

**Tamias obscurus.** By Troy L. Best and Nancy J. Granai

Published 2 December 1994 by The American Society of Mammalogists

***Tamias obscurus* J. A. Allen, 1890**

**Dusky Chipmunk**

*Tamias obscurus* J. A. Allen, 1890:70. Type locality "San Pedro [Mártir] Mountains [near Vallecitos—Callahan, 1977:195], lower [=Baja] California, Mexico."

**CONTEXT AND CONTENT.** Order Rodentia, Suborder Sciuromorpha, Family Sciuridae. The genus *Tamias* contains 25 species (Wilson and Reeder, 1993). *T. obscurus* is in the subgenus *Neotamias*, and in the *merriami* species group with *T. bulleri*, *T. merriami*, and *T. palmeri* (Levenson et al., 1985). Three subspecies of *T. obscurus* are recognized (Hall, 1981):

*T. o. davisi* (Callahan, 1977:193). Type locality "Barker's Reservoir, 1300 meters (m), 16 km SW of Twentynine Palms, San Bernardino Co., California."

*T. o. meridionalis* (Nelson and Goldman, 1909:23). Type locality "Aguaje de San Esteban, about 25 miles northwest of San Ignacio, Lower [=Baja] California, Mexico (altitude about 1,200 ft.)."

*T. o. obscurus* J. A. Allen, 1890:70, see above.

**DIAGNOSIS.** *Tamias obscurus* (Fig. 1) is sympatric or parapatric with *T. merriami* and *T. speciosus*. However, *T. panamintinus* approaches within 80 km of the range of *T. obscurus* in the Providence Mountains, California.

*Tamias obscurus* and *T. merriami* are sympatric in the San Bernardino Mountains north of San Gorgonio Pass and in the San Jacinto Mountains of southern California. *T. merriami* occurs northward to the Sierra Nevada, whereas *T. obscurus* occurs southward into Baja California (Blankenship and Bradley, 1985; Callahan, 1976; Hall, 1981; Nelson, 1922). Spermatozoa of *T. obscurus* and *T. merriami* are similar (Callahan, 1976), but the two species can be distinguished by the ossa genitalia (Blankenship, 1985; Callahan, 1977). The summer pelage of adult *T. obscurus* is paler, less yellowish, and there is more reddish in the dark dorsal stripes than in *T. merriami* (Callahan, 1977). Further, *T. obscurus* is smaller, has a shorter tail and hind foot, and has a smaller and flatter cranium. These differences are less pronounced in the San Bernardino Mountains than in other zones of sympatry. In the San Bernardino Mountains and elsewhere, the two species are 100% separable by discriminant analysis of skull and body measurements (Callahan, 1976). In the San Jacinto Mountains, adults of *T. obscurus* and *T. merriami* are distinguishable by ventral coloration; hairs of the throat and upper chest are gray (usually black at the base) in *T. o. davisi* and whitish in *T. merriami* (this criterion is not valid in the San Bernardino Mountains where these hairs have black bases in both species—Callahan, 1977).

Sonograms of the chips of *T. obscurus* and *T. merriami* are characterized by a symmetrical inverted-V shape. The calls of *T. obscurus* and *T. merriami* differ in frequency of origin of upsweep, top of upsweep, bottom of downsweep, and length of chip (Blankenship and Brand, 1987). In addition, *T. obscurus* is closely tied to single-leaf pinyon (*Pinus monophylla*) woodland in the San Bernardino Mountains, whereas *T. merriami* usually is found in more mesic forest, primarily, coniferous forest. Habitats occupied by these chipmunks are more useful than calls for distinguishing between these species (Blankenship, 1985).

Unlike *T. o. obscurus* and *T. o. meridionalis*, which have karyotype A of *Tamias*, *T. o. davisi* cannot be distinguished from *T. merriami* on the basis of gross chromosomal morphology because both have karyotype B. Two adult specimens of *T. merriami* resemble *T. obscurus* in coloration, but the baubella and skulls are typical of *T. merriami* (Callahan, 1977).

*Tamias obscurus* is sympatric with *T. speciosus* in the San Bernardino and San Jacinto mountains, California (e.g., Big Bear Lake, Sugarloaf Mountain, Heart Bar State Park, and San Jacinto Peak—Blankenship, 1985). However, recent fieldwork on San Jacinto Peak indicates that *T. speciosus* may no longer occur there (J. R. Callahan, in litt.). Examination of 11 allozymes revealed that *T. obscurus* differs from *T. speciosus* by the presence of a fast-band esterase-1 and that *T. obscurus* differs from *T. amoenus* in relative mobility of esterase-3 (Blankenship and Bradley, 1985), but allozymes of *T. obscurus* do not differ consistently from those of *T. merriami* (Blankenship, 1985; Blankenship and Bradley, 1985). *T. panamintinus* resembles *T. obscurus* in having reddish stripes and a flattened cranium (Fig. 2), but *T. panamintinus* is smaller than *T. obscurus* and the ossa genitalia of the two species differ (Callahan, 1976).

**GENERAL CHARACTERS.** In summer pelage (July–September), the top of the head is pale smoke-gray, shaded with pinkish cinnamon, and bordered on the sides with a narrow stripe of bister or snuff brown. Sides of the nose are clay color or cinnamon buff. The dark facial stripes are mikado brown and the ocular stripe is fuscous black around the eye. The pale facial stripes are pale smoke-



FIG. 1. *Tamias obscurus davisi* in Joshua Tree National Monument, Riverside Co., California. Photograph courtesy of H. E. Broadbooks.

