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Spilogale gracilis.

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Spilogale gracilis Merriam, 1890a

Western Spotted Skunk

Spilogale gracilis Merriam, 1890a:83. Type locality "Grand Cañon of the Colorado (altitude 3,500 feet), [Coconino County,] Arizona, north of San Francisco Mountain."

CONTEXT AND CONTENT. Order Carnivora, family Mephitidae, genus *Spilogale* (Dragoo and Honeycutt 1997). Traditionally, skunks of the genera *Spilogale, Conepatus,* and *Mephitis* were included in the family Mustelidae, subfamily Mephitinae, but Dragoo and Honeycutt (1997), based on analyses of mitochrondrial DNA (mtDNA) sequences, found that these genera plus the stink-badgers (*Mydaus*) formed a clade separate from other mustelids. Thus, they placed members of the clade in a separate family.

At various times, spotted skunks in western North America were treated as specifically distinct (Davis and Schmidly 1994; Hall and Kelson 1952, 1959; Jones et al. 1992; Kinlaw 1995) and at other times *gracilis* was considered a subspecies of *S. putorius* (Hall 1981; Ramírez-Pulido et al. 1996; Seton 1929; Van Gelder 1959; Wozencraft 1993). Hall and Kelson (1952) suggested that proof of intergradation between eastern and western forms ultimately would be found. Later they (Hall and Kelson 1959:929) claimed that "Most workers are of the opinion that the genus *Spilogale* is monotypic, or has, at most, 2 or 3 species." Nevertheless, they cited no references in support of their contention. In the most recent morphologic and morphometric treatment of the genus *Spilogale,* Van Gelder (1959) recognized only 2 species: *S. putorius* and *S. pygmaea.* Based on specimens from southern Texas, deemed intermediate between smaller animals with more extensive white to the west and larger, blacker individuals to the east, he subsumed *S. gracilis,* and all of its former subspecies, into *S. putorius.* He did not find evidence of intergradation between eastern and western populations through the remainder of the midsection of the continent (Van Gelder 1959:251, figure 4).

Subsequently, eastern and western spotted skunks were determined to have bacula of different shape and size (Mead 1966) and to be reproductively isolated temporally (Mead 1968b), creating justification for recognition of *S. gracilis* as a distinct species. Based on analyses of cytochrome *b* and a region of the mtDNA D-loop, separation of *S. gracilis* and *S. putorius* as distinct species was supported (Dragoo et al. 1993). The latter authors suggested (Dragoo et al. 1993:264) that "if there is gene flow between the eastern and the western forms in the United States it is probably occurring via Central American forms." Herein, we review information available on spotted skunks (other than *S. pygmaea* and *S. angustifrons* sensu Hall and Kelson 1959) in the Rocky Mountains and westward not considered by Kinlaw (1995).

Hall and Kelson (1959) included 10 subspecies in *S. gracilis.* Hall (1981) acknowledged Van Gelder's (1959) recognition of only 7 races in the same geographic region, but he retained the delineation between western and eastern forms on the range map (Hall 1981:1016, map 518) from Hall and Kelson's (1959) treatment of the genus. He placed all 7 within *S. putorius.* These races, herein considered subspecies of *S. gracilis,* are as follows:

S. g. amphialus Dickey, 1929:158. Type locality "2½ miles north of ranch house near coast, Santa Rosa Island, Santa Barbara County, California."

S. g. gracilis Merriam, 1890a:83, see above (*saxatilis* Merriam and *tenuis* Howell are synonyms).

S. g. latifrons Merriam, 1890b:15. Type locality "Roseburg, Douglas County, Oregon" (*olympica* Elliot is a synonym).

S. g. leucoparia Merriam, 1890b:11. Type locality "Mason, Mason County, Texas" (*ambigua* Mearns, *arizonae* Mearns, and *texensis* Merriam are synonyms).

S. g. lucasana Merriam, 1890b:11. Type locality "Cape St. Lucas, Lower California," [Mexico].

S. g. martirensis Elliot, 1903:170. Type locality "Vallecitos, San Pedro Martir mountains, Lower California, [Mexico,] 9,000 feet elevation" (*microdon* Howell is a synonym).

S. g. phenax Merriam, 1890b:13. Type locality "Nicasio, Marin County, California" (*microrhina* Hall is a synonym).

DIAGNOSIS. Western spotted skunks (Fig. 1) are black with 3 pairs of longitudinal white stripes anteriorly and 3 pairs of vertical white stripes posteriorly (Van Gelder 1959). Originally, the western spotted skunk was described as: "Longer and more slender than the eastern *S. putorius,* with a much longer tail" (Merriam 1890a:83). Frontal white patch on forehead also was described as rounded and much longer than broad. Skull (Fig. 2) was claimed to be much flatter and zygomata wider than in *S. putorius,* and frontoparietal region depressed to level of cranium (Merriam 1890a). Bacula (Fig. 3) of western forms are 11–18 mm long (*n* not provided) and lightly curved whereas those of eastern forms are 14–24 mm long (*n* not provided) and strongly curved (Mead 1966). We know of no other gross morphologic feature that can be used to separate *S. gracilis* and *S. putorius* reliably. However, *S. gracilis* breeds in September, undergoes delayed implantation, and gives birth in April, whereas *S. putorius* breeds in March–April and gives birth in May–June (Mead 1968b). Thus, the 2 species are considered reproductively isolated (Genoways and Jones 1968; Hall 1981; Jones et al. 1982; Kinlaw 1995).

GENERAL CHARACTERS. The western spotted skunk is the size of a half-grown domestic cat and is decidedly weasel (*Mustela*)-like in overall conformation. One pair of longitudinal stripes lies dorsally and parallels the spine, a 2nd pair parallels the dorsal pair but extends over shoulders and anteriorly in front of ears onto forehead and nose, and a 3rd pair extends from the shoulder posteriorly to midflank then curves dorsally to form the 1st ventral stripe. The latter stripe sometimes joins the 1st or 2nd lateral stripes or fragments thereof. The 2nd vertical stripe extends from knee to near base of tail and the 3rd vertical stripe often is manifested as a spot on rump. The tip, and in some instances, the dorsal portion of tail are white (Howell 1906; Van Gelder 1959). Distal tail hairs can be spread to form a huge white plume (Bailey 1936). In rare individuals, normally black portions of the pelage may be reddish or brownish and normally white portions may be grayish or

FIG. 1. Photograph of a western spotted skunk. Photograph reprinted from Verts and Carraway (1998) with permission of the photographer, Ronn Altig.

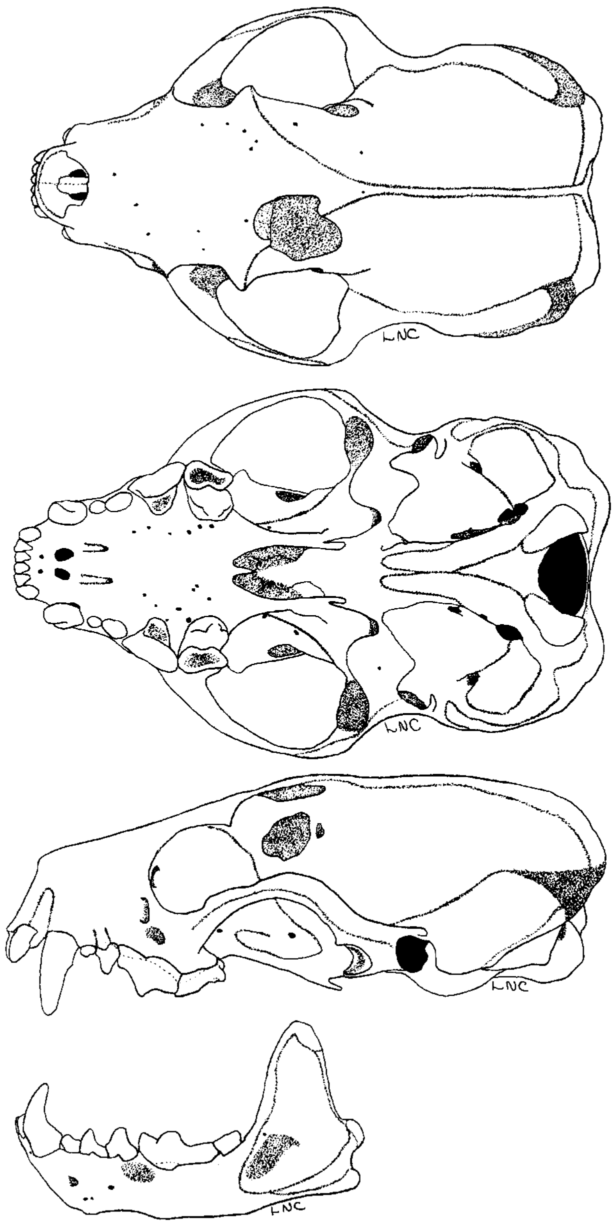

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult male *Spilogale gracilis* (Oregon State University Department of Fisheries and Wildlife mammal collection [OSUFW] 2640; from 13 miles N, 4⅓ miles E Florence, Lane Co., Oregon). Greatest length of skull is 59.95 mm. Irregular-shaped area in frontal region is result of skrjabingyliasis.

yellowish. Van Gelder (1959) considered the grayish coloration was from black hairs scattered among white stripes and the yellowish tinge likely was from earwax or urine. However, J. W. Dragoo (in litt.) suggested that the yellow coloration more likely was caused by a diet with excessive protein because the yellow fur of individuals fed a low protein diet turned white. The color pattern may be aposematic (Pocock 1908) or cryptic (Howell 1906; Seton 1929). Howell (1906) claimed color markings varied relatively little among nominal races, but Van Gelder (1959) considered color markings, combined with body size, constituted the primary differences among races. Cuticular scales on guard hairs of *S. gracilis* are wider than long (mosaic) with crenated margins (Short 1978).

Feet are pentadactyl and plantigrade. Toes of manus have recurved claws ca. 7 mm long, whereas those of pes are about one-half as long and straighter.

Averages and ranges of external measurements (in mm) for spotted skunks from 2 regions in California, respectively, now considered within the range of *S. g. phenax* (Grinnell et al. 1937), were: total length, 385 (345–421), 405 (386–451); length of tail, 150 (139–155), 146 (126–170); and length of hind foot, 42 (39–44), 45 (40–55) for females (*n* = 4 and *n* = 10) and 419 (356–467), 443 (415–473); 159 (130–182), 152 (135–170); and 47 (44–50), 48 (43–52) for males (*n* = 19 and *n* = 11). Hall (1926a), based on a small sample of males and data from Howell (1906), claimed that body length decreased and tail length increased from north to south in *S. g. phenax.* Averages and ranges of external measurements (in mm) for 8 female and 14 male (in parentheses) *S. g. leucoparia* from Trans Pecos, Texas (Patton 1974), were: total length, 370, 331–403 (398, 346–446); length of tail, 138, 123–164 (138, 101–161); and length of hind foot, 41, 36–43 (44, 37–49). Averages and ranges of the same dimensions for 5 females and 4 males (in parentheses) of the same race from Sinaloa (Genoways and Jones 1968) were: 356.2, 332–385 (391, 360–417); 131.8, 115–144 (140.3, 130–153); and 41.2, 39.0–43.9 (46, 43–49). The same dimensions for 7 female and 13 male *S. g. latifrons* from British Columbia (Cowan and Guiguet 1960) were: 378, 368–383 (403, 370–434); 122, 104–148 (128, 110–140); and 44, 41–47 (48, 44–52). The same dimensions for 27 females and 26 males of the same race from west of the Cascade Range in Oregon (Verts and Carraway 1998) were: 386, 330–457 (411, 356–453); 125, 96–150 (132, 102–162); and 45, 40–52 (49, 42–54); and for 8 female and 9 male *S. g. gracilis* from east of the Cascade Range in Oregon the dimensions were: 373, 356–385 (409, 380–455); 138, 125–155 (144, 115–163); and 40, 38–43 (46, 43–50).

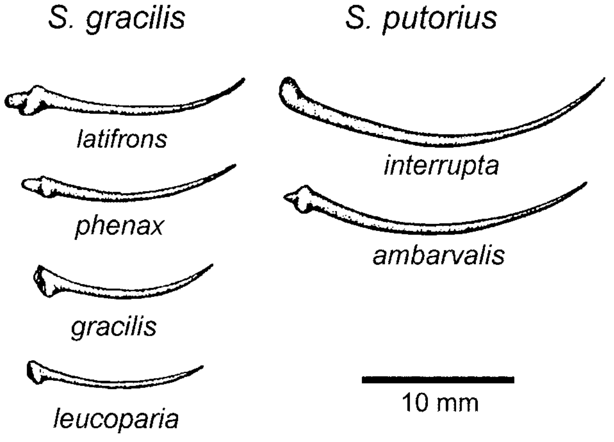

FIG. 3. Bacula of adults of 4 subspecies of *Spilogale gracilis* in comparison with those of 2 subspecies of *S. putorius* (redrawn after Mead 1966:15, figure 6).

Averages and ranges of skull measurements (in mm) of *S. gracilis* from 2 regions in California, respectively, now considered within the range of *S. g. phenax* (Grinnell et al. 1937), were: condylobasal length, 52.8 (50.8–57.0), 52.9 (50.4–55.5); zygomatic breadth, 32.7 (31.5–34.7), 34.0 (31.1–36.2); mastoid breadth, 29.8 (28.5–32.1), 29.4 (28.7–30.6); interorbital breadth, 14.4 (14.0–14.7), 14.6 (13.6–15.3); and width of rostrum, 12.4 (11.7–13.6), 12.9 (12.4–13.4) for females (*n* = 6 and *n* = 10) and 56.3 (52.9–59.8), 58.9 (55.5–62.4); 36.1 (33.9–38.7), 38.3 (35.4–40.8); 32.4 (31.0–34.8), 33.5 (31.7–35.0); 15.5 (14.2–17.1), 16.1 (14.5–17.4); and 13.9 (12.8–14.9), 14.7 (13.3–15.9) for males (*n* = 20 and *n* = 10). Averages and ranges of skull measurements (in mm) for female (*n* = 4 or 5) and male (*n* = 3 or 4; in parentheses) *S. g. leucoparia* from Sinaloa (Genoways and Jones 1968) were: condylobasal length, 48.6, 46.7–49.9 (52.6, 51.7–53.7); occipitonasal length, 45.0, 42.7–46.7 (49.3, 48.6–49.7); zygomatic breadth, 30.4, 29.6–31.3 (33.4, 33.1–33.9); mastoid breadth, 28.0, 27.7–28.3 (29.2, 28.8–29.7); interorbital breadth, 13.4, 12.8–14.6 (14.4, 13.6–14.9); cranial height, 16.5, 15.2–17.6 (17.1, 16.4–18.1); and length of maxillary toothrow, 16.5, 16.4–17.4 (17.1, 16.5–17.8). Averages and ranges for skull dimensions of 6 or 7 females and 10 males (in parentheses) of the same race from Trans Pecos, Texas (Patton 1974) were: condylobasal length, 49.50, 45.86–52.64 (52.77, 47.10–58.10); zygomatic breadth, 32.51, 30.61–35.36 (34.12, 29.62–37.12); mastoid breadth, 29.37, 28.70–30.05 (30.71, 27.83–35.38); palatal length, 18.97, 17.60–20.80 (20.33, 17.25–21.88); and postorbital constriction, 14.52, 13.88–15.43 (14.63,

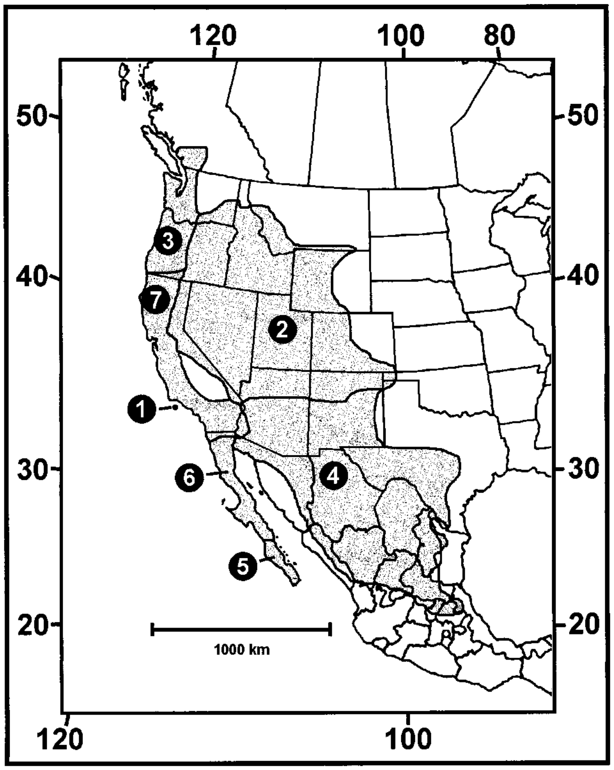

FIG. 4. Distribution of *Spilogale gracilis*. Subspecies are: 1, *S. g. amphialus*; 2, *S. g. gracilis*; 3, *S. g. latifrons*; 4, *S. g. leucoparia*; 5, *S. g. lucasana*; 6, *S. g. martirensis*; and 7, *S. g. phenax*. Map redrawn from Hall (1981:1016, map 518); Hall and Kelson (1959:930, map 472); and Van Gelder (1959:251, figure 4) with modifications.

13.95–15.56). Averages and ranges for skull dimensions of 27 female and 26 male (in parentheses) *S. g. latifrons* from west of the Cascade Range in Oregon (Verts and Carraway 1998) were: condylobasal length, 54.10, 50.46–59.03 (57.70, 52.32–62.62); basilar length, 47.22, 43.81–51.53 (50.56, 45.44–55.71); zygomatic breadth, 34.42, 32.49–38.45 (37.24, 32.87–41.78); cranial breadth, 25.53, 23.79–28.98 (26.76, 24.51–28.91); interorbital breadth, 15.54, 14.40–16.63 (16.53, 14.77–19.57); length of mandible, 34.63, 32.34–39.26 (37.26, 32.88–40.48); and length of maxillary toothrow, 17.55, 16.46–18.78 (18.45, 17.09–20.61). The same dimensions for 7 or 8 female and 9 male (in parentheses) *S. g. gracilis* from east of the Cascade Range in Oregon (Verts and Carraway 1998), in order, were: 48.79, 47.73–49.68 (54.51, 50.49–56.91); 43.06, 42.01–44.30 (48.09, 45.04–50.10); 31.19, 29.77–33.20 (35.27, 32.93–37.84); 23.67, 22.31–24.37 (24.48, 23.17–26.40); 13.34, 12.70–14.36 (14.61, 13.49–15.82); 30.56, 29.67–31.67 (34.66, 33.02–36.48); and 15.58, 14.88–16.17 (17.05, 15.88–18.24). Body mass of striped skunks in Trans Pecos, Texas, ranged from 227 to 482 g for females and 336 to 734 g for males (Patton 1974). Males average ca. 6% longer and 40% heavier than females (Verts and Carraway 1998).

Mass of dry lens of eye is the best criterion of age in the western spotted skunk, but mass and length of baculum, obliteration of cranial sutures, ankylosis of epiphyses to diaphyses of long bones, and presence of pigmented sites of implantation also provide useful information regarding age. These criteria, combined with average dates of parturition, can provide estimates of age to within 1–2 months (Mead 1967).

DISTRIBUTION. *Spilogale gracilis* occurs from southwestern British Columbia (Canada), northern Idaho, and northern Wyoming south through the western three-fourths of Wyoming, montane regions of Colorado, the panhandle of Oklahoma, southwestern Texas, eastern Nuevo Leon to southern Guanajuato then westward and southward to the Pacific Ocean and Baja California Sur (Mexico) (Fig. 4—Hall 1981; Hall and Kelson 1959; Van Gelder 1959). *S. gracilis* also occurs on the Santa Barbara Islands, California. Western spotted skunks do not occur in extreme western Sonora and Sinaloa. One was caught at 2,560 m in California (Orr 1943) and the type of *S. g. martirensis* was collected at 2,744 m in Baja California, Mexico (Elliot 1903). Contrary to the claim of Servín et al. (1995), the 1st record of the species in Durango was recorded by Baker and Baker (1975).

FOSSIL RECORD. Fossils of *Spilogale* from within the present distribution of *S. gracilis* were recovered from the La Brea tar pools (California) of Pleistocene age (Stock 1929) and Curtis Ranch (Arizona) of early Irvingtonian age (Kurtén and Anderson 1980). The only extralimital record is from Medicine Hat (Alberta, Canada) of Sangamonian age (Kurtén and Anderson 1980). *Spilogale* is presumed of Central American origin and thought to have extended its range northward during retreat of Wisconsinan glaciation (Ewer 1973). During the hypothesized northward movement, a western branch that possibly was the progenitor of the spotted skunks now occupying areas west of the Rocky Mountains split from an eastern branch that likely became those now occupying areas in the Great Plains and eastward (Van Gelder 1959).

FORM AND FUNCTION. Comparative myology of *S. gracilis*, *Mephitis mephitis*, and *Martes americana* illustrates that *S. gracilis* differs from *Mephitis* by absence of omohyoid and part of scalenus longus, a relatively larger serratus posterior superior, and more extensive origins of spinotrapezius and elavotrapezius. It differs from *Martes* by undifferentiated psoas muscles, absence of longissimus capitis, coracobrachialis, epitrochlearis, tensor fasciae latae, presemimembranosus, relatively larger stylohyoideus, more equal size of the 4 parts of the pectoralis, no direct origin of rhomboideus from skull, large area of insertion of cleidomastoideus, origin of gracilis and sartorius by fleshy fibers, tendinous insertion of gracilis, absence of caudal head of semitendinosus, and longus colli extending posteriorly only to 5th thoracic vertebra (Hall 1926c). *S. gracilis* was considered closely related to, but somewhat more advanced than, *M. mephitis* especially regarding musculature that provides greater adaptability and agility (Hall 1926c). *Spilogale* has no abdominal skin gland as found in *Martes* and *Gulo* (Hall 1926b). Dental formula is i 3/3, c 1/1, p 3/3, m 1/2, total 34 (Hall and Kelson 1959).

Osteological structure of *Spilogale* has been described in detail and most bony elements are either smaller than in *Conepatus* and *Mephitis*, or intermediate in size or structure between these 2 genera (Van De Graaff 1969). Although skeletal structure of *Spilogale* more closely resembles that of *Mephitis* than of *Conepatus*, several differences from both genera exist. In *Spilogale* the thyrohyal and ceratohyal both arise dorsally from the basihyal, whereas in *Mephitis* the ceratohyal is ventral to the thyrohyal. *Spilogale* has 8 sternebra; other skunks have 9. Xiphisternum is a thin, upright, roughened plate of bone; however, in *Conepatus* and *Mephitis* it is "pyramidal with a flattened, dorsal base" (Van De Graff 1969:79). Vertebral formula for *Spilogale* is 7 C, 14 T, 7 L, 2 S, 23 Ca, total 53; *Conepatus* and *Mephitis* each have 16 thoracic, and 5 and 3–6 lumbar, and 21 and 24–25 caudal vertebrae, respectively (Van De Graaff 1969). Prezygapophyses and associated articular fossae of the 1st thoracic vertebra are distinct and separate from lamina, much as in *Conepatus*. Articular surfaces face dorsomedially to form a more interlocking type of articulation than is present in *Mephitis*, thus allowing less ventral flexion of vertebral column in *Spilogale*. Unlike *Conepatus* and *Mephitis*, transverse processes of 2nd thoracic vertebra have narrower terminal ends than bases. As with *Conepatus* and *Mephitis*, sacrum is composed of 2 fused vertebrae; however, in *Spilogale* neural spines of vertebrae are ankylosed, thus forming "a continuous plate along the dorsal length of the lamina" (Van De Graff 1969:128). Triquetral of carpus articulates with pisiform and has a long body that extends toward palm; in *Conepatus*, this is absent and in *Mephitis*, it is only a small ventral knob. The lesser multangular articulates with 1st and 2nd metacarpals. The dual articulation is unique to *Spilogale*. Lateral and medial borders of ischium have no ridges for muscle attachment. Tibia is not as inflected and anterior border of proximal extremity is not as enlarged as in *Conepatus* and *Mephitis*.

Other than size and shape of bacula, no gross differences were detected in morphology or histology of reproductive tracts of male *S. gracilis* and *S. putorius* (Mead 1970). Vasa differentia are dorsal and parallel to epididymides, pass through inquinal canal, and extend cranially. After entering the prostate they extend diagonally to its midpoint then turn abruptly and open onto colliculus seminalis. Distal ends of vasa differentia are not enlarged to form ampullae, but open via narrow slits into prostatic urethra, which is 8–10 mm long and contains a swelling in the middorsal wall. The prostate gland, the only accessory sex gland present, is well developed (ca. 7 by 7 by 3 mm in nonreproductive individuals and ca. 11 by 16 by 9 mm in reproductively active individuals); although possessing some indentations, it is not bilobed. Muscular urethra is ca. 12 mm long and extends from prostate to base of penis. Penis is ca. 35–40 mm long and attached to ischii by connective tissue and crura is attached by bulbo- and ischiocavernous muscles. Glans penis is 13–25 mm long and completely ensheathed by prepus. Baculum (Fig. 3) is embedded in the glans dorsal to urethra (Mead 1970).

Western spotted skunks are equipped with muscle-encapsulated musk glands that can eject yellowish musk through 2 papillae located immediately inside the anal sphincter. (*E*)-2-butene-l-thiol, 3-methyl-1-butanethiol, and 2-phenylethanethiol compose 89–98% of the volatile compounds in musk, but phenylmethanethiol, 2-methyl-quinoline, 2-quinoline methanethiol, bis[(*E*)-2-butenyl] disulfide, (*E*)-2-butenyl 3-methylbutyl disulfide, and bis(3-methylbutyl) disulfide also are present in small amounts (Wood et al. 1991). Proportions of the 3 major components of the musk differ between males and females: 36%, 30%; 48%, 66%; and 5%, 2%, respectively. Also, musk of *S. gracilis* differs from that of *M. mephitis* by presence of 2-phenylthanethiol, deletion of 3 thioacetate derivatives, and different proportions of various compounds (Wood 1990; Wood et al. 1991). Such differences possibly account for the odor of the musk of the former species being considered more pungent or acrid, but spreading less widely (Dalquest 1948; Hall 1946).

Suprachiasmatic nuclei, that portion of diencephalon of the brain responsible for mediating circadian rhythms, occur bilaterally, commence (mean) 515 μm ± 89 *SD* behind the anterior border of the optic chiasm, and are 1,175 ± 114 μm long, 1,046 ± 77 μm high, and 779 ± 153 μm wide. Shortest cells within the nuclei are 9.6 ± 2.0 μm, whereas those above the nuclei are ≥14.9 ± 3.5 μm and cells above the optic chiasm average 24.0 ± 4.3 μm. Fibers of the retinohypothalamic tract are located in the medial and ventral region of the suprachiasmatic nuclei (May et al. 1985).

Average plasma level of luteinizing hormone in pregnant western spotted skunks at 120 days before implantation was 4.9 ng/ml ± 0.8 *SE* ($n = 11$) and increased gradually to 7.9 ± 1.2 ng/ml ($n = 334$) ca. 1 week before implantation. In general, luteinizing hormone levels in nonpregnant skunks were higher with 9.3 ± 2.0 ng/ml ($n = 8$) and 9.4 ± 3.2 ng/ml ($n = 5$) at 130 days and a few days before average date of implantation for pregnant skunks, respectively (Foresman and Mead 1974). Luteinizing hormone levels in pregnant skunks were stimulated by injections of luteinizing hormone–releasing hormone, but pituitary responsiveness did not increase signficantly from week 8 through week 1 before implantation, suggesting that the period of delayed implantation was "not a result of pituitary inability to respond to hypothalamic control during this period" (Foresman et al. 1974:102).

Average duration of the preimplantation period was reduced from 199 days ± 5.1 *SD* to 148 ± 33.6 days by daily injections of 0.5 mg prolactin and increased to 251 ± 3.2 days by daily injections of 1.5 mg bromocriptine (a dopamine agonist). Gonadotropin-releasing hormone agonist from minipumps had no significant effect on length of the preimplantation period (Berria et al. 1989b). Thus, prolactin may be the "primary pituitary hormone responsible for increased luteal activity and subsequent blastocyst implantation" (Berria et al. 1989b:232). Average prolactin levels in plasma ranged from 3.5 to 9.5 ng/ml in January–April, then increased to nearly 12 ng/ml by late April and to 17.1 ng/ml by early May near the time of nidation (Kaplan et al. 1991). Also, melatonin released from implanted Silastic capsules delayed the rise in plasma prolactin and timing of implantation, possibly by delaying the photoperiod-associated rise in prolactin. Thus, neurons of the anterior hypothalamic area may be "involved in regulating the preimplantation pattern of [prolactin] secretion" (Kaplan et al. 1991:996). Also, in vitro secretion of prolactin from pituitaries excised during long-day photoperiods was significantly greater than from those excised during short-day photoperiods (Rozell and Mead 1993). Prolactin secretion was not inhibited by melatonin, but melatonin reduced the inhibitory effects of dopamine on secretion of prolactin during both photoperiods and in presence or absence of the pars tuberalis; thus, the pars tuberalis may not effect the inhibitory action of melatonin on prolactin in the absence of the hypothalamus as formerly believed (Rozell and Mead 1993).

Although estrogen was not detected by gas chromotography during the preimplantation period, levels increased gradually during the postimplantation period (Mead and Eik-Nes 1969a). However, average plasma estrogen levels in pregnant western spotted skunks during embryonic diapause as determined by radioimmunoassay ranged from 3 to 18 pg/ml; levels were less variable and significantly lower in females with activating blastocysts (Ravindra and Mead 1984). Estradiol alone or combined with progesterone inhibits uterine protein synthesis and secretion (Mead et al. 1979). "Estrogen is required for development of tall columnar luminal epithelium" in the uterus of the western spotted skunk (Hirzel et al. 1999:490).

Average diameter of corpora lutea increased from <1.1 mm in November to ca. 1.2 mm in December–March, then increased again to ca. 1.9 mm in April, but declined to ca. 1.5 mm in May (Mead and Eik-Nes 1969b). During embryonic diapause, corpora lutea contain undifferentiated granulosa cells (12–20 μm) and differentiated granulosa lutein cells (20–45 μm). The 2 types of cells were present in about equal numbers 2 days before nidation, whereas larger cells predominated 8–12 h before implantation and were the only type present 24 h after nidation (Sinha and Mead 1975). Other cellular changes during transformation include the elongate nucleus becoming spherical, small amounts of granular and agranular endoplasmic reticulum becoming a large amount of the agranular type in membranous whorls, the small Golgi complex becoming well developed, rod-shaped mitochondria with both platelike and tubular cristae becoming rounded with tubular cristae predominating, and the smooth plasma membrane becoming plicated and ruffled (Mead 1981).

Average plasma progesterone levels in nonpregnant western spotted skunks remained ≤4.3 ng/ml throughout the year, whereas those of pregnant skunks increased from ca. 0.5 ng/ml in November to >20.0 ng/ml in April (Mead and Eik-Nes 1969b). During implantation, progesterone levels were 8–16.6 ng/ml (Sinha and Mead 1976). After implantation, progesterone levels declined from ca. 23.5 ng/ml to ca. 8.2 ng/ml at parturition (Mead and Eik-Nes 1969b). Hysterectomy had no significant effect on production of progesterone, thus "neither embryos nor placentae were an essential source of luteotropin" and "the uterus played no significant role in regulating the life span of the corpora lutea of pregnancy" (Mead and Swannack 1978:379). However, hypophysectomy reduced progesterone levels within 40 days, had no effect on luteal histology, and prolonged the preimplantation period, suggesting that the pituitary is essential for nidation (Mead 1975). The increase in progesterone during the preimplantation period enhances the number of proteins and quantity of each uterine protein, but other hormones likely are involved in protein synthesis before implantation (Mead et al. 1979). Progesterone administered in implanted Silastic capsules or as medroxyprogesterone acetate by injection maintained blastocyst viability in females for 120 days after ovariectomy, but did not shorten the preimplantation period or induce implantation (Mead et al. 1981). However, steroids, in combination with progesterone, that possibly induce implantation could not be identified, suggesting that the luteal factor may not be a steroid (Ravindra et al. 1984). Blastocysts undergoing delay produce several large protein molecules not produced by activated preimplantation embryos (Rourke and Mead 1982).

Estrogen receptors and progesterone receptors were detected by immunocytochemistry "in luminal and glandular epithelium, endometrial stroma, vasculature, and myometrium of the uterus during the period of delayed implantation" (Mead and Eroschenko 1995: 827). Reduction in staining intensity in both types of receptors occurred during the peri-implantation period with greