

Sorex ornatus. By James G. Owen and Robert S. Hoffmann

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Sorex ornatus Merriam, 1895

Ornate Shrew

- Sorex ornatus* Merriam, 1895:79. Type locality "head of San Emigdio Canyon, Mount Piños, [Kern Co.] California."
Sorex californicus Merriam, 1895:80. Type locality "Walnut Creek, Contra Costa County, Calif."
Sorex oreinus Elliot, 1903:172. Type locality "Aguaje de las Fresas, San Pedro Martir mountains, Lower California, Mexico, 6,000 feet elevation." Synonym of *S. ornatus*.
Sorex lagunae Nelson and Goldman, 1909:27. Type locality "Sierra Laguna, Lower California, Mexico (5,500 ft.)."
Sorex californicus juncensis Nelson and Goldman, 1909:27. Type locality "Socorro, 15 miles south of San Quintin, Lower California, Mexico." (recognized as *Sorex juncensis* by Jackson, 1928:172).
Sorex sinuosus Grinnell, 1913:187. Type locality "Grizzly Island, near Suisun, Solano County, California."
Sorex willetti von Bloeker, 1941:163. Type locality "Avalon Canyon, Santa Catalina Island, Los Angeles County, California."

CONTEXT AND CONTENT. Order Insectivora, Family Soricidae, Subfamily Soricinae, Tribe Soricini, Genus *Sorex*, Subgenus *Otisorex* (Findley, 1955; Repenning, 1967). About 59 species are recognized in the genus *Sorex*, which has a Holarctic distribution. The *S. ornatus* species group is divided into three to five species. *S. nanus* and *S. tenellus* are each monotypic (Hoffmann and Owen, 1980; Jackson, 1928); *S. ornatus* is polytypic and contains seven to nine subspecies (Hall, 1981; Junge and Hoffmann, 1981). The taxa *juncensis* and *sinuosus* are usually considered species (cf. Hall, 1981), but were arranged as subspecies of *S. ornatus* by Junge and Hoffmann (1981). Brown and Rudd (1981) and Williams (1979) also considered *sinuosus* a subspecies. Thus the following subspecies are currently recognized.

- Sorex ornatus californicus* Merriam, 1895, see above. First use of name combination (Jackson, 1922:264).
Sorex ornatus juncensis Nelson and Goldman, 1909, see above. First use of name combination (Junge and Hoffmann, 1981:34).
Sorex ornatus lagunae Nelson and Goldman, 1909. First use of name combination (Jackson, 1928:169).
Sorex o. ornatus Merriam, 1895, see above.
Sorex ornatus relictus Grinnell, 1932:389. Type locality "Buena Vista Lake, 290 feet altitude, Kern County, California."
Sorex ornatus salicornicus von Bloeker, 1932:131. Type locality "Playa del Rey, Los Angeles County, California."
Sorex ornatus salarius von Bloeker, 1939:94. Type locality "salt-marsh at the mouth of the Salinas River, Monterey County, California."
Sorex ornatus sinuosus Grinnell, 1913. First use of name combination (Williams, 1979:426).
Sorex ornatus willetti von Bloeker, 1941. First use of name combination (von Bloeker, 1967:247).

DIAGNOSIS. The subgenus *Otisorex* lacks a postmandibular canal, and the pigmented ridges on the unicuspid, extending from apices to cingula, are usually well developed (Findley, 1955; Diersing and Hoffmeister, 1977; Hoffmann and Peterson, 1967; Junge and Hoffmann, 1981). *Sorex ornatus* can be distinguished from other species of the subgenus *Otisorex* by the following combination of characters: 1) upper third unicuspid tooth smaller than fourth; 2) condylobasal length of skull 14.7 to 17.1 mm; 3) medial tine of upper first incisor tooth contained entirely within pigmented area; 4) upper toothrow not crowded, with distinct triangular space between postero-medial edge of the fifth unicuspid and antero-medial edge of premolar (Fig. 1). Junge and Hoffmann (1981) provided a key to *Sorex* of the United States and Canada.

GENERAL CHARACTERS. Small shrews, weighing an average of 5.12 g (2.9 to 8.7; n = 70; Fig. 2); tail short relative to

length of head and body. Means and ranges of external measurements (mm) are: total length, 99.4 (80 to 110; n = 116); length of tail, 37.5 (28 to 46; n = 117); length of hindfoot, 12.1 (9 to 14; n = 107). Cranial measurements (mean, range in mm) are: condylobasal length, 16.30 (14.7 to 17.1; n = 89); palatal length, 6.82 (6.1 to 8.1; n = 112); interorbital breadth, 3.31 (2.9 to 3.7; n = 111); cranial breadth, 7.96 (7.4 to 8.8; n = 92); and cranial