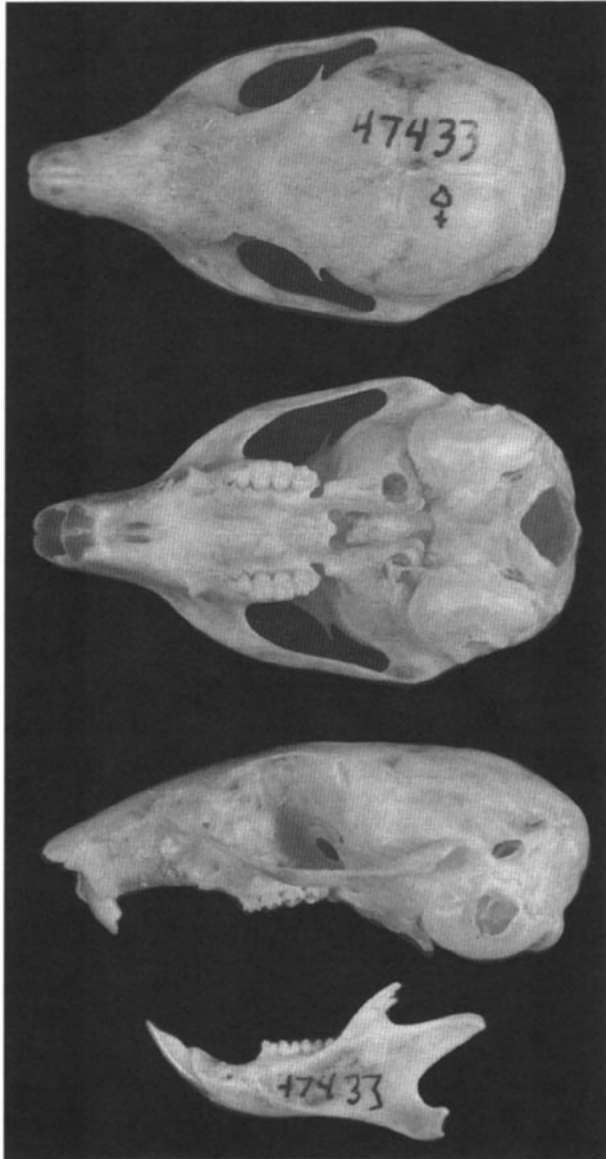


FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of *Tamias o. obscurus* from near Vallecitos, Sierra San Pedro Mártir, Baja California, Mexico (female, University of New Mexico Museum of Southwestern Biology 47433). Greatest length of cranium is 35.5 mm. Photographs by T. H. Henry.

gray. The ears are mouse gray or chaetura drab, washed on the posterior one-half with pale buff or soiled whitish. The postauricular patches are grayish white. The dark dorsal stripes are mikado brown or russet, with the median one blackish in the posterior one-half. The median pair of pale stripes is smoke-gray or pale smoke-gray. The outer pair is grayish white. The sides are sayal brown, shoulders are pale smoke-gray with pinkish buff, and rump and thighs are grayish white mixed with clay color or cinnamon giving a general tone near neutral gray. The hind feet are cinnamon buff or pinkish buff, and the forefeet are pinkish buff. The tail is fuscous black dorsally, overlaid with pinkish buff. Ventrally, the tail is tawny, bordered with fuscous black and edged with pinkish buff. The underparts are creamy white. The color of winter pelage (November) is similar to that of summer pelage, but the general tone of the upperparts is darker in the dorsal stripes, which usually are less distinct and often nearly indistinguishable. The sides are washed with pale sayal brown or cinnamon buff (color nomenclature follows Ridgway, 1912—Howell, 1929).

Average measurements (in mm) of males and females of *T. o. obscurus*, males and females of *T. o. davisii*, and sexes combined of

*T. o. meridionalis*, respectively, are: greatest length of cranium, 36.2, 37.0, 37.3, 37.7, 34.7; rostral length, 13.5, 13.8, 13.9, 14.0, 12.7; length of braincase, 22.7, 23.2, 23.4, 23.7, 22.3; length of maxillary toothrow, 5.7, 5.9, 5.7, 5.9, 5.5; length of nasals, 11.5, 12.0, 12.0, 12.0, 10.6; zygomatic breadth, 19.6, 19.9, 20.0, 20.4, 18.5; depth of cranium, 13.7, 13.7, 14.0, 14.0, 13.3; least interorbital breadth, 8.4, 8.4, 8.5, 8.6, 8.6; cranial breadth, 17.5, 17.5, 17.6, 17.7, 16.6; rostral breadth, 8.3, 8.3, 8.4, 8.4, 7.6; width of nasals, 2.2, 2.2, 2.5, 2.2, 2.3; length of head and body, 127.8, 130.8, 127.8, 134.7, 114.0; length of tail, 91.9, 94.7, 96.2, 98.9, 102.4; length of hind foot, 33.5, 34.2, 34.1, 34.5, 33.1 (Callahan, 1977). The mass of adults is 56–90 g (Jameson and Peeters, 1988; Larson, 1964).

Although one study failed to detect sexual dimorphism in length of head and body (Levenson, 1990), females are larger than males in this character, greatest length of cranium, length of braincase, and length of maxillary toothrow in *T. o. davisii* and *T. o. obscurus*. Females of *T. o. davisii* are larger than males in zygomatic breadth and males are larger than females in width of nasals; in *T. o. obscurus*, females are larger than males in rostral length and length of nasals (Callahan, 1977).

In a sample of *T. o. obscurus* from the San Pedro Mártir Mountains, Baja California, there was considerable intraspecific variation in the amount of brownish suffusion beneath the surface of the pelage, which was strong to nearly absent. In some of these chipmunks, the general color of the dorsal surface was paler and grayer than in others (Allen, 1890). Farther south, *T. o. meridionalis* is smaller, grayer, and the braincase is narrower and less inflated than in *T. o. obscurus* (Nelson and Goldman, 1909). Bacula of *T. o. meridionalis* and *T. o. obscurus* are indistinguishable (Fig. 3), except the basal portion is wider in *T. o. obscurus*. Baubella of these two subspecies are similar, except the angle formed by the basal and distal sections is more acute in *T. o. obscurus* (Callahan, 1975). Compared with those of *T. o. davisii* and *T. o. obscurus*, the skull of *T. o. meridionalis* is smaller and narrower, but has greater interorbital breadth. *T. o. meridionalis* is small, with a long tail averaging 47% of total length (42% in *T. o. davisii* and *T. o. obscurus*); its pelage is paler than that of *T. o. obscurus* (Callahan, 1977).

**DISTRIBUTION.** *Tamias obscurus* occurs as a series of disjunct populations from the San Bernardino and San Jacinto mountains southeastward across the desert ranges of southern California and central Baja California as far south as the Sierra de San Francisco (Fig. 4; Blankenship and Bradley, 1985; Callahan, 1976, 1977; Howell, 1929; Miller and Stebbins, 1964; Nelson, 1922). The dusky chipmunk occupies the lower Sonoran, upper Sonoran, transition, and Canadian life zones, at elevations of 300–3,000 m elev. (Blankenship, 1985; J. R. Callahan, in litt.; Howell, 1929).

