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Sorex palustris.

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Sorex palustris Richardson, 1828

American Water Shrew

Sorex palustris Richardson, 1828:517. Type locality "marshy places, from Hudson's Bay to the Rocky Mountains."

Neosorex navigator Baird, 1857:11. Type locality "Fort Vancouver, Washington Territory."

Neosorex albibarbis Cope, 1862:188. Type locality "Profile Lake, Franconia Mountains, Grafton Co., New Hamshire."

CONTEXT AND CONTENT. Order Insectivora, Family Soricidae, Subfamily Soricinae, Genus *Sorex*, Subgenus *Otisorex* (Findley, 1967; Junge and Hoffmann, 1981). Nine or 10 subspecies of *Sorex palustris* are recognized, depending on whether *S. alaskanus* is considered to be a distinct species or a subspecies of *S. palustris*. Jackson (1926) originally described and later discussed (Jackson, 1928) *S. alaskanus* as a separate species. However, van Zyll de Jong (1983) apparently considers *S. alaskanus* a subspecies of *S. palustris* (although he does not specifically comment on this taxonomic change, he suggested that a revision of the subspecies of *S. palustris* is needed). Hall (1981) and Junge and Hoffmann (1981) also questioned the taxonomic status of *S. alaskanus*, but they did not propose specific revisions. The nine formally recognized subspecies of *S. palustris* include:

S. p. albibarbis (Cope, 1862:188), see above.

S. p. brooksi Anderson, 1934:134. Type locality "Black Creek, 150 ft., Comox District, E coast Vancouver Island, British Columbia."

S. p. gloveralleni Jackson, 1926:57. Type locality "Digby, Digby Co., Nova Scotia" (renaming of *Neosorex palustris acadicus* Allen preoccupied by *S. acadicus* Gilpin).

S. p. hydrobadistes Jackson, 1926:57. Type locality "Withee, Clark Co., Wisconsin."

S. p. labradorensis Burt, 1938:1. Type locality "Red Bay, Strait of Belle Isle, Labrador."

S. p. navigator (Baird, 1857:11), see above.

S. p. palustris Richardson, 1828:57, see above.

S. p. punctulatus Hooper, 1942:1. Type locality "6 mi, NW Durbin, Shavers Fork of Cheat R., 3600 ft., Randolph Co., West Virginia."

S. p. turneri Johnson, 1951:110. Type locality "Fort Chimo (on the eastern bank of the Koksoak River, lat. 58° 8′ N., long. 68° 15′ W.), Ungava District, Quebec, Canada."

DIAGNOSIS. *Sorex palustris* is a large shrew (Fig. 1) with measurements of adults (in mm) ranging as follows: total length, 130 to 170; tail length, 57 to 89; length of hind foot, 18 to 22 (Ingles, 1965; Johnson, 1951; van Zyll de Jong, 1983). The tail is distinctly bicolored (dark above, light below) or, more rarely, concolor. The hind feet are conspicuously fimbriated; similar specialized hairs also are found on the front feet (van Zyll de Jong, 1983). The pelage, although highly variable geographically and seasonally, is generally black or gray frosted dorsally and white tinged with gray or brown ventrally. The chin usually is lighter in color than other body regions (Dalquest, 1948; van Zyll de Jong, 1983).

The skull is large and each side of the upper jaw has five unicuspid teeth; the fourth unicuspid is larger than the third (Fig. 2). The protocones of M1 and M2 usually lack a cuplike posterior lobe; each premolar bears a distinctive, medially directed, pigmented ridge. The osseous bridge over the infraorbital canal is relatively narrow, and the lacrimal and infraorbital foramina are located anterior to the M1–M2 interface. The anterior part of the rostrum is comparatively short and not curved ventrally (Hall, 1981; Kurtén and Anderson, 1980; van Zyll de Jong, 1983).

GENERAL CHARACTERS. The dental formula is i 3/1, c 1/1, p 3/1, m 3/3, total 32. Skull measurements of adults (means and ranges in mm) are: condylobasal length, 20.1, 19.1 to 21.7 ($n = 93$); cranial breadth, 9.7, 9.0 to 10.9 ($n = 88$); interorbital breadth, 3.8, 3.4 to 4.4 ($n = 95$); palatal length, 8.4, 8.1 to 8.8 ($n = 9$); cranial height, 5.5, 5.3 to 5.6 ($n = 5$); length of upper tooth row, 9.3, 9.2 to 9.5 ($n = 5$); length of maxillary tooth row, 7.6, 7.4 to 7.7 ($n = 9$); breadth across second molars, 5.8, 5.7 to 6.0 ($n = 5$); and maxillary width, 5.9, 5.4 to 6.5 ($n = 70$; Johnson, 1951; Pagels and Tate, 1976; van Zyll de Jong, 1983; Whitaker et al., 1975). Despite their extensive geographic distribution, differences in cranial and external measurements among subspecies are not great (Jackson, 1928; van Zyll de Jong, 1983).

Jackson (1928) stated that males and females did not differ in color, size, or proportions, but van Zyll de Jong (1983) reported the average mass of sexually active males (13 to 18 g) was significantly greater than that of adult females (8 to 12 g). Conaway (1952) documented the following differences between samples of adult male and female water shrews from Montana: mean body mass ($\pm SD$) of 25 males (15.4 ± 1.3 g) was significantly greater than that of 27 females (12.3 ± 1.3 g), and the total length of 38 males (153.4 ± 5.4 mm) was significantly greater than that of 39 females (149.4 ± 5.2 mm). No significant sexual differences were found in tail length, length of hindfoot, or color (Conaway, 1952).

DISTRIBUTION. The geographic distribution of the nine named subspecies of the water shrew (Fig. 3) includes the cooler, boreomontane regions of North America, much of Canada, southwestern Alaska, and northern and mountainous regions of the United States (Hall, 1981; Jackson, 1928; Junge and Hoffmann, 1981). Although *S. palustris* has been collected in the Lower Sonoran life zone (Presnall and Hall, 1936), its ecological distribution is more typically limited to the Canadian and Hudsonian life zones (Borell and Ellis, 1934; Dalquest, 1948).

FOSSIL RECORD. The stratigraphic range of *S. palustris* extends from the late Pleistocene (Illinoian) to the Recent with fossils identified from the following local faunas: Arkansas—Peccary Cave; Kansas—Mt. Scott, Duck Creek, and Robert; Kentucky—Welsh Cave; Missouri—Crankshaft Pit; New Mexico—Muskox Cave; Okla-

FIG. 1. *Sorex palustris navigator*, mounted specimen. WSC #46-221, adult female, Tucannon Ranger Station, Columbia Co., Washington. Total length of body = 70 mm (photograph by S. R. Antell).

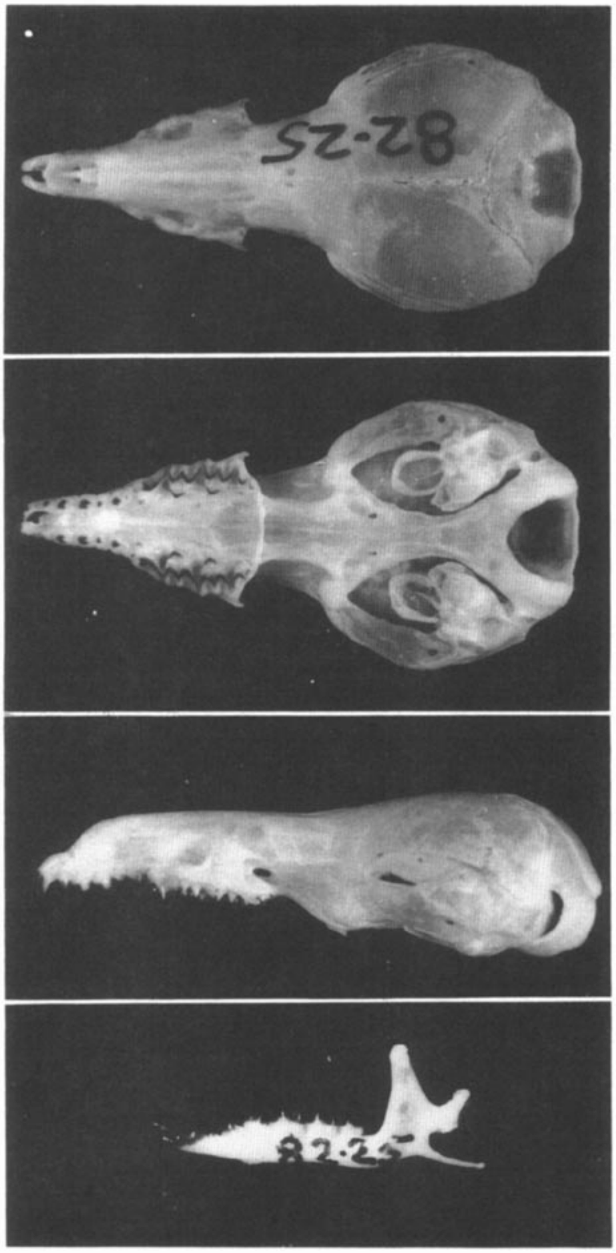

FIG. 2. Dorsal, ventral, and lateral views of skull, and lateral view of mandible of *Sorex palustris* (WSC #82-25, female, Salt Creek, Mt. Adams, Skamania Co., Washington). Greatest length of skull = 20.6 mm (photograph by S. R. Antell).

