schmeck (1968) studied the predatory behavior of *O. leucogaster* adults toward cricket prey. A single subject was reported to kill as many as 40 crickets in a two-hour period.

Ruffer (1965*c*) described patterns of courtship and copulation for northern grasshopper mice. In 174 heterosexual pairings observed, initial sexual recognition occurred when the two subjects moved in a small circle 10 to 15 cm in diameter. This was followed by naso-anal and naso-nasal contact. After another period of circling and naso-anal contact, the male followed the female around the enclosure, frequently sniffing her genitalia. This pattern of circling and grooming continued with a variable number of interruptions of activity until the male mounted the female from the rear. Intromission occurred while the male held his forepaws on the shoulders of the female. During a copulatory lock, the pair would often roll on their sides for up to two seconds. The female terminated the sequence by moving away and grooming. The entire 10-phase courtship sequence required up to three hours for completion (Ruffer, 1965*c*). Ewer (1968), in reviewing the description by Ruffer (1965*c*) of the copulatory behavior of *O. leucogaster*, concluded that it was the most complex pattern of courtship yet described for the Rodentia.

Lanier and Dewsbury (personal communication) provided a quantitative description of the copulatory behavior of northern grasshopper mice. In 50 tests, 10 different adult males were paired to satiety with female partners in hormone-induced estrus. For these pairings, there was a mean of 3.8 copulatory locks with a mean lock duration (MLD) of 60.4 seconds. In tests employing females in postpartum estrus, the mean number of locks was 9.3 with a MLD of 32.8 seconds. Fourteen females failed to become pregnant when tests were interrupted after a single lock. If these same females remained with their male partners until satiety, 25% became pregnant. Facilitation of sperm transfer by multiple locks has also been observed for *O. toridus* pairs (Dewsbury and Janzen, 1972).

O. leucogaster parents are particularly solicitous of the young and will actively defend the nest against human disturbances (Egoscue, 1960; Scudder *et al.*, 1967). When young were replaced in the home cage after inspection, both parents carried them back to the nest area. The female spends considerable time grooming the head and back of her pups until they reach 14 days of age. Males were not observed to assist in such grooming (Ruffer, 1964). Scudder *et al.* (1967) suggested that the slow maturation, relative to that of other cricetids, allows a longer period of development of behavioral characters, particularly those associated with predation. Ruffer (1965*c*) observed parents leaving insect remains near the nest for young animals between 10 and 16 days of age.

Northern grasshopper mice are nocturnal and are rarely active during daylight hours under captive conditions (Bailey and Sperry, 1929; Egoscue, 1960). The time and amount of activity of adult grasshopper mice maintained in outdoor enclosures is influenced by the lunar cycle and daily weather conditions. Mice are most active when the moon is below the horizon or when there is a heavy cloud cover with light or intermittent rains. Activity is greatly reduced during a full moon or heavy, prolonged rainfall (Jahoda, 1970*a*, 1973). Grasshopper mice are active throughout the year, with no evidence of hibernation (Ruffer, 1964). In the extreme northern portions of the range, mice may take refuge in outdoor cellars, underground caverns, or burrows (Bailey and Sperry, 1929).

The vocal behavior of grasshopper mice was first described by Bailey and Sperry (1929). They noted a short, sharp squeak produced in rapid succession by mice when threatened or when pursuing prey, and a long, shrill whistle frequently heard on spring or summer nights. The latter call was thought to function as a hunting or mating call, or possibly both. In addition to the squeaks and whistles, Egoscue (1960) described a low birdlike chirp of protest that was heard when two grasshopper mice were attempting to feed from the same food source. He also noted the variety of calls produced by the nestlings during the course of feeding and moving about the nest. Ruffer (1964) described four types of calls produced by grasshopper mice: (1) a squeak call given by young 0 to 4 days of age and adults during agonistic encounters, (2) a high-pitched chirping call given as an alarm call during a vigorous fight, (3) a high-pitched whistle lasting an average of 0.8 seconds and (4) a call similar to the whistle, but broken so that it sounded like two shortened calls. The entire latter type of call lasted an average of 0.9 seconds. Both types of whistles were thought to provide a means of intraspecific communication and localization (Ruffer, 1964, 1966). Hildebrand (1961) recorded a representative whistle call of an adult *O. leucogaster* and reported the sound wave to be nearly a sine curve with a frequency of 10 kHz (10,000 cycles per second).

Burrows provide *O. leucogaster* with essential protection from the high diurnal temperatures characteristic of a xeric habitat. Ruffer (1965) observed adult male-female pairs for a three day period in outdoor enclosures (5 by 5 by 1 m) that contained a sand substrate and native plant species. Four types of burrows were constructed, including nest burrows, retreat burrows, cache burrows, and miscellaneous burrows. Nest burrows were constructed and utilized by male-female pairs for such activities as sleeping, care of the young, and retreat. A typical nest burrow was shallow and U-shaped with a mean length of 48 cm and a mean depth below the surface of 14 cm. A centrally located nest chamber averaged 12 cm long, 9 cm wide, and 7 cm high. Two entrances were constructed, although only one normally was used. During one July day, surface temperatures fluctuated 27°C (49°F), whereas the temperature within the nest burrow fluctuated only 7°C (12°F). Retreat burrows were constructed at a 45° angle to the horizontal and averaged 25 cm in length with a maximum depth of 20 cm. These burrows were used if a subject was frightened while moving about the enclosure. Seeds were stored in cache burrows scattered at various locations about the enclosure. Each cache burrow was dug at an angle of less than 45° with the horizontal and averaged 10 cm in length. The burrow was filled with seeds, then covered with a thin layer of sand. Several other burrow types were observed, including defecation burrows and territorial sign posts. Defecation sites were 5 cm long and were dug at a 90° angle to the horizontal. Territorial signpost burrows were less than 3 cm in length and served to mark the boundary of a territory. After constructing a signpost burrow, the subject often took a sand bath in it to further advertise the location of the boundary (Ruffer, 1965*b*).