**FOSSIL RECORD.** The genus *Tamias* evolved by the early Miocene (Black, 1972). No fossils of *T. obscurus* are known.

**FORM AND FUNCTION.** Post-breeding pelage is bright; the five dark dorsal stripes are conspicuous and of a bright-chestnut color. The central stripe is black on the lateral one-half. The four gray dorsal stripes also are accentuated, and the flanks are tawny ochraceous or ochraceous rufous. Summer and winter pelages of *T. obscurus* differ markedly (Elliot, 1903). By spring or early summer, winter pelage is worn and lacks stripes (Howell, 1929). In California, a male at Mountain Spring, San Diego Co., was in summer pelage on 15 May; on 4 and 12 August, two were molting at Barker's Reservoir, San Bernardino Co. (Callahan, 1976). In the Laguna Hanson Mountains, Baja California, summer pelage appeared on the head and anterior dorsum of a male on 8 June. At Vallecitos, Baja California, on 14 July, an adult female had a similarly worn pelage on the posterior dorsum, with new pelage covering the anterior one-half of the body (Howell, 1929). In the San Pedro Mártir Mountains, Baja California, in May, several were molting, some had post-breeding pelage, but most had pelage that was worn and ragged (Allen, 1893). In the Sierra de San Francisco, Baja California, an adult male was molting on 27 June (Larson, 1964). In the Sierra Juárez, Baja California, adults had acquired the summer pelage by mid-June (Callahan, 1976).

As in all members of the subgenus *Neotamias*, the dental formula is i 1/1, c 0/0, p 2/1, m 3/3, total 22 (Howell, 1929; Ingles, 1965). The hypohyal of the hyoid is cylindrical in populations at the southern limit of the range. Where sympatric with *T. merriami*,

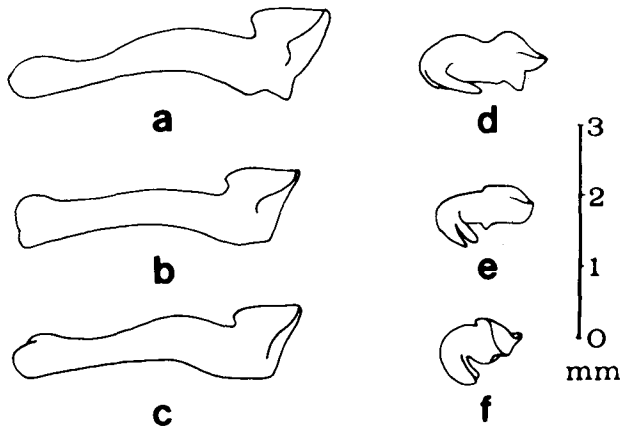


FIG. 3. Ossa genitalia of *T. obscurus*, right, lateral view (f, right anterolateral): a-c, bacula; d-f, baubella (a and d, *T. o. obscurus*; b and e, *T. o. davisii*; c and f, *T. o. meridionalis*—Callahan, 1977).

the hypohyal of *T. obscurus* is narrow, thick, and has a cross-section approximating a fat ellipse (Callahan, 1976). The baculum of one *T. o. davisii* had been broken; there was symmetric calcification along the broken edge (Callahan, 1976).

**ONTOGENY AND REPRODUCTION.** In California, it has been reported that *T. obscurus* may have more than two litters of three or four young each per year (Jameson and Peeters, 1988), but *T. obscurus* may have only one litter each year (J. R. Callahan, in litt.). *T. o. davisii* has a long breeding season, which may begin early in January. Females had embryos on 26 January and 22 April; on 23 March an 8-week-old juvenile was observed. On 28 May, an estrous female was observed on Sugarloaf Mountain, and on 5 August one was lactating and had acquired the summer pelage (Callahan, 1976; Miller and Stebbins, 1964).

In Baja California, *T. o. meridionalis* begins breeding early in the year; nests containing juveniles were present in February, and two subadults were observed in mid-July. These subadults were molting into summer pelage, and two non-lactating adult females were in summer pelage. Apparently, some young also are born in late April or May. In the Sierra Juárez at 1,500 m elev., breeding begins by early March; a two-thirds-grown juvenile was observed here on 11 June (Callahan, 1976), but there was no evidence of lactation in early May (Allen, 1890). In the San Pedro Mártir Mountains, several half-grown young were observed 6–28 May (Allen, 1893). Near San Gregorio, a female and three young were found in a cavity of a cardon cactus (*Pachycereus pringleyi*) in February. Another individual was two-thirds grown in mid-July. Thus, there may be early and late breeding individuals. A male was in breeding condition in late June, but no females were lactating in mid-July (Callahan and Davis, 1976). An adult male from Sierra de San Francisco was in breeding condition on 27 June; it had an enlarged bulbourethral gland and pendulous testes (Larson, 1964).

Physical characteristics of *T. o. meridionalis*, such as its small size, long tail, narrow skull, and pale coloration, may be desert adaptations; however, the pale coloring may be a characteristic of old individuals (Callahan, 1977). No published information is available on ontogeny and longevity, but one *T. obscurus* is known to have lived for 10 years in captivity (J. R. Callahan, in litt.).