homa—Dolby Springs; Pennsylvania—New Paris No. 4; Tennessee—Robinson Cave; Texas—Howard Ranch; Utah—Silver Creek; Virginia—Clarks Cave and Natural Chimneys; and Wyoming—Little Box Elder, Bell, and Little Canyon Creek. Of these, Peccary Cave, Mt. Scott, Duck Creek, Robert, Crankshaft Pit, Muskox Cave, Dolby Springs, and Howard Ranch lie outside the present geographic range of *S. palustris*. The small number of fossils of water shrews (relative to other species) found at most sites suggests that population densities during the Pleistocene were low, thus similar to estimates for extant populations. The distribution of fossils indicates the geographic range of the water shrew during the Pleistocene extended farther south and to slightly lower elevations than currently (Guilday et al., 1971; Harris, 1985; Kurtén and Anderson, 1981; McMullen, 1975, 1978; Stephens, 1960).

The maxillae and dentaries from Pleistocene deposits in Kansas and Oklahoma are indistinguishable from Recent forms (McMullen, 1975, 1978; Stephens, 1960). Kurtén and Anderson (1981) considered the extinct lake shrew, *S. lacustris* ancestral to *S. palustris*.

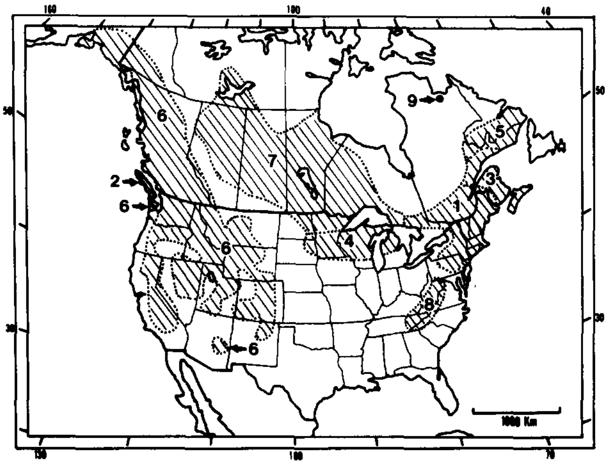

FIG. 3. Distribution of *Sorex palustris*: 1, *S. p. albibarbis*; 2, *S. p. brooksi*; 3, *S. p. gloveralleni*; 4, *S. p. hydrobadistes*; 5, *S. p. labradorensis*; 6, *S. p. navigator*; 7, *S. p. palustris*; 8, *S. p. punctulatus*; 9, *S. p. turneri* (redrawn from Hall, 1981).

FORM AND FUNCTION. Semi-aquatic species in four genera of the Soricidae exhibit a general trend for an increasingly greater degree of modification to a semi-aquatic existence as follows: *Sorex*, *Neomys*, *Chimarrogale*, *Nectogale*. *S. palustris* and *S. benderii* tend to have fewer and less-developed anatomical adaptations to the aquatic environment than other semi-aquatic species of shrews (Hutterer, 1985; Pruitt, 1957). In comparison to terrestrial species, semi-aquatic shrews are characterized by a larger brain case, a larger foramen magnum, a broader and larger thorax, longer tibias, and longer digits on the hind feet (Hutterer, 1985).

The feet of *S. palustris* have a fringe of stiff hairs (fibrillae) located on the outer and inner margins of the front and hind feet and toes (Fig. 4); the longest fibrillae (1.25 mm) are found along the outer margins of the hind feet. The large, fimbriated hind feet provide the main thrust for swimming (van Zyll de Jong, 1983). The guard hairs are comparatively thin (49 μm) and are characterized by short, wide, overlapping cuticular scales that incompletely encircle the hair shaft (Short, 1978). Guard hairs of soricine shrews are "H"-shaped in cross section (Vogel and Kopchen, 1978); the longitudinal grooves have numerous ridges with the number greater in more aquatic genera (Hutterer, 1985). *Nectogale* has 4 times the number of ridges as *S. palustris*. These ridges may improve the ability of the hair to retain air underwater. Distal ends of guard hairs are flattened possibly to repel water (Hutterer, 1985; Hutterer and Hurter, 1981).