When pairs of *O. leucogaster* were released into an enclosure that contained the burrows of other species (*Dipodomys ordii* or *Perognathus hispidus*), they would utilize the abandoned nest burrows as a place of retreat during the first night while constructing their own burrow system (Ruffer, 1964, 1965*b*).

Although most of the diet of *O. leucogaster* is animal material (Flake, 1973), there are several reports that adult mice hoard seeds under captive conditions. Ruffer (1965b) observed that grasshopper mice hoarded seeds in specific cache burrows and in the nest burrow chamber. Bailey and Sperry (1929) stated that food storage may be a common behavior of grasshopper mice during the onset of winter. Nest boxes were filled to capacity with sunflower seeds. The food stores were not utilized if other food was provided. The hoarding behavior of *Onychomys* may be of critical importance to survival during winter months when arthropod populations are greatly reduced as a source of food.

Russell and Findley (1954) reported observing a grasshopper mouse swim 12 feet across a stream. In the laboratory, Ruffer (1964) found that three of five mice escaped to a large container of water when frightened. The three swam an average of 24 feet each. Boice (1972) observed that wild-trapped *O. leucogaster* consumed 230 mm³ of water per g of body weight. Amounts of water consumed over the first five days in captivity averaged 7500 mm³ per day.

Harriman (1973) reported that 70% of a sample of laboratory-reared *O. leucogaster* were able to maintain body weight increases similar to those of control animals when placed on a schedule of total dietary self-selection from an array of semi-purified and purified nutrients. Over a 60-day test period, mice fed a standard laboratory chow diet had an average caloric intake of 298 ± 42 cal/g/day whereas mice on a self-selection schedule consumed 306 ± 39 cal/g/day. Water consumption averaged 134 ± 25 mm³/g/day for controls and 90 ± 19 mm³/g/day for the self-selection group. A test diet composed of the nutrients mixed in quantities reflecting consumption rates by a group of self-selectors proved as adequate as laboratory chow in maintaining the body weights of a group of captive mice (Harriman, 1973).

Two of three wild-trapped *O. leucogaster* exhibited long periods of immobility (median time greater than six minutes) when suddenly exposed to an open field arena. Associated with these periods of immobility were decreases in heart rates, transient cardiac arrhythmias, and increases in respiratory rates (Hofer, 1970).

Harriman (personal communication) reported that 3% of wild-trapped *O. leucogaster* exhibit convulsive seizures in the laboratory. The onset of seizures is especially pronounced when the mice are exposed to novel stimuli. Attempts to inbreed seizure-prone individuals were unsuccessful. The seizure activity described by Harriman appears identical to that described for *O. torridus* (McCarty and Southwick, 1975).

GENETICS. The diploid chromosome number of *O. leucogaster* is 48. The 46 autosomes consist of metacentrics, submetacentrics, and subtelocentrics. The X chromosome is submetacentric and the Y chromosome is subtelocentric (Hsu and Benirschke, 1967). Where *O. leucogaster* occurs sympatrically with *O. torridus*, there is no evidence of character displacement (Van Cura and Hoffmeister, 1966).

The pattern of inheritance of dichromatism (color phases) in a laboratory population of *O. l. utahensis* was studied by Egoscue (1963). Two distinct color phases were observed in adult animals trapped in southcentral Tooele County, Utah, a pale phase (upper parts buff colored) and a melanistic phase (upper parts blackish-brown to black). Melanistic animals were especially rare in nature, with only four recorded over several years of trapping. Breeding tests demonstrated that the melanistic phase was inherited as a simple autosomal recessive in the presence of the pale phase. The small percentage of melanistic animals from the study area probably reflects the greater camouflaging ability provided by the pale phase pelage against the pale, sandy substrate of the vegetated dunes. In north-central Arizona, Van Cura and Hoffmeister (1966) described melanistic phase *O. l. fuliginosus* from the cinder beds around the San Francisco Mountains in Coconino County, Arizona. Animals in the pale phase were common from the desert regions of eastern Arizona (*O. l. pallescens*).

REMARKS. For this account, the subspecies *O. l capitulatus* was regarded as synonymous with *O. l. fuliginosus* (Van Cura and Hoffmeister, 1966). Citations to original descriptions were not consulted directly; rather, all references were taken from Hollister (1914) or Van Cura and Hoffmeister (1966).

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Principal editor of this account was SYDNEY ANDERSON.

R. McCARTY, DEPARTMENT OF PATHOBIOLOGY, SCHOOL OF HYGIENE AND PUBLIC HEALTH, THE JOHNS HOPKINS UNIVERSITY, 615 NORTH WOLFE STREET, BALTIMORE, MARYLAND 21205.