**ECOLOGY.** The range of the dusky chipmunk lies within the California and Vizcaino Desert biotic provinces, which extend from southern California across the international boundary to include the Sierra Juárez, Sierra San Pedro Mártir, and the western slopes of these mountains to the Pacific coast in northern and central Baja California. This is an area of extreme aridity to moderate rainfall (Goldman and Moore, 1946). *T. obscurus* commonly is found in pinyon-juniper (*Pinus-Juniperus*) woodlands ( $\geq 1,200$  m) and pine-oak (*Pinus-Quercus*) forests. Often it is found in the vicinity of granite outcroppings and talus, sometimes with manzanita (*Arctostaphylos glauca*) or sagebrush (*Artemisia*) present (Callahan, 1976). *T. obscurus* is found along dry northern slopes in the San Bernardino Mountains from their eastern end to the western limit of the pinyon

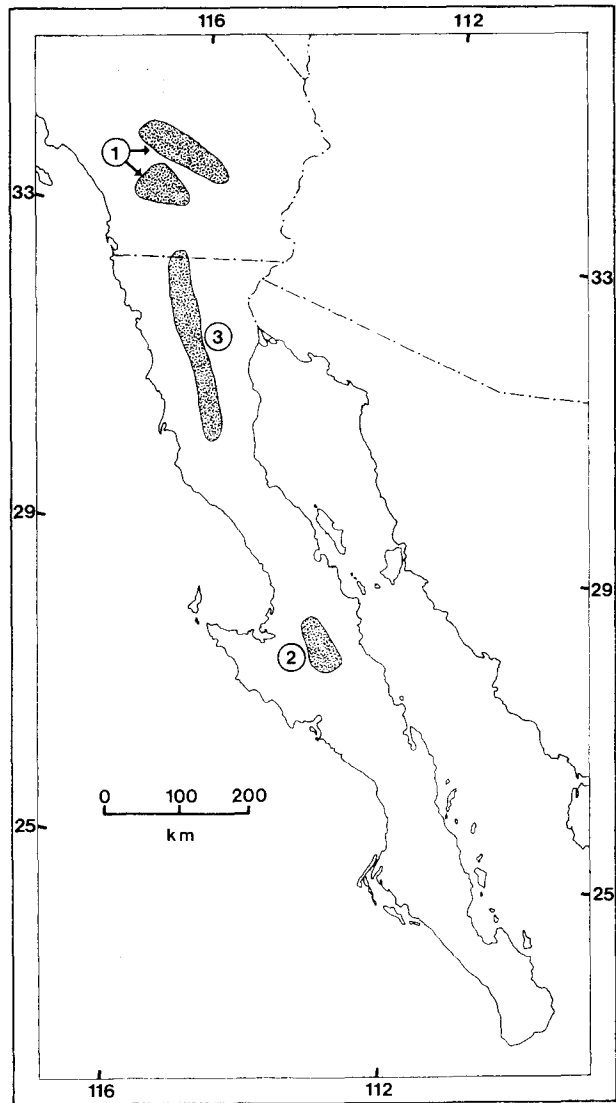


FIG. 4. Distribution of *Tamias obscurus* in California and Baja California (Hall, 1981): 1, *T. o. davisii*; 2, *T. o. meridionalis*; 3, *T. o. obscurus*.

woodlands, and from the desert to the lower edge of the coniferous forest up to 3,000 m elev. (Blankenship, 1985). In the San Pedro Mártir Mountains, *T. obscurus* is almost exclusively a rock-dwelling species. It is present on every large mass of granite boulders, which are common in its geographic range (Allen, 1893).

At least four populations of *T. o. davisii* may be isolated by low desert barriers. San Geronio Pass and the Coachella Valley separate chipmunks of the San Jacinto and Santa Rosa mountains from those to the north, and the Morongo Valley separates those of the eastern San Bernardino Mountains from the Little San Bernardino Range (Callahan, 1976). Another isolated population occurs on Eagle Mountain (Miller and Stebbins, 1964). North of San Geronio Pass, *T. o. davisii* is restricted largely to arid, rocky situations in upper Sonoran pinyon-juniper woodland  $< 2,100$  m elev. It is abundant in this habitat from the desert slope of the San Bernardino Mountains eastward through the desert ranges of Joshua Tree National Monument. *T. o. davisii* occurs up to 2,550 m elev. on the desert slope of Sugarloaf Mountain where it is associated with ponderosa pine, incense cedar, and serviceberry (*Amelanchier alnifolia*). *T. o. davisii* usually is seen among boulders, although it may occur in clearings with rotting logs and stumps. Apparently, *T. o. davisii* enters the lodgepole pine-chinquapin belt in the vicinity of Round Valley (Callahan, 1976). In the San Jacinto Mountains, *T. o. davisii* occurs at elevations of 1,735 (Dark Canyon) to 2,745 m (San Jacinto Peak), but one occurred at 1,372 m (Kenworthy). *T. o. davisii* occupies the transition life zone at 1,735 m and typically is associated with

ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), white fir (*Abies concolor*), Engelmann oak (*Quercus engelmannii*), and incense cedar (*Libocedrus decurrens*—Callahan, 1977). At the 2,745-m location on San Jacinto Peak, *T. o. davisii* occupies the Canadian life zone, and is associated with lodgepole pine and chinquapin (*Pinus contorta*—*Castanopsis sempervirens*—J. R. Callahan, in litt.). In the Santa Rosa Mountains, *T. o. davisii* occurs from 1,500 to  $\geq 2,440$  m elev. At lower elevations, its habitat includes live oak (*Quercus chrysolepis*) and chaparral (e.g., *Adenostoma*), whereas at higher elevations it inhabits pine-oak-cedar forest (Callahan, 1977).

*Tamias o. obscurus* occurs in the higher chaparral and forested areas of the Sierra Juárez and Sierra San Pedro Mártir of northern Baja California (Huey, 1964). This subspecies is at least as common in pinyon-juniper woodland as in ponderosa pine forest, and it is abundant at 1,370–1,525 m elev. in rock outcroppings along the road from El Condor to Laguna Hanson (Callahan, 1977).

*Tamias o. meridionalis* is one of the rarest mammals in Baja California, where its range is an area <40 km in diameter. Here it lives in lava-bound palm-cactus associations (Huey, 1964). *T. o. meridionalis* is known only from the lower Sonoran life zone, although patches of upper Sonoran oak woodland apparently occur within its range (Callahan, 1977). It occurs among the cacti near the mouth of San Pablo Canyon (Nelson, 1922). Common plants associated with *T. o. meridionalis* are elephant tree (*Bursera microphylla*), foothill paloverde (*Cercidium microphyllum*), brittlebush (*Encelia farinosa*), barrel cactus (*Ferocactus peninsulæ*), ocotillo (*Fouquieria peninsularis*), organpipe cactus (*Lemaireocereus thurberi*), palo blanco (*Lysiloma candida*), pitaya agria (*Machaerocereus gummosus*), cochal (*Myrtillocactus cochal*), blue fan palm (*Erythea armata*), wild fig (*Ficus palmeri*), common mesquite (*Prosopis juliflora*), chokecherry (*Prunus*), Bonpland willow (*Salix bonplandiana*), whitethorn (*Acacia constricta*), jatropha (*Jatropha cinerea*), cholla and prickly pear cacti (*Opuntia*), cardon cactus, and palo fierro (*Pithecellobium confine*—Callahan, 1976; Callahan and Davis, 1976).