Water shrews are capable of sustaining forced dives of 31.1 to 47.7 s before becoming exhausted, longer than feral *Mus musculus* of similar size (22 s), but less than predicted by an extrapolation of metabolic performance in seals (*Cystophora cristata*; Calder, 1969). During dives, air trapped in the fur reduces heat loss by 50% compared to fur from which the air layer is removed, therefore, the ability of the fur to hold air may not be an adaptation specific to diving. Forced submersions in water temperatures similar to that of summer streams (10 to 12°C) resulted in a cooling rate of 1.43°C/30 s; shrews held on the surface of the water cooled at a rate of 1.03°C/30 s. Water shrews cooled from 39.7°C to about 34°C exhibited slower movements and some loss of coordination, but they suffered no lasting effects; after a short delay, rewarming occurred at approximately 1°C/min (Calder, 1969).

Oxygen consumption of five water shrews (mean mass = 11.3 g) ranged from 4.7 to 10.9 cc g^{-1} h^{-1}; the mean rate of oxygen consumption (n = 80 measurements) was 7.8 cc g^{-1} h^{-1}. This compares to a mean rate of 15.8 cc g^{-1} h^{-1} for *S. cinereus* and 5.3 cc g^{-1} h^{-1} for *Blarina brevicauda* (Morrison et al., 1959; Sorenson, 1962). In captivity, water shrews used or stored 10.3 to 14.6 g of food per day (Conaway, 1952; Sorenson, 1962). Based on food use and oxygen consumption, Sorenson (1962) estimated the food requirement of water shrews to be 0.95 g g^{-1} day^{-1}.

Water shrews are capable of reducing their metabolic demands, thereby allowing them to dive year-round in cold mountain streams. They have enzymes that function well at low temperatures, and that may facilitate daily torpor (Boernke, 1977). Additional metabolic energy is conserved though nasal cooling; the nasal tract has a temperature gradient that shows only a slight temperature difference between inhalent and exhalant air, yet a substantial difference between exhalant air and the cribiform plate (Schmid, 1976).

Water shrews molt in fall and spring; winter pelage is somewhat paler than summer pelage (Jackson, 1928). Fall molt is the first molt following birth and is similar for young and old animals. Winter pelage appears first on the flanks or mid-dorsal region and spreads from this center; a second center may develop on the rostrum. Spring molt proceeds anterior to posterior with the summer pelage first evident on the rostrum. In Montana, fall molt occurs during late July and August and spring molt occurs from February to March (Conaway, 1952).

Flank glands, composed of enlarged sweat and sebaceous glands, are present in all shrews. In *S. palustris*, flank glands appear as small (approximately 8 mm) ovals of oily white hairs located posterior to the ribs (Conaway, 1952; Pearson, 1946; van Zyll de Jong, 1983). Conaway (1952) reported that flank glands were not visible on immature males or on females, regardless of reproductive condition. Although flank glands are typically less evident in female shrews, their absence in female water shrews is a unique condition for soricids (Conaway, 1952).

Conaway (1952) noted a positive relationship between development of flank glands and testicular mass in male water shrews. Wrigley (1969) reported a strong musky odor could be detected near specimens with enlarged flank glands, considered nauseating when a captive water shrew became excited or frightened (Svihla, 1934). Because flank glands of most shrew species are highly developed in breeding males and anestrous females, Pearson (1946) suggested that odors produced may facilitate mutual avoidance and territoriality. Hawes (1976), however, noted that the period of most intense territoriality and strict avoidance usually occurs before the odor-producing glands develop.

In coping with their environment, water shrews seem to use their sensory abilities synergistically; however, the relative acuity and functional significance of individual senses are not well understood (Sorenson, 1962). Conaway (1952) reported that water shrews had difficulty locating minnows unless the minnows were moving, and Svihla (1934) reported that a captive individual often failed to recognize snails (Gasteropoda) unless the snails were contacted by the shrew's vibrissae or muzzle. Buckner (1970), however, reported that water shrews could see submerged minnows from a distance of 12 to 15 cm above the water surface. Sorenson (1962) attempted to resolve the role of vision in water shrew activities by covering their eyes with viscous hair wax; although his technique proved inconclusive, he suggested that vision probably was adequate over short distances, but that it may be used in conjunction with a kinesthetic memory.

The vibrissae and sensitive muzzle of water shrews seem to aid in detection of prey (especially when diving), and the vibrissae also may serve as lateral feelers in confined areas (Sorenson, 1962; Svihla, 1934). Hutterer (1985) considered the relatively large brain of semi-aquatic shrews to be a response to the enlargement of the trigeminal system that innervates the vibrissae. However, when Sorenson (1962) clipped the vibrissae of a water shrew, its activity seemed unaffected and its ability to locate food seemed unimpaired. This led Sorenson (1962) to conclude that vibrissae were not a primary mechanism for locating food.

The hearing ability of water shrews seems acute to distances of 3 m (Sorenson, 1962), particularly for high-pitched sounds (Svihla, 1934). Sorenson (1962) observed that water shrews emit an almost continuous high-pitched squeak whenever they run; such behavior led him to suspect that water shrews are capable of echolocation.

Some shrew species can be distinguished by characteristic odors they emit; these odors possibly serve as sexual attractants or in species recognition (Hamilton, 1940; Hawes, 1976; Skarén, 1964). Captive water shrews frequently sniff the air, and their odor on traps was found to attract other water shrews (Sorenson, 1962).

ONTOGENY AND REPRODUCTION. Conaway (1952) concluded that the rate of tooth wear is relatively constant throughout the lifespan of a water shrew. By measuring tooth wear of 119 water shrews trapped throughout the year, Conaway (1952) described two distinct age classes: first-year shrews born during the current spring or summer, and second-year shrews born the previous spring or summer. In Montana, the mean mass (±*SD*) of first-year males (9.7 ± 1.1 g) was significantly less than that of second-year males (15.4 ± 1.3 g); a similar relationship was found for females (9.7 ± 0.6 g vs 12.3 ± 1.6). The maximum lifespan for water shrews is about 18 months (Conaway, 1952).

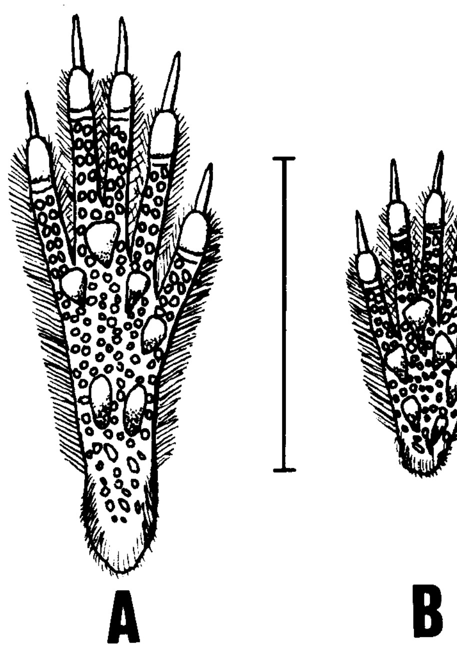

FIG. 4. Feet of *Sorex palustris*: A, right hind foot, B, right front foot. Scale = 10 mm (illustration by D. W. Stinson).

Of 61 first-year males collected in Montana between May and November, none exhibited evidence of reproductive activity (Conaway, 1952). Testes of immature males were small (0.4 to 4.0 mg), seminiferous tubules were solid, and only spematogonia and Sertoli cells were present. Water shrews mature earlier and with greater individual variation than reported for other *Sorex* species (Conaway, 1952). Sexual maturation, marked by testicular enlargement and spermatogenesis, began in December or January. The combined mass of both testes in mature males exceeded 110 mg. Sperm were first present in testes on 24 January, and were found in testes of all second-year males collected from 1 February to August (Conaway, 1952).

Conaway (1952) also examined 58 female water shrews from Montana; in sexually immature females ovaries are small and composed principally of stroma and primary follicles, and the uteri are thin walled with inconspicuous glands. The earliest indication of ovarian activity was 4 January. Reproductive maturation was characterized by an enlargement and vascularization of the ovaries, appearance of Graafian follicles, and enlargement and glandular proliferation of the uteri. Females seemed to become estrus asynchronously throughout late winter and early spring. The first pregnant water shrew was caught 24 February. All second-year females caught between 24 January and August were in various stages of reproductive activity. Three females were reproductively active in June of their first year, but similar to *S. ornatus*, *S. vagrans*, and *S. fumeus* (Hamilton, 1940; Owen and Hoffmann, 1983), most female water shrews do not reproduce until after their first winter (Conaway, 1952).

The corpora lutea of water shrews are similar to those of *Blarina* (Conaway, 1952; Pearson, 1944). The corpora lutea attain maximum size when embryos are in the early limb-bud stage, and regress about the time of parturition (Conaway, 1952). Absence of corpora lutea in 14 near-estrous females caught between 25 January and 2 April led Conaway (1952) to suggest that ovulation is not spontaneous, but induced by copulation, as reported for other shrews (Hamilton, 1940; Pearson, 1944). Adult females produce two or three litters per breeding season (Conaway, 1952). The gestation period in water shrews is not known, but for most shrews is approximately 21 days (van Zyll de Jong, 1983). Conaway (1952) estimated that the duration of gestation and lactation in the water shrew does not exceed 10 weeks. Embryo counts range from three to 10, with six being the most common (Jackson, 1928; Negus and

Findley, 1959; Whitaker et al., 1975). There are six mammae, two pair abdominal and one pair inguinal (Borell and Ellis, 1934).