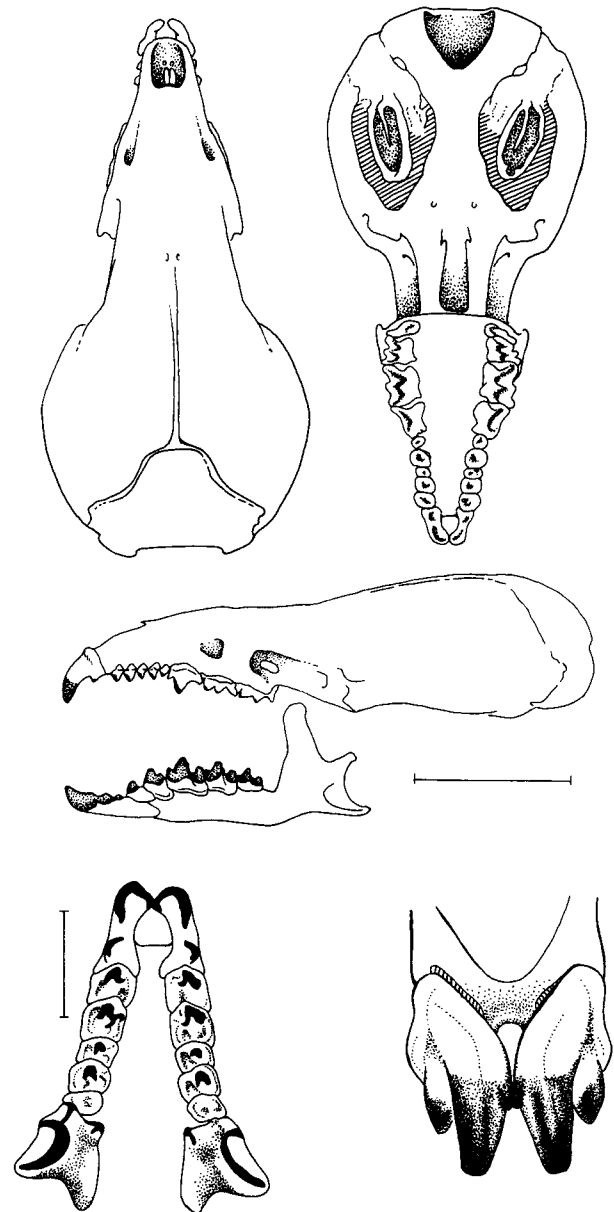


FIGURE 1. Dorsal, ventral, and lateral views of skull of *Sorex ornatus californicus* (MVZ 74572, Avon, Contra Costa Co., California); scale represents 5 mm. Modified from Hall, 1981, by permission of author. Bottom: left, occlusal view of upper anterior tooththrow (AMNH 9002); right, frontal view of first upper incisors (CAS 3941); both *S. ornatus californicus* (scale represents 2 mm).

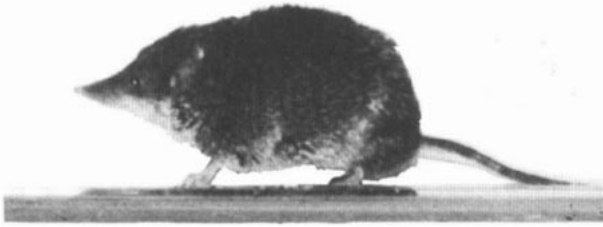


FIGURE 2. Captive ornate shrew (*S. ornatus*). Photograph by J. R. Newman, courtesy R. L. Rudd.

height, 4.59 (3.9 to 5.1; $n = 76$). These external and cranial measurements are based on specimens from throughout the ranges of *S. o. ornatus* and *S. o. californicus*. The former, more southerly subspecies is significantly larger, with a relatively longer tail, than the latter, which occupies the northern part of the species range. Clines of decreasing size northward are also found in other species of *Sorex* (Mezhzherin, 1964). Other salt marsh or palustrine subspecies with limited ranges are of variable size, either somewhat larger (*relictus*, *sinuosus*), smaller (*saliarius*, *salicornicus*), or close to *S. o. ornatus*.

The skull is relatively flat and broad, and depressed interorbitally (Fig. 1). Foramen magnum is relatively dorsal, positioned more into supraoccipital and less into basioccipital (Jackson, 1928). The foramina magna of *S. monticolus* and *S. ornatus* have been figured in rear and ventral views by Jackson (1928). Summer pelage is drab brownish dorsally, grading gradually into ventral color which is paler, more grayish to buffy in most populations. Winter pelage is similar, but slightly darker dorsally and lighter ventrally, sometimes approaching grayish-white. The tail is indistinctly bicolored, brown above and gray below. There is a tendency for size to become larger, and ventral fur darker, from north to south. The darkest subspecies is *S. o. sinuosus*, which is almost black both dorsally and ventrally in winter pelage, and only slightly browner in summer pelage.

DISTRIBUTION. *Sorex ornatus* occurs in California from about 39°N latitude southward discontinuously to the tip of Baja California; the subspecies *S. o. willetti* occurs on Santa Catalina Island (Fig. 3). According to von Bloeker (1967), trapping in mountains and canyons of Santa Cruz and Santa Rosa Islands may reveal shrews there. Altitudinally ornate shrews extend from coastal marshes at sea level to about 2,400 m in the San Jacinto Mountains (Grinnell and Swarth, 1913). *Sorex o. sinuosus* is known only from near sea level on islands and tidal marshlands of San Pablo and Suisun Bays, California. Other subspecies also have restricted palustrine or salt-marsh distributions. The known ranges of the subspecies are plotted in Fig. 3.