*Tamias obscurus* uses burrows with entrances protected by large boulders. At Black Mountain (2,100 m elev.), one burrow was a straight tunnel >90 cm in length and >7.5 cm in diameter; angle of descent was ca. 45°. Another burrow was in a rock crevice in a narrow canyon. The natural opening was 10.2 by 3.8 cm, and the vestibule, which was littered by gnawed acorn hulls, was ca. 30 by 45 cm. At Black Mountain (1,950 m elev.), a burrow was situated in a partially hollow, rotten log that was lying on a steep hillside. The burrow began in the log, continued into the ground, and was 5.7–7.6 cm in diameter (Callahan, 1976). Burrow systems have short side branches that may serve as turn-around points or for deposition of fecal pellets. A winter den of an adult had a large nest chamber with a rock ceiling formed by an over-hanging boulder; numerous acorn shells, one sprouted acorn, and a stripped pine cone were cached under the eaves. The ceiling was covered with beads of condensed moisture, which may have provided a source of water. A den of this type may be inaccessible to many predators (Callahan and Estep, 1982).

In Baja California, *T. o. meridionalis* often has night shelters (Larson, 1986) and nests in cavities in cardon cacti. Standing and fallen cacti may be used as nest sites. Nests in standing cacti usually are 3–4.5 m aboveground. Each of two such nests had a single opening ca. 45 mm in diameter; neither contained food or nesting material. One of the nests had an opening that was 38 by 43 mm, and volume of the chamber was 870 cm<sup>3</sup>. Ladder-backed woodpeckers (*Dendrocopos scalaris*) make similar, but usually larger, nest cavities, and it is likely that chipmunks use these cavities if they are abandoned or unfinished. In captivity, *T. o. meridionalis* used its incisors to scrape the interior of cardboard nestboxes until the walls were paper thin. This habit suggests that existing nests may be enlarged and modified (Callahan, 1976).

Plant fibers used in nests are prepared in one of two ways. The dusky chipmunk draws a piece of dead root or stem slowly between its teeth, so that the outer layer curls up and accumulates at one side of the mouth, or the chipmunk loosens a fiber by gnawing, then strips it away from the root or stem. Pine straw, leaves, and similar nest materials are used without modification. An underground nest made of plant fibers with coffeeberry-redberry (*Rhamnus*) leaves at the rear, had a volume of 600 cm<sup>3</sup>, was 45 cm from the nearest exit, and was 35 cm underground. Another nest made of pine straw

was 1,000 cm<sup>3</sup> in volume, 82 cm from the nearest exit, and 45 cm underground (Callahan and Estep, 1982).

*Tamias o. meridionalis* eats a variety of seeds, fruits, and flowers, but captive specimens refused to eat insects and meat (Callahan and Davis, 1976). *T. o. davisii* feeds largely on acorns, pinyon seeds, and berries of manzanita and junipers. One *T. o. davisii* on Santa Rosa Mountain (2,100 m elev.) had a piece of acorn in its mouth. Throughout most of its range *T. obscurus* does not have access to permanent water (Callahan, 1976), but *T. o. meridionalis* usually occurs near free water (Larson, 1964).

At sites in the San Bernardino Mountains where *T. obscurus* is not sympatric with *T. merriami*, the presence of *T. obscurus* is correlated with presence of *Opuntia*, density of trees, crown cover, and basal area of xerophytic vegetation types. Based on regression analysis, single-leaf pinyon, which produces nuts that dusky chipmunks feed on in late summer, is the most significant plant species (Blankenship, 1985). Where *T. obscurus* coexists with *T. merriami* in southern California, zones of overlap are narrow and there is evidence of competitive exclusion (Callahan, 1976). Often, localities of sympatry are drainage areas and canyons in which the transition zone extends into the upper Sonoran zone or where the topography is such that a vegetational mosaic is formed (Blankenship, 1985). In the San Bernardino Mountains, *T. obscurus* occupies the pinyon-juniper belt below *T. merriami*. In the San Jacinto Mountains, it occupies the transition life zone above *T. merriami* (Callahan, 1976). North of San Gorgonio Pass, the point at which *T. merriami* replaces *T. obscurus* coincides with the juncture of the transition and upper Sonoran life zones. *T. speciosus* also may occur here, but it is more typical of the Canadian life zone. South of San Gorgonio Pass, *T. speciosus* again occupies the Canadian zone, but the other two species are reversed in zonation. In the San Jacinto Mountains, at higher elevations *T. obscurus* is replaced by *T. speciosus* and at lower elevations by *T. merriami*. Similar habitat occurs at the summit of Thomas Mountain (2,075 m elev.), but until a recent expansion of the range of *T. obscurus*, this peak was occupied exclusively by *T. merriami* (Callahan, 1977; Davis and Callahan, 1992). *T. obscurus* is the only chipmunk in the Santa Rosa Mountains and occupies the upper Sonoran and transition zones. *T. panamintinus*, where it approaches the range of *T. obscurus* in the Providence Mountains, apparently occupies habitat equivalent to that of adjacent populations of *T. obscurus* (Callahan, 1976).

Other mammals occurring in the same habitats as *T. obscurus* are *Sorex ornatus*, *Scapanus latimanus*, *Sylvilagus bachmani*, *Tamiasciurus douglasii*, *Ammospermophilus leucurus*, *Spermophilus beecheyi*, *Thomomys bottae* (Nelson, 1922), *Dipodomys simulans*, *Peromyscus boylei*, *P. maniculatus*, *P. truei*, *Neotoma fuscipes*, *Ovis canadensis*, *Odocoileus hemionus*, *Felis concolor*, *Lynx rufus*, *Canis latrans*, *Urocyon cinereoargenteus* (Nelson, 1922), and *Bassariscus astutus* (Callahan, 1976). Although some reptiles and mammals probably prey on *T. obscurus*, the only recorded attempt of predation was by a sharp-shinned hawk (*Accipiter striatus*), which dived at a calling female; the hawk was not successful (Callahan, 1981).