Conaway (1952) reported that all lactating females showed evidence of a postpartum ovulation. Corpora lutea of four nonpregnant postpartum females were in a stage of development corresponding to that of early implantation. Because embryos in these four shrews may have been resorbed, the success of postpartum pregnancies is uncertain (Conaway, 1952).

ECOLOGY. *Sorex palustris* is rarely found far from water (Conaway and Pfitzer, 1952; Jackson, 1928; Starrett et al., 1952). Although it is typically found along edges of swift-flowing streams with rocks, logs, crevices, and overhanging banks (Baker, 1983; Banfield, 1974; Conaway, 1952), it also has been collected near slow-moving streams (Davis, 1939), dry ephemeral creek beds (Kinsella, 1967), and small springs (Wible, 1946). Extensive sampling of all habitat types in Manitoba produced 130 specimens, 92% of which were trapped in hydric habitats and 8% in mesic habitats. Some water shrews were collected in areas with herb, shrub, and tree cover, but most were trapped in grass-sedge marshes and willow (*Salix*)-alder (*Alnus*) shrub zones along creeks and ponds; few water shrews were caught in wet habitats (such as sedge-moss or heather-moss bogs or tamarack (*Larix*) swamps) that lacked open, moving water or did not support an abundant invertebrate fauna (Wrigley et al., 1979). Water shrews also are caught frequently in willow-grass or willow-sedge associations (Brown, 1967; Negus and Findley, 1959; Reichel, 1986).

Clark (1973) found water shrews most common in habitats with approximately 75% ground cover. Such ground cover may be necessary to maintain high moisture levels in the microhabitat and to support abundant invertebrates and plant foods (Wrigley et al., 1979). In Manitoba, the local distributions of water shrews and beaver (*Castor canadensis*) are similar; beaver dams increase the marsh-shrub edges of streams and create habitat with quiet pools, running water, and moist humus (Wrigley et al., 1979).

Water shrews can be trapped in live traps, snap traps, or pitfalls (Brown, 1967; Conaway, 1952; Sorenson, 1962), although 4.4-l pitfall traps containing a few centimeters of water seem to be the most efficient method (Brown, 1967). Poor trapping success relative to other sympatric species of shrews suggests that water shrew densities are low (Kirkland and Schmidt, 1982; Nagorsen and Peterson, 1981). Buckner and Ray (1968) retrapped two marked individuals and estimated (method not stated) the home range of water shrews to be 0.2 to 0.3 ha. Movement patterns indicate that water shrews use regular tracks along stream banks (Goodwin, 1932).

Water shrews are primarily insectivorous (Conaway, 1952; Conaway and Pfitzer, 1952; Sorenson, 1962); however, Whitaker and Schmeltz (1973) found that slugs (Gastropoda) and earth-worms (Annelida) accounted for 49% of the diet, and Whitaker and French (1984) found slugs and snails composed 19% of the diet. Clark (1973) found that green plants composed 13% of the stomach volume compared with 3.8% reported by Whitaker and Schmeltz (1973) and 0% reported by Whitaker and French (1984). The fungus *Endogone* was found in 25% of the stomachs analyzed by Whitaker and French (1984). Hamilton (1930) thought it unlikely that water shrews obtained a substantial portion of their diet from aquatic life; however, both Conaway (1952) and Linzey and Linzey (1973) found that 49% of stomachs analyzed contained aquatic organisms. Insects commonly recorded in the diet include stonefly nymphs (Plecoptera), mayflies (Ephmeroptera), caddis flies (Tricoptera), tipulid larvae (Diptera) and other dipterans, and crickets (Gryllidae; Hamilton, 1930; Sorenson, 1962; Whitaker and Schmeltz, 1973). Water shrews also feed on spiders (Araeae), leeches (Hirundinea), dead mice (Muridae) fish (Teleostei), and salamander (*Dicamptodon ensatus*) larvae (Conaway, 1960; Dalquest, 1948; Jackson, 1928; Nussbaum and Maser, 1969; Svihla, 1934), and they are known to feed on fish eggs at hatchery ponds (Banfield, 1974). In the field, *S. palustris* was observed to prey on common shiners (*Notropis cornutes*) and salmon (taxon not reported) parr by grasping the fish by the belly then dragging them onto shore (Buckner, 1970; Lampman, 1947). Nussbaum and Maser (1969) witnessed a water shrew feeding on a sculpin (*Cottus* sp.) and a larval Pacific giant salamander; in each instance, the prey was siezed by the head and seemed to immobilized.