FOSSIL RECORD. Compton (1937) assigned a palate with unworn dentition from the Pleistocene of the Rancho La Brea asphalt to *S. ornatus*, but could not make positive identification. Wilson (1933) tentatively assigned two right mandibular rami from Pleistocene Carpinteria asphalt to *S. ornatus*. Schultz (1938) referred a left mandibular ramus from the McKittrick fauna to *S. ornatus*, but thought that this material might be of Recent age. Miller (1971) discussed Pleistocene vertebrates of the Los Angeles Basin. He reported two species of shrews, *Notiosorex crawfordi* and *S. ornatus*, from the Newport Bay Mesa fauna (Locality 1067). *S. ornatus* was considerably more numerous than *N. crawfordi* at this locality but was much less numerous than *N. crawfordi* at Rancho La Brea.

Findley (1955) hypothesized that a lineage of shrews ancestral to *S. ornatus* migrated into southwestern California during the Illinoian glaciation. This stock became isolated and evolved into *S. ornatus* during the relatively warmer and drier climatic conditions that prevailed in the Sangamonian interglacial. Walker (1980) found remains of a cranium of *Sorex* in a vertical fissure in a rock on San Miguel Island, California. Prior to his discovery the only shrew known from the Channel Islands was a unique specimen, *S. o. willetti*, reported by von Bloeker (1941, 1967). Walker (1980) compared dimensions of the cranium from San Miguel Island with those of the holotype of *S. o. willetti* and with mainland *S. ornatus*. Both *S. o. willetti* and the San Miguel Island specimen have cranial dimensions larger than mainland *S. ornatus*, and Walker (1980) suggested that the San Miguel Island specimen might represent a distinct race.

There has been considerable speculation concerning biotic dis-

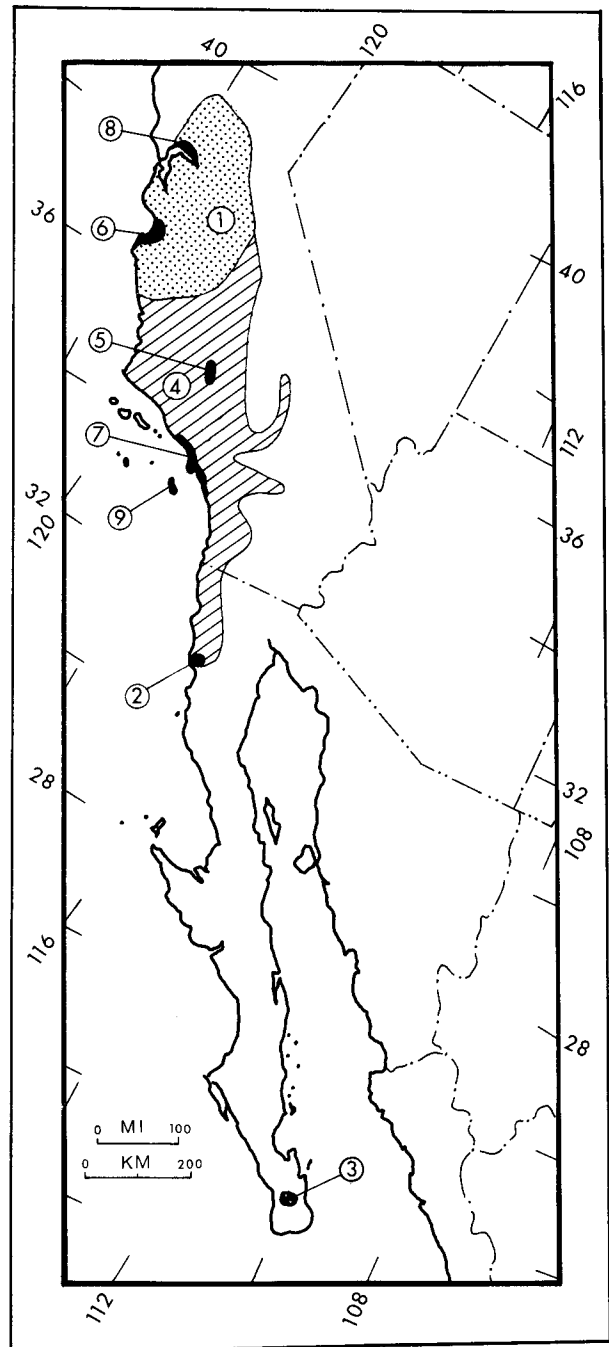


FIGURE 3. Distribution of the ornate shrew (*S. ornatus*), modified from Hall, 1981. (Bipolar oblique conic conformal projection.) Approximate ranges of recognized subspecies: 1, *S. o. californicus*; 2, *S. o. juncensis*; 3, *S. o. lagunae*; 4, *S. o. ornatus*; 5, *S. o. relictus*; 6, *S. o. saliarius*; 7, *S. o. salicornicus*; 8, *S. o. sinuosus*; 9, *S. o. willetti*.

persal to the Channel Islands (Werner and Johnson, 1980). On the basis of mammalian distribution in the Channel Islands, von Bloeker (1967) proposed that Santa Catalina Island (the only island on which *Sorex* had been found) has been connected to the mainland by a bridge which disappeared by the early Pleistocene. Thus isolated, this population differentiated into the insular endemic *S. o. willetti*.

If the ornate shrew reached and became established on Santa Catalina Island by the early Pleistocene as proposed by von Bloeker (1967), then *S. ornatus* must have evolved before this time. Findley (1955) suggested that *S. ornatus* diverged during the Sangamonian-Wisconsin interval, a time far later than the early Pleistocene. Thus, the hypotheses of von Bloeker (1967) and Findley (1955) concerning the date of origin of *S. ornatus* are in conflict. Von Bloeker's

proposed land bridge connection between Santa Catalina Island and mainland California was questioned by Savage (1967) who, on the basis of the distribution of the reptiles, amphibians, and mammals of the Channel Islands, suggested that these islands were colonized by chance dispersal over water. The presence of barn owl remains in the deposit containing the shrew cranium on San Miguel Island suggested to Walker (1980) that raptorial birds may have acted as dispersal agents. Walker (1980) also argued for a role by American Indians in carrying animals to the Channel Islands. Wenner and Johnson (1980) found scant geological evidence to support a postulated land bridge connection between the mainland and the Northern Channel Islands, and presented both biological and anthropological arguments which they conclude "strongly suggests that a combination of 'sweepstakes' dispersal and Indian transport most plausibly explains the origin and distribution of land animals on the Northern Channel Islands."

FORM AND FUNCTION. At 20°C the average maximum metabolic rate of *S. o. sinuosus* is about 6.0 Kcal/day (Newman and Rudd, 1978a). The average minimum metabolic rate is about 4.5 Kcal/day which approximates that of other species of *Sorex*. As in other *Sorex*, the metabolic rate of the ornate shrew is higher than predicted basal values. This increased rate is attributed, in part, to a high activity level (Newman and Rudd, 1978a). Only in post-absorptive, fasted animals at 15 min before death do minimal metabolic rates approach predicted basal values. The reduced rate of metabolism of fasted shrews is associated with reduced activity. Shrews fasted at 20°C lived from 5 to 23 h and lost from 8 to 10% of their body weight (Newman and Rudd, 1978a). Maximum metabolic rates during periods of activity are 20 to 50% higher than minimum rates during inactivity.

The metabolic rate and weight of *S. o. sinuosus* decrease during winter (Newman and Rudd, 1978a). Such functional reduction in metabolism may be an adaptation to the more rigorous energetic demands of this season (Gebczynski, 1965; Mezhzherin, 1969). Both weight and metabolic rate increase in *S. o. sinuosus* during spring and early summer (Newman and Rudd, 1978a), and nocturnal metabolic rate exceeds diurnal rate (Newman and Rudd, 1978a; Rust, 1978). These increases in the weight and metabolism of the ornate shrew co-occur with sexual maturation and reproductive activity (Brown, 1974a; Rudd, 1955a; Rust, 1978). Late summer metabolic rates are intermediate between those of spring and winter (Newman and Rudd, 1978a).

Breeding *S. o. sinuosus* have higher energy needs than non-breeding shrews but, instead of consuming more calories, they develop an increased assimilation efficiency (Rust, 1978). Newman (1970) estimated an assimilation efficiency of 65% in reproductively active *S. o. sinuosus* and 42% in reproductively inactive shrews.

Newman and Rudd (1978b) observed torpidity in *S. o. sinuosus* maintained in the laboratory. Some individuals became inactive with a reduced breathing rate; such shrews could be aroused only by active stimulation. Newman and Rudd (1978b) found that "the animal, during these deep sleeps, could be handled and even pushed over without immediately righting itself. After awakening, the animal acted normally with sharp and quick reflexes." The duration of torpidity varied from a few min to 1 h. The ad libitum availability of food minimized the possibility that starvation was the cause of the torpid condition.

The average caloric value of *S. ornatus* is about 4.82 Kcal/g of dry-weight (Newman, 1977). This value is similar to those of *S. minutus* and *Neomys fodiens* (Myrcha, 1969) and rodents (Kaufman et al., 1975). There is slight sex and seasonal variation in caloric content; the caloric value of a pregnant female with four embryos did not differ from that of non-pregnant females.

The most widely distributed subspecies of the ornate shrew, *S. o. ornatus*, has been reported from dry chaparral-covered slopes (Grinnell, 1933) and thus appears to be relatively tolerant of the absence of drinking water. Two other shrews of the *Sorex ornatus* group, *S. tenellus* and *S. nanus*, also occur in xeric situations (Hoffmann and Owen, 1980).

The summer molt in *S. ornatus* may occur from late February until mid-July, though most specimens are in full summer pelage by May. *S. ornatus* usually molts again during September and early October. By late October and early November, the winter coat is frequently full. Specimens from colder mountainous areas may commence autumn molt earlier than specimens from warmer lowland areas (Jackson, 1928).

Brown (1974a) described sexual dimorphism in the innominate bone of *S. ornatus*. Sexually immature males and females have only qualitative differences in this bone. The innominate of sexually mature males exhibits increased ossification and size when compared to that of sexually mature females. Robust development of this bone

in males was interpreted as an adaptation for increased support of the adult male genitalia (Brown, 1974a). There are no published reports on other elements of the post-cranial skeleton.

Dental formula is probably $i\ 3/1, c\ 1/1, p\ 3/1, m\ 3/3$, total 32 (Vaughan, 1978; see also Kindahl, 1960). Homologies of these teeth are uncertain, and Repenning (1967) advocated referring to them as incisors; antemolars, including unicuspid and molariform (fourth) premolar; and molars.

ONTOGENY AND REPRODUCTION. The reproductive period in *Sorex ornatus* (including *S. o. sinuosus*) from the San Francisco Bay area appears to extend from late February through September to early October (Brown, 1974a; Rudd, 1955a; Rust, 1978). Most breeding occurs from early spring through May, and is by shrews born the previous year. Reproduction decreases from late spring through mid-summer but increases again in late summer. Reproduction at this time may be by shrews born in late summer of the previous year that do not reach sexual maturity until late in the breeding season. A few young-of-the-year born in early spring may also mature by late summer and reproduce then (Rudd, 1955a). Breeding in the first year of life is uncommon in both *S. vagrans* and *S. ornatus* (Rudd, 1955a) but may occur more often in *S. ornatus*. Rudd (1955a) suggested that *S. ornatus* may have a slightly later breeding season than *S. vagrans*; he found little evidence to suggest that females produce second litters. Adult males are heavier than adult females during the breeding season but may decline in weight later whereas post-reproductive females continue to gain weight (Rudd, 1955a). Embryo counts range from four to six (Jackson, 1928; Newman, 1977). There are no published data on gestation period or embryonic and post-natal development, but other small shrews have a gestation period of about 21 days (Conaway, 1958).

ECOLOGY. *Sorex o. sinuosus* inhabits brackish-water marshes of the Upper Sonoran life zone along the northern boundaries of Suisun and San Pablo bays, with populations extending eastward to Grizzly Island and westward to the mouth of Petaluma Creek (Grinnell, 1933; Rudd, 1955b). The climate of the San Francisco Bay area is Mediterranean. Rain falls mainly from November to April and averages about 457 to 635 mm per year. However, the aridity of long, dry summers is ameliorated for marsh-dwelling *Sorex* by high summer tides; shrews may be water stressed only in September and October (Johnston and Rudd, 1957). Vegetation of the San Francisco Bay area was discussed by Hinde (1954), Johnston and Rudd (1957), and Rudd (1955b). Presence of shrews is associated with vegetation structure rather than species composition. Shrews prefer low, dense vegetation which affords plentiful invertebrates for food, along with adequate cover and nesting places (Johnston and Rudd, 1957; Rudd, 1955b). *S. o. sinuosus* may remain within its home range during extreme tidal flooding and not seek higher ground (Hadaway and Newman, 1971). Williams (in press) reported that habitat loss or degradation has endangered *S. o. sinuosus* and that this subspecies should be considered for state and federal Endangered status.

Newman (1970) estimated energy flow through *S. o. sinuosus*. Densities in shrew populations vary with seasons and habitats. The most favorable habitat supported shrew densities of as many as 111 per ha. Energy flux through the Suisun shrew population was estimated to be about 260,979 Kcal per ha per year. Low efficiency of digestion yielded an estimated energy intake of 326,040 to 518,700 Kcal per ha per year. *S. o. sinuosus* is the second largest small mammal consumer of energy in the salt marsh community. Shrew populations did not appear to be limited by food availability but may effect invertebrate density and diversity (Newman, 1970).

Sorex ornatus occurs mainly in brackish or saline marshes near sea level (*S. o. juncensis*, *salarius*, *salicornicus*, *sinuosus*) and in riparian and palustrine upland habitat (*S. o. californicus*, *lagunae*, *ornatus*, *relictus*), but shrews of the subspecies *ornatus* and *californicus* may extend onto grassy hillsides and dry chaparral slopes (Grinnell, 1933; von Bloeker, 1967). There are no habitat descriptions for the Santa Catalina Island endemic *S. o. willetti*. Von Bloeker (1967) suggested that it might be found in "stream-bearing canyons . . . although not necessarily close to water." Williams (in press) reported on the distribution, habitat, population status, and recommended management of the subspecies *S. o. relictus*, *S. o. salicornicus*, *S. o. sinuosus*, and *S. o. willetti*.

Ornate shrews rarely live more than about 12 to 16 months (Rudd, 1955a) and populations turn over annually. Populations in early spring consist of adults born the previous year. Summer populations are composed of old adults and young-of-the-year. By autumn most old adults have died and populations consist mainly of young-of-the-year (Newman, 1976; Rudd, 1955a). Vestal (1938)

cited *S. o. californicus* as a biotic associate of *Neotoma fuscipes*, having found two specimens of this shrew in the base of two woodrat houses. Von Bloeker (1937) reported skeletal material of *S. ornatus californicus* from litter at the base of an owl roost in San Benito Co., California. This was the first record of *S. o. californicus* from San Benito Co. Henry (1932) found oocysts of the coccidian, *Eimeria soricis* sp. nov., in the intestine of *S. o. californicus*.

BEHAVIOR. *Sorex ornatus* is active day and night (Newman and Rudd, 1978a; Pearson, 1959; Rust, 1978). Nocturnal/diurnal activity ratios vary with season and reproductive condition in *S. o. sinuosus*, but nocturnal activity predominates, especially during the breeding season (Rust, 1978). Newman and Rudd (1978a) reported that captive *S. o. sinuosus* exhibited 8 to 12 periods of activity per h with durations of from a few s to 10 min. Rust (1978) observed that captive *S. o. sinuosus* maintained cycles of activity and inactivity with periods of about 1 h, and that these shrews were active about 24% of each 24-h period. The intensity of activity and its distribution within a 24-h period varies with reproductive condition (Rust, 1978). Old adult (sexually mature) ornate shrews are very active in the spring, concurrent with spring reproduction, but by early summer are less active. Some young-of-the-year, presumably born in early spring, are sexually mature by late summer and are relatively active then (Rust, 1978). Others, born later in the season, are still sexually immature by late summer and are comparatively inactive then (Rust, 1978).

Newman (1976) observed territorial defense of nest sites in captive *S. ornatus*. Rust (1978) noted that breeding *S. o. sinuosus* were more active in the corners of their cages than nonbreeding shrews and speculated that this site-specific activity reflected territorial patrolling.

The following behavioral observations on captive *S. vagrans* and *S. ornatus* are drawn mainly from Rudd (1953). Captive shrews lived up to 6.5 months on a ration described by Pearson (1950). When the shrews were given a dead mouse, its cranium and abdominal cavities were opened to expose the brain and liver. With adequate food and water, male and female pairs of each species lived together without antagonism but sometimes attempted to kill each other if food and water supplies were inadequate. Rudd (1953) did not observe burrowing activity in leaf litter on the cage floors. However, burrowing appears to occur in the natural habitat. Pearson (1959) observed an ornate shrew appear at the entrance of a small hole in the ground, rapidly twitch its nose and retreat down the hole. Pearson (1959) suggested that during hot summer weather in dry habitats, *S. ornatus* restricts its daytime activity to burrows of gophers, moles, and microtines. Glass vials, simulating burrows, were used as sleeping places by most shrews and for refuge when frightened (Rudd, 1953). The shrews used exercise wheels. Some became possessive of the wheels and displayed a reduced tendency for concealment when using them. Shrews often competed for use of the exercise wheels with the winner appearing to be the animal which could first start it turning. If shrews met, they would back off as if startled, and one or both would run to concealment. Sometimes after backing away, shrews would stop and face each other while emitting shrill, threatening squeaks. During such encounters the mouth was open and the head turned sideways. Usually males retreated, suggesting female dominance. Similar behaviors occurred in male-male encounters, one male being dominant. Immature shrews were not antagonistic. Several, about 2 months old, were easily kept together for 6 weeks. However, when food was absent, two of the animals were eaten by the others. The five remaining shrews lived together for 6 more weeks. Juvenile siblings appeared less antagonistic toward one another than non-sibs and slept huddled together.

Shrews have sometimes been reported to have died from fright (Jackson, 1928; Orr, 1949). While duck hunting, Orr (1949) reported capturing a specimen of *S. o. sinuosus* at about 0800 h and putting it into an empty shell box. During the ensuing hour shotgun shots were fired, some near the box. One hour later, at 0900 h, the shrew was found dead. The animal showed no signs of injury and was assumed by Orr (1949) to have died of fright or shock. However, Pearson (1950) reported that in his experience shrews could withstand considerable trauma and that deaths usually were from experimentation or neglect; in the case reported by Orr, an hour without food may have been sufficient trauma.

GENETICS. Brown (1971) investigated the karyotypes of several taxa of the subgenus *Otisorex*: *S. ornatus californicus*, *S. sinuosus* (= *S. o. sinuosus*), *S. v. vagrans*, *S. v. halicoetes*, *S. "vagrans" ssp.* (= *S. monticolus*; see Hennings and Hoffmann, 1977), and *S. bendirii*. All of these taxa had identical diploid chromosome numbers of 54, but differed in fundamental number (FN). The karyotypes of *S. o. sinuosus* and *S. o. californicus* were identical

(that is, $2n = 54$, $FN = 76$), but are fully separable from that of *S. vagrans*, which exhibited $2n = 54$, $FN = 58$ to 64 (Brown, 1971, 1974b; Brown and Rudd, 1981), suggesting that pericentric inversions were instrumental in the evolution of the karyotype of these *Otisorex* shrews.

REMARKS. Rudd (1955b) studied morphological variation in *Sorex* from tidal marshlands along the north shore of San Francisco Bay, California. In marshes along Suisun Bay, Rudd (1955b) described a population of shrews which he referred to as *S. sinuosus* but which were intermediate in color and in several mensural characters between topotypical *sinuosus* and upland *S. ornatus californicus*. A resemblance in pelage between *sinuosus* and *ornatus* in this area was also implied by Jackson (1928). In the absence of apparent differential selective forces acting on these marshland populations, Rudd (1955b) postulated that hybridization produced the observed intermediacy.

Melanism in the pelage of *Sorex* from salt marshes was noted by Green (1932), Grinnell (1913, 1932), and von Bloeker (1932) but may not be correlated with salinity (Grinnell, 1913); darkened fur also occurs in the freshwater marsh form, *S. o. relictus* (Grinnell, 1932). Melanism in palustrine-dwelling forms may be related to the darkened soils produced by decaying vegetation (von Bloeker, 1932) and probably affords some protective coloration.

Rudd (1955b) also described a population of shrews at the mouth of Toly Creek of San Pablo Bay with characters intermediate between *S. vagrans vagrans* and *S. sinuosus*. Rudd (1955b) postulated that the vagrant and ornate shrews hybridized in this area. These findings led Ingles (1965) and Hall (1981) to suggest that a future reviser might arrange both *sinuosus* and *ornatus* as subspecies of *S. vagrans*, the latter name having priority. However, genic introgression may be contraindicated. Brown and Rudd (1981) could not subsequently find *S. vagrans* in the Toly Creek area. All shrews that they examined from there had karyotypes identical to those of *S. o. californicus* and *S. o. sinuosus*. Brown and Rudd (1981) concluded that "populations from Toly, Novato, and San Antonio creeks and from the Petaluma River that were once considered *S. vagrans* or hybrids are now considered as slightly differentiated populations of *S. ornatus californicus*."

LITERATURE CITED

- Brown, R. J. 1971. A comparative study of the chromosomes of some Pacific coast shrews (Genus *Sorex*). Unpubl. Ph.D. dissert., Univ. California, Davis, 51 pp.
- 1974a. Sexual dimorphism in the pelvic girdle of the ornate shrew, *Sorex ornatus*. *Wasmann J. Biol.*, 32:99–104.
- 1974b. A comparative study of the chromosomes of three species of shrews, *Sorex bendirii*, *Sorex trowbridgii*, and *Sorex vagrans*. *Wasmann J. Biol.*, 32:303–326.
- Brown, R. J., and R. L. Rudd. 1981. Chromosomal comparisons within the *Sorex ornatus*-*S. vagrans* complex. *Wasmann J. Biol.*, 39:30–35.
- Compton, L. V. 1937. Shrews from the Pleistocene of the Rancho La Brea asphalt. *Univ. California Publ., Dept. Geol. Sci. Bull.*, 24:85–90.
- Conaway, C. H. 1958. Maintenance, reproduction and growth of the least shrew in captivity. *J. Mamm.*, 39:507–512.
- Diersing, V. E., and D. F. Hoffmeister. 1977. Revision of the shrews *Sorex merriami* and a description of a new species of the subgenus *Sorex*. *J. Mamm.*, 58:321–333.
- Elliott, D. G. 1903. Descriptions of apparently new species and subspecies of mammals from California, Oregon, the Kenai Peninsula, Alaska, and Lower California, Mexico. *Field Columb. Mus., Publ. 74, Zool. Ser.*, 3:153–173.
- Findley, J. S. 1955. Speciation of the wandering shrew. *Univ. Kansas Publ., Mus. Nat. Hist.*, 9:1–68.
- Gebczynski, M. 1965. Seasonal and age changes in the metabolism and activity of *Sorex araneus* Linnaeus, 1758. *Acta Theriol.*, 10:303–331.
- Green, M. M. 1932. An unrecognized shrew from New Jersey. *Univ. California Publ. Zool.*, 38:387–388.
- Grinnell, J. 1913. The species of the mammalian genus *Sorex* of west-central California. *Univ. California Publ. Zool.*, 10:179–195.
- 1932. A relic shrew from central California. *Univ. California Publ. Zool.*, 38:389–390.
- 1933. Review of the Recent mammal fauna of California. *Univ. California Publ. Zool.*, 40:71–234.
- Grinnell, J., and H. S. Swarth. 1913. An account of the birds and mammals of the San Jacinto area of southern California. *Univ. California Publ. Zool.*, 10:197–406.

- Hadaway, H. C., and J. R. Newman. 1971. Differential responses of five species of salt marsh mammals to inundation. *J. Mamm.*, 52:818-820.
- Hall, E. R. 1981. *The mammals of North America*. Second ed. John Wiley and Sons, New York, 1:xv + 600 + 90.
- Hennings, D., and R. S. Hoffmann. 1977. A review of the taxonomy of the *Sorex vagrans* species complex from western North America. *Occas. Papers Mus. Nat. Hist., Univ. Kansas*, 68:1-35.
- Henry, D. P. 1932. Observations on coccidia of small mammals in California, with descriptions of seven new species. *Univ. California Publ. Zool.*, 37:279-290.
- Hinde, H. P. 1954. Vertical distribution of salt marsh phanerogams in relation to tide levels. *Ecol. Monogr.*, 24:209-225.
- Hoffmann, R. S., and J. G. Owen. 1980. *Sorex tenellus* and *Sorex nanus*. *Mamm. Species*, 131:1-4.
- Hoffmann, R. S., and R. S. Peterson. 1967. Systematics and zoogeography of *Sorex* in the Bering Strait area. *Syst. Zool.*, 16:126-136.
- Ingles, L. G. 1965. *Mammals of the Pacific states*. Stanford Univ. Press, Stanford, California, xii + 506 pp.
- Jackson, H. H. T. 1922. New species and subspecies of *Sorex* from western North America. *J. Washington Acad. Sci.*, 12:262-264.
- 1928. A taxonomic review of the American long-tailed shrews (Genera *Sorex* and *Microsorex*). *N. Amer. Fauna*, 51:1-218.
- Johnston, R. F., and R. L. Rudd. 1957. Breeding of the salt marsh shrew. *J. Mamm.*, 38:157-163.
- Junge, J. A., and R. S. Hoffmann. 1981. An annotated key to the long-tailed shrews (genus *Sorex*) of the United States and Canada, with notes on Middle American *Sorex*. *Occas. Papers Mus. Nat. Hist., Univ. Kansas*, 94:1-48.
- Kaufman, D. W., G. A. Kaufman, and J. G. Weiner. 1975. Energy equivalents for sixteen species of xeric rodents. *J. Mamm.*, 56:946-949.
- Kindahl, M. 1960. Some aspects of the tooth development in Soricidae. *Acta Odont. Scandinavia*, 17:203-237.
- Merriam, C. H. 1895. Synopsis of the American shrews of the genus *Sorex*. *N. Amer. Fauna*, 10:57-98.
- Mezhzherin, V. A. 1964. Dehnel's phenomenon and its possible explanation. *Acta. Theriol.*, 8:95-114. (In Russian, English summary.)
- 1969. Energetics of populations and evolution of the shrews *Sorex*, *Insectivora*, *Mammalia*. Pp. 149-156, in *Energy flow through small mammal populations* (K. Peterusewicz and L. Ryszkowski, eds.). PWN-Polish Sci. Publ., Warsaw, 298 pp.
- Miller, W. E. 1971. Pleistocene vertebrates of the Los Angeles Basin and vicinity (exclusive of Rancho La Brea). *Sci. Bull., Los Angeles Co. Mus. Nat. Hist.*, 10:1-124.
- Myrcha, A. 1969. Several changes in caloric value, body water and fat in some shrews. *Acta Theriol.*, 16:211-227.
- Nelson, E. W., and E. A. Goldman. 1909. Eleven new mammals from lower California. *Proc. Biol. Soc. Washington*, 22:23-28.
- Newman, J. R. 1970. Energy flow of a secondary consumer (*Sorex sinuosus*) in a salt marsh community. *Dissert. Abst.*, 32B:883.
- 1976. Population dynamics of the wandering shrew *Sorex vagrans*. *Wasmann J. Biol.*, 34:235-250.
- 1977. Energy value of the shrew, *Sorex ornatus*. *Acta Theriol.*, 22:274-275.
- Newman, J. R., and R. L. Rudd. 1978a. Minimum and maximum metabolic rates of *Sorex sinuosus*. *Acta Theriol.*, 23:371-380.
- 1978b. Observations of torpor-like behavior in the shrew, *Sorex sinuosus*. *Acta Theriol.*, 23:446-448.
- Orr, R. T. 1949. Death from fright in long-tailed shrews. *J. Mamm.*, 30:195-196.
- Pearson, O. P. 1950. Keeping shrews in captivity. *J. Mamm.*, 31:351-352.
- 1959. A traffic survey of *Microtus-Reithrodontomys* runways. *J. Mamm.*, 40:169-180.
- Repenning, C. A. 1967. Subfamilies and genera of the Soricidae: classification, historical zoogeography, and temporal correlation of the shrews. *Geol. Surv. Prof. Paper*, 565:1-74.
- Rudd, R. L. 1953. Notes on maintenance and behavior of shrews in captivity. *J. Mamm.*, 34:118-120.
- 1955a. Age, sex and weight comparisons in three species of shrews. *J. Mamm.*, 36:323-338.
- 1955b. Population variation and hybridization in some Californian shrews. *Syst. Zool.*, 4:21-34.
- Rust, A. K. 1978. Activity rhythms in the shrews, *Sorex sinuosus* Grinnell and *Sorex trowbridgii* Baird. *Amer. Midland Nat.*, 99:369-382.
- Savage, J. M. 1967. Evolution of the insular herpetofaunas. Pp. 219-227, in *Proceedings of the Symposium on the biology of the California Islands*, Santa Barbara (R. N. Philbrick, ed.). Santa Barbara Botanic Garden, Santa Barbara, California, 363 pp.
- Schultz, J. R. 1938. A late Quaternary mammal fauna from the tar seeps of McKittrick, California. *Carnegie Inst. Washington Publ.*, 487:111-215.
- Vaughan, T. A. 1978. *Mammalogy*. Second ed. W. B. Saunders, Philadelphia, x + 518 pp.
- Vestal, E. H. 1938. Biotic relations of the wood rat (*Neotoma fuscipes*) in the Berkeley Hills. *J. Mamm.*, 19:1-36.
- von Bloeker, J. C., Jr. 1932. Three new mammals from the salt marsh areas in southern California. *Proc. Biol. Soc. Washington*, 45:131-138.
- 1937. Mammal remains from detritus of raptorial birds in California. *J. Mamm.*, 18:360-361.
- 1939. Two new shrews from west-central California. *Proc. Biol. Soc. Washington*, 52:93-96.
- 1941. A new shrew from Santa Catalina Island, California. *Bull. Southern California Acad. Sci.*, 40:163-164.
- 1967. Land mammals of the southern California Islands. Pp. 245-266, in *Proceedings of the symposium on the biology of the California Islands*, Santa Barbara (R. N. Philbrick, ed.). Santa Barbara Botanic Garden, Santa Barbara, California, 363 pp.
- Walker, P. L. 1980. Archeological evidence for the recent extinction of three terrestrial mammals on San Miguel Island. Pp. 703-713, in *The California Islands: proceedings of a multidisciplinary symposium* (D. M. Power, ed.). Santa Barbara Mus. Nat. Hist., Santa Barbara, California, 787 pp.
- Wenner, A. M., and D. L. Johnson. 1980. Land vertebrates on the California Channel Islands: sweepstakes or bridges? Pp. 497-530, in *The California Islands: proceedings of a multidisciplinary symposium* (D. M. Power, ed.). Santa Barbara Mus. Nat. Hist., Santa Barbara, California, 787 pp.
- Williams, D. F. 1979. Checklist of California mammals. *Ann. Carnegie Mus. Nat. Hist.*, 48:425-433.
- In press. Mammalian species of special concern in California. California Dept. Fish and Game, Nongame Wildl. Invest., Final Rep., Project E-W-4, IV-14.1.
- Wilson, R. W. 1933. Pleistocene mammalian fauna from the Carpinteria asphalt. *Carnegie Inst. Washington Publ.*, 440:59-76.

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