Coccidian oocysts were found in 41% of *T. obscurus*. Eimerians included: *Eimeria cochisensis*, *E. dorsalis*, *E. tamiasciuri*, and *E. wisconsinensis* (Hill and Duszynski, 1986). Ectoparasites recovered from nests of *T. obscurus* include the flea *Monopsyllus fornacis* and the mite *Androlaelaps casalis* (Callahan and Estep, 1982).

**BEHAVIOR.** *Tamias obscurus* is active throughout the year (Jameson and Peeters, 1988). Greatest daily activity takes place early in the morning and late in the afternoon; *T. obscurus* is inactive in mid-day (Larson, 1986).

The dusky chipmunk sometimes calls from bushes 1.0–1.5 m above the ground, but usually it is not found in trees (Allen, 1893). When it is disturbed in nests located in cavities of cardon cacti, squeaking calls are emitted. Calls include the chip, chuck, chipper, and trill. The chip usually is given from the top of a boulder, and may continue for  $\geq 5$  min; the rate is 100–165 chips/min, and each chip is accompanied by a flip of the tail. The chuck (up to ca. 160/min) seems to cause other chipmunks to remain quiet and hidden; a second concealed individual, however, also may give the chuck. The chip usually is given by an exposed individual near its den. In campgrounds and other public areas, chipmunks appear careless and may give the chip when distant from their burrows. Unlike the ventriloquial chuck, which has a narrow frequency range,

the chip has a wide frequency range and is located easily. Whereas the chuck causes other chipmunks to be quiet, the chip causes them to be noisy; it is an allelomimetic call given in a variety of contexts. *T. obscurus* does most of its chipping in summer, when population densities are high and lactating females remain near their nests. As an alarm call, the chip pinpoints the location of a predator without appreciable risks to the caller (which is near its burrow); a population producing a chorus of chips may disorient the predator. Often, the trill follows the chips (or is interspersed with a rapid series of chips) and is heard in situations of high-intensity alarm. The chipper, a jumbled series of notes is given by an individual that has been startled and is racing for cover (Callahan, 1976).

Frequency ranges (in kHz) of the chip call of *T. obscurus* in the San Bernardino and San Jacinto mountains, respectively, are: origin of upsweep, 1.0–1.8, 1.0–2.0; top of upsweep, 14.1–16.0, 12.5–16.0; bottom of downsweep, 1.0–5.0, 1.0–4.8; length of chips (in s), 0.027–0.050, 0.030–0.057. The two populations are significantly different for top of upsweep. Thus, intraspecific differences in chips are present (Blankenship and Brand, 1987).

Although chip calls of *T. obscurus* and *T. merriami* are acoustically similar, males have not been observed to approach a displaying female of the other species, even where habitats interdigitate. A male *T. merriami* sniffed at the spot where a pair of *T. obscurus* had appeared to copulate the day before, suggesting that olfactory cues are operative at close range. The call used by the female for solicitation is the same as the chip, which is given by both sexes in the presence of a ground predator, but inhibited in the presence of a raptor. It is an explosive, abruptly terminated, easily located call with much noise and a wide range in frequency. Chip calls of the estrous female tend to be produced in bursts or irregular series, rather than in the steady, rapid-fire fashion that often characterizes high-intensity, directed alarm bouts. The vocal display is conspicuous and entails risk for the female (Callahan, 1981).

The female, ca. 3–5 days prior to estrus, begins to spend a great deal of time sitting on exposed perches and calling loudly for periods  $\geq 10$ –30 min, interspersed with bouts of grooming and periods of inactivity. This behavior may occupy 3–4 h/day over a period of several days. Males may come from distances  $>200$  m; they respond to the female by approaching silently and in a hesitant, jerky manner. Upon arrival, the male sniffs the genital area of the female or the perch where she has been displaying. At this stage, the female responds by moving away, sometimes uttering a faint growl if the male follows. One male gathered nest material near the female's den, suggesting that males establish temporary billets during this period. By the onset of estrus, two to six or more males have arrived in her home range. Estrus lasts a few hours and largely is occupied with pursuit of females by males and male vocalization. At some point the female stops and allows one member of the leading pack of males to copulate with her; usually, the successful male is one of a group of approximately equal rank at the top of the dominance hierarchy. During and after the mating chase, the female abruptly ceases to display or vocalize (Callahan, 1981).

Males that survive the breeding season often appear to be in poor condition. They return to their burrows in a bedraggled state in May, and do not reappear until August or September. They become inactive later in autumn than females, but emerge a month or so earlier in spring, perhaps because of limited opportunity to store a winter cache. Thus, males and females spend similar percentages of the year aboveground, but the harshest months are experienced by the males. Females, by staying in place, may force males to assume the risks of dispersal and to disappear at a time when their presence might result in competition for food resources (Callahan, 1981).

When a male *T. dorsalis* was placed in a cage containing a female *T. obscurus*, it approached the female in a hesitant manner, giving a series of low hiccup-like notes resembling the chuck. It stopped vocalizing after ca. 30 s and attempted to copulate with the female, who showed no hostility. This activity was observed daily for the next 2 weeks, although no further vocalizations were heard (Callahan, 1976).

Some females move their young to a new underground burrow in summer rather than to a tree den. No remnants of a winter food cache were found in a simple underground burrow occupied by a lactating female and five juveniles in April. The limited debris suggested a brief occupancy; apparently, the female had not overwintered there. One litter occupied a tree cavity 60 cm above the ground in a live oak in April. These juveniles were at least 8 weeks

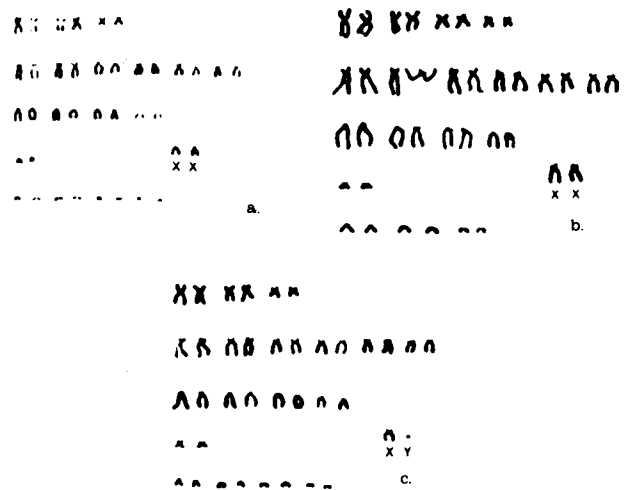


FIG. 5. Karyotypes of (a) a female *Tamias o. obscurus*, (b) a female *T. o. davisii*, and (c) a male *T. o. meridionalis* (Callahan, 1977).

old and no adult was present, so it was not possible to determine if this was the maternal summer den. Juveniles disperse widely and explore virtually any existing pocket gopher (*Thomomys*) burrow, hollow tree, or other natural cavity, apparently establishing temporary residences and then moving on. Such exploratory behavior likely accounts for the wide range of den structures used (Callahan and Estep, 1982).

**GENETICS.** *Tamias obscurus* had an average heterozygosity of 0.0220 and one polymorphic locus (red cell phosphoglucosaminase) among 20 allozymes (Levenson et al., 1985). *T. o. obscurus* and *T. o. meridionalis* have karyotype A of *Tamias* and *T. o. davisii* has karyotype B (Fig. 5). In the type A karyotype of *T. o. obscurus* and *T. o. meridionalis* (Callahan, 1977), the diploid karyotype contains 38 chromosomes including three pair of large metacentric, six pair of large submetacentric, four pair of large acrocentric, one pair of small metacentric, and four pair of small acrocentric chromosomes. The X chromosome is submetacentric and the Y is acrocentric (Sutton and Nadler, 1969). In the type B karyotype of *T. o. davisii* (Callahan, 1977), the diploid karyotype contains 38 chromosomes including four pair of large metacentric, six pair of large submetacentric, four pair of large acrocentric, one pair of small metacentric, and three pair of small acrocentric chromosomes. The X chromosome is submetacentric and the Y is acrocentric (Sutton and Nadler, 1969).

**REMARKS.** Based upon structure of the ossa genitalia, skull, karyotype, and habitat differences, *T. obscurus* is considered to be distinct from *T. merriami* (Callahan, 1975). The nearest relative of *T. obscurus* appears to be *T. bulleri*. Bacula of these two species are similar and do not closely resemble those of any other member of the genus. The baubella of these species differ in that the base is unfolded in *T. bulleri* (Callahan, 1977).

Phenetic analysis of morphologic characters placed *T. obscurus* in the same cluster as *T. bulleri*, *T. canipes*, *T. cinereicollis*, *T. dorsalis*, and *T. durangae*. A cladistic analysis of electrophoretic data placed *T. obscurus* with *T. dorsalis*, *T. merriami*, *T. palmeri*, and *T. panamintinus* (Levenson et al., 1985; Nadler et al., 1985).

Currently, chipmunks previously assigned to the genus *Eutamias* are included in the genus *Tamias* (Levenson et al., 1985; Nadler et al., 1969, 1977; Wilson and Reeder, 1993). Indications that *Eutamias* and *Tamias* may be distinct genera include divergence in the late Miocene (Ellis and Maxson, 1979; Hafner, 1984), differences in pattern of dorsal stripes, structure of the hyoid, chromosomes, dental formulas, bacula (Hoffmeister, 1986), microcomplement-fixation reactions, and allozymes (Ellis and Maxson, 1979; Hafner, 1984).

*Tamias* is from the Greek *tamias* meaning a storer or distributor. The specific epithet is from the Latin *obscurus* meaning dusky (Jaeger, 1955). Additional common names include Lower California

chipmunk (Elliot, 1905), San Pedro Mártir chipmunk, peninsula chipmunk (Gordon, 1943), and chaparral chipmunk (Jameson and Peeters, 1988).

We thank L. L. Thornton, A. M. Coffman, and other personnel in the Interlibrary Loan Department at the Auburn University R. G. Draughton Library for their assistance in obtaining articles from other institutions, and K. A. Howard for preparing Fig. 4. J. B. Armstrong, J. R. Callahan, R. B. Forbes, and R. S. Lishak critically evaluated an early draft of the manuscript. This is journal article no. 15-923339 of the Alabama Agricultural Experiment Station.

#### LITERATURE CITED

- ALLEN, J. A. 1890. A review of some of the North American ground squirrels of the genus *Tamias*. *Bulletin of the American Museum of Natural History*, 3:45-116.
- . 1893. On a collection of mammals from the San Pedro Martir region of Lower California, with notes on other species, particularly of the genus *Sitomys*. *Bulletin of the American Museum of Natural History*, 5:181-202.
- BLACK, C. C. 1972. Holarctic evolution and dispersal of squirrels (Rodentia: Sciuridae). *Evolutionary Biology*, 6:305-322.
- BLANKENSHIP, D. J. 1985. Reproductive isolating mechanisms of southern California chipmunks: a systematic evaluation of *Tamias obscurus* Allen, 1890 and *T. merriami* Allen, 1889 (Rodentia: Sciuridae). Ph.D. dissert., Loma Linda University, Loma Linda, California, 137 pp.
- BLANKENSHIP, D. J., AND G. L. BRADLEY. 1985. Electrophoretic comparison of two southern California chipmunks (*Tamias obscurus* and *Tamias merriami*). *Bulletin of the Southern California Academy of Sciences*, 84:48-50.
- BLANKENSHIP, D. J., AND L. R. BRAND. 1987. Geographic variation in vocalizations of California chipmunks *Tamias obscurus* and *T. merriami*. *Bulletin of the Southern California Academy of Sciences*, 86:126-135.
- CALLAHAN, J. R. 1975. Status of the peninsula chipmunk. *Journal of Mammalogy*, 56:266-269.
- . 1976. Systematics and biogeography of the *Eutamias obscurus* complex (Rodentia: Sciuridae). Ph.D. dissert., The University of Arizona, Tucson, 184 pp.
- . 1977. Diagnosis of *Eutamias obscurus* (Rodentia: Sciuridae). *Journal of Mammalogy*, 58:188-201.
- . 1981. Vocal solicitation and parental investment in female *Eutamias*. *The American Naturalist*, 118:872-875.
- CALLAHAN, J. R., AND R. DAVIS. 1976. Desert chipmunks. *The Southwestern Naturalist*, 21:127-130.
- CALLAHAN, J. R., AND D. Q. ESTEP. 1982. Tree and ground nests of southern *Eutamias*. *The Southwestern Naturalist*, 27:234-238.
- DAVIS, R., AND J. R. CALLAHAN. 1992. Post-Pleistocene dispersal in the Mexican vole (*Microtus mexicanus*): an example of an apparent trend in the distribution of southwestern mammals. *The Great Basin Naturalist*, 52:262-268.
- ELLIOT, D. G. 1903. A list of mammals collected by Edmund Heller, in the San Pedro Martir and Hanson Laguna mountains and the accompanying coast regions of Lower California with descriptions of apparently new species. *Field Columbian Museum Publication 79, Zoological Series*, 3:199-232.
- . 1905. A check list of mammals of the North American continent the West Indies and the neighboring seas. *Field Columbian Museum Publication 105, Zoological Series*, 6:1-701.
- ELLIS, L. S., AND L. R. MAXSON. 1979. Evolution of the chipmunk genera *Eutamias* and *Tamias*. *Journal of Mammalogy*, 60:331-334.
- GOLDMAN, E. A., AND R. T. MOORE. 1946. The biotic provinces of Mexico. *Journal of Mammalogy*, 26:347-360.
- GORDON, K. 1943. The natural history and behavior of the western chipmunk and the mantled ground squirrel. *Oregon State Monographs, Studies in Zoology*, 5:1-104.
- HAFNER, D. J. 1984. Evolutionary relationships of the Nearctic Sciuridae. Pp. 3-23, in *The biology of ground-dwelling squirrels: annual cycles, behavioral ecology, and sociality* (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln, 459 pp.
- HALL, E. R. 1981. *The mammals of North America*. Second ed. John Wiley & Sons, New York, 1:1-600 + 90.
- HILL, T. P., AND D. W. DUSZYNSKI. 1986. Coccidia (Apicomplexa: Eimeriidae) from sciurid rodents (*Eutamias*, *Sciurus*, *Tamiasciurus* spp.) from the western United States and northern Mexico with descriptions of two new species. *Journal of Protozoology*, 33:282-288.
- HOFFMEISTER, D. F. 1986. *Mammals of Arizona*. The University of Arizona Press and The Arizona Game and Fish Department [Tucson], 602 pp.
- HOWELL, A. H. 1929. Revision of the American chipmunks (genera *Tamias* and *Eutamias*). *North American Fauna*, 52:1-157.
- HUEY, L. M. 1964. The mammals of Baja California, Mexico. *Transactions of the San Diego Society of Natural History*, 13:85-165.
- INGLES, L. G. 1965. *Mammals of the Pacific states: California, Oregon, and Washington*. Stanford University Press, Stanford, California, 506 pp.
- JAEGER, E. C. 1955. *A source-book of biological names and terms*. Third ed. Charles C Thomas Publisher, Springfield, Illinois, 323 pp.
- JAMESON, E. W., JR., AND H. J. PEETERS. 1988. *California mammals*. University of California Press, Berkeley, 403 pp.
- LARSON, E. A. 1964. The peninsula chipmunk in Baja California. *Journal of Mammalogy*, 45:634.
- . 1986. Merriam's chipmunk on Palo Escrito in the Santa Lucia Mountains of California. Part II. The individual in relation to its environment with recorded episodes of naturalistic behavior. Waucoba Press, Big Pine, California, 283 pp.
- LEVENSON, H. 1990. Sexual size dimorphism in chipmunks. *Journal of Mammalogy*, 71:161-170.
- LEVENSON, H., R. S. HOFFMANN, C. F. NADLER, L. DEUTSCH, AND S. D. FREEMAN. 1985. Systematics of the Holarctic chipmunks (*Tamias*). *Journal of Mammalogy*, 66:219-242.
- MILLER, A. H., AND R. C. STEBBINS. 1964. *The lives of desert animals in Joshua Tree National Monument*. University of California Press, Berkeley, 452 pp.
- NADLER, C. F., R. S. HOFFMANN, AND D. M. LAY. 1969. Chromosomes of the Asian chipmunk *Eutamias sibiricus* Laxmann (Rodentia: Sciuridae). *Experientia*, 25:868-869.
- NADLER, C. F., R. S. HOFFMANN, AND H. LEVENSON. 1985. Biochemical and morphological relationships among Holarctic chipmunks. *Acta Zoologica Fennica*, 170:19-23.
- NADLER, C. F., R. S. HOFFMANN, J. H. HONACKI, AND D. POZIN. 1977. Chromosomal evolution in chipmunks, with special emphasis on A and B karyotypes of the subgenus Neotamias. *The American Midland Naturalist*, 98:343-353.
- NELSON, E. W. 1922. Lower California and its natural resources. *National Academy of Sciences, First Memoir*, 16:1-194.
- NELSON, E. W., AND E. A. GOLDMAN. 1909. Eleven new mammals from Lower California. *Proceedings of the Biological Society of Washington*, 22:23-28.
- RIDGWAY, R. 1912. *Color standards and color nomenclature*. R. Ridgway, Washington, D.C., 340 pp.
- SUTTON, D. A., AND C. F. NADLER. 1969. Chromosomes of the North American chipmunk genus *Eutamias*. *Journal of Mammalogy*, 50:524-535.
- WILSON, D. E., AND D. M. REEDER (EDS.). 1993. *Mammal species of the world: a taxonomic and geographic reference*. Second ed. Smithsonian Institution Press, Washington, D.C., 1206 pp.

Editors of this account were J. ALDEN LACKEY and KARL F. KOOPMAN. Managing editor was JOSEPH F. MERRITT.

T. L. BEST AND N. J. GRANAL, DEPARTMENT OF ZOOLOGY AND WILDLIFE SCIENCE AND ALABAMA AGRICULTURAL EXPERIMENT STATION, 331 FUNCHESS HALL, AUBURN UNIVERSITY, ALABAMA 36849-5414.