Predators of water shrews include garter snakes (*Thamnophis ordinoides*), water snakes (*Natrix sipedon*), weasels (*Mustela* sp.), and brown trout (*Salmo trutta*; Grierson, 1948; Jackson, 1961; Linzey and Linzey, 1973; Wetzal and Shelar, 1964). Hawks (Accipitridae), owls (Strigiformes), mink, brook and rainbrow trout (*Salvelinus fontinalis* and *Salmo gairdneri*), black bass (*Micropterus* sp.), pickerel (*Esox* sp.), walleye (*Stizostedion vitrem*), and possibly large frogs (*Rana* sp.) may occasionally prey on water shrews (Jackson, 1961; Marshall, 1951).

Although *S. palustris* shares three parasites (*Amorphacarus hengererorum*, *Miyatrombicula esoensis*, and *Pygmephorus horridus*) with *S. hoyi*, its parasite fauna generally is different from that of other shrews (Whitaker and French,1948). Other ectoparasites reported from *S. palustris* include: mites—*Androlaelaps fahrenholzi*, *Crytolaelaps* sp., *Dermacarus newyorkensis*, *Echinonyssus talpae*, *Euphaemogamasus liponyssoides*, *E. nidi*, *Glycyphagus hypudaei*, *Haemogamasus ambulans*, *H. liponyssoides*, *H. reidi*, *Hirstionyssus talpae*, *Myocoptes* sp., *Myonyssus jamesoni*, *Naemoloelaps glosgowi*, *Orycterxenus soricis*, *Potomyobia claparedei*, *P. brevisetosa*, *Pygmephorus moreohorridus*, and *Xenoryctes nudus*; chiggers—(*Cheladonta ouachitensis*, *Eushongastia blarinae*, *E. jonesi*, *E. peromysci*, *Neotrombicula cavicola*, and *N. microti*; fleas—*Corrodopsylla curvata*, *Doratopsylla blarinae*, *Megabothris abantis*, *Nearctopsylla hyrtaci*; and ticks—*Dermacentor andersoni*, *D. variabilis*, *Ixodes angustus*, *I. cookei*, and *I. muris* (Conaway, 1952; Sorenson, 1962; Thomas et al., 1980; Whitaker et al., 1975; Whitaker and Schmeltz, 1973). Internal parasites include nematodes—*Porrocaecum americana* and *P. encapsulatum* from under the skin, *Capillaria rauschi* from the stomach, and an apparently undescribed *Capillaria* from the bladder; and cestodes—*Hymenolepis* sp. in the duodenum, and *Tetrahydridium* sp. in the coelomic cavity (Conaway, 1952).

BEHAVIOR. Water shrews are capable divers and often enter the water to capture prey or to elude danger (Banfield, 1974; Davis, 1939). In winter, water shrews continue to use the water by swimming under the ice (van Zyll de Jong, 1983). When diving, the shrews propel themselves by a walking motion of all four feet (Jackson, 1928; Svihla, 1934). Howell's (1924) claim that water shrews swim by kicking both hind feet in a froglike manner evidently is incorrect. Water shrews also can walk on the surface of either calm or turbulent water (Jackson, 1928; Findley et al., 1975). Jackson (1928) attributed this ability to the presence of small air globules trapped in the fibrillae of the hind feet.

While underwater, *S. palustris* often forages by probing into the substrate with its snout. Remaining underwater is difficult because during a dive a water shrew is surrounded by a silvery layer of air that causes it to surface and float like a cork whenever it stops paddling (Banfield, 1974; Svihla, 1934). Fur of water shrews often begins to wet after a few minutes of activity in the water, whereupon, the shrew returns to the bank and dries its fur by rapidly working over its body with its hind feet for 10 to 30 s (Conaway, 1952, 1960). On land, *S. palustris* is as agile as other shrews (Dalquest, 1948).

Activity patterns of 13 captive water shrews housed in groups of 1 to 7 individuals over a 14-month period were characterized by two periods of hyperactivity; one major activity peak occurred between sunset and 2300 h and a second occurred 1 h before sunrise (Sorenson, 1962). Active and sleeping phases were on a 1.5-h rhythm; the active phase lasted approximately 30 min and the sleeping phase lasted approximately 57 min. At the start of a typical active phase, shrews drank, wandered for 1 to 2 min, then ate. Eating was followed by "exploration behavior." Shrews frequently interrupted periods of hyperactivity to sniff the air, scratch, or eat. After an active phase, water shrews usually entered a nest, walked around in small circles within the nest depression, then curled into a tight ball and slept (Sorenson, 1962).

Feeding periods by captive water shrews typically are short (30 to 90 s); the mean interval between successive periods of feeding was 10 min ($n = 51$). When feeding on large items, captive water shrews usually tear off small pieces by grasping the food with their teeth then vigorously jerking their heads upward while holding the food down with their forefeet. Smaller items often are lifted and held by the forefeet (Sorenson, 1962). Captive water shrews are able to capture small fish (up to 6 cm long) by killing them with a bite through, or directly behind the head (Conaway, 1952; Sorenson, 1962). When supplied with over 100 aquatic insects, captive water shrews cached most of them, one at a time, in a hollow log. Small fish cached in logs were excavated and partially eaten within 3 to 4 weeks. Captive water shrews usually drink immediately after eating, sleeping, or being released from a confined area. They drink by scooping water with their mouths then raising their muzzles (Sorenson, 1962).

Captive water shrews frequently built new nests or destroyed and rebuilt old nests. After making numerous trips to gather nesting materials, the shrews positioned themselves in the center of the materials, then made a series of quick turns while using their feet and legs to form a depression. The walls of the nest were formed by a stitching motion of the muzzle. Nests were constructed in tunnels and in or under hollow logs. Of 10 nests examined, the mean diameter was approximately 8 cm, and the largest was 33 cm in diameter (Sorenson, 1962). Siegler (1956) found a nest, constructed of sticks and leaves, just above the water line in a beaver lodge.

Captive *S. palustris* frequently used tunnels dug by *Peromyscus*, but the shrews also dug several short (less than 13 cm) tunnels of their own. Shrews dug with their forefeet and threw the soil out of the tunnel with their hind feet; tunneling activity usually occurred during short bursts of hyperactivity or following antagonistic encounters. While in a tunnel, shrews flattened their bodies dorsoventrally by extending their limbs against the sides of the tunnel. Shrews sometimes hid or blocked the entrance to a tunnel with sticks and dirt (Sorenson, 1962).

In captivity, water shrews generally were solitary and most intraspecific behavior was antagonistic. Most encounters between water shrews were brief with one shrew quickly retreating unmolested. Occasionally, severe fighting occurred, particularly in the confined spaces of tunnels or hollow logs. Such fighting usually began by both shrews emitting a series of high-pitched squeaks while they remained 3 to 5 cm apart. If neither shrew retreated, one shrew raised up onto its hind limbs exposing its light-colored ventral surface and continued to squeak until the other shrew retreated. If both shrews rose up onto their hindlimbs, they slashed at each other with their teeth until one managed to grasp the other; they then fell to the ground and continued to slash at each other as they rolled into a tight ball. If the fighting continued, head and tail injuries often were incurred. Fighting ended when one of the shrews either retreated or seemingly could no longer continue. Defeated shrews seldom engaged in another fight during their retreat, but the winner frequently engaged in conflicts with other shrews that it happened to encounter. After a fight, both combatants usually curled the distal end of their tails into a loop; tails usually remained in this position for a relatively long period of time (Sorenson, 1962).

Sorenson (1962) found that male and female water shrews were equally prone to fight. No dominance hierarchy was evident inasmuch as the outcome of aggressive encounters between shrews did not seem to depend on body size or on the area in which the encounter took place. Rudd (1953) reported that captive *S. vagrans*, *S. ornatus*, and *S. sinuosus* did not kill each other as long as food was available. Although food was available at all times, five of 13 water shrews in Sorenson's (1962) study died as a result of intraspecific fighting, and one partially cannibalized its victim. When water shrews were kept in captivity with *Peromyscus*, there was mutual avoidance (Sorenson, 1962).

Captive water shrews neither defended individual nests nor nested in social groups. Nests usually were separated by 30 to 46 cm. Shrews did not appear to defend particular food caches but seemed to eat from any cache. Sometimes food was marked by defecation which seemed to cause other shrews to avoid it temporarily. When relatively few shrews were housed together, Sorenson (1962) found that they defecated in middens located at the corners of the pen; however, as more shrews were added to the enclosure, deposition eventually became indiscriminate. Middens and food marking were the only behaviors that could be interpreted as territorial (Sorenson, 1962).

GENETICS. Although no idiogram for *S. palustris* has been published, George (1984) reported the karyotype as 2N = 44. She also reported that 12 *S. palustris* from British Columbia, California, and New Mexico exhibited polymorphisms at six [malic enzyme, glucose-6-phosphate dehydrogenase, glutamate-oxaloacetate transaminase 1, esterase, peptidase B (leucyl-glycyl-glycine), and glucose-phosphate isomerase] of 26 presumptive loci assayed. Estimated mean heterozygosity (H) was 0.016 and percent polymorphism was 0.231 (George, 1984).

REMARKS. The generic name *Sorex* is from the Latin *soric* meaning "shrew mouse" and the specific name *palustris* is from Latin and means "dwelling in marshes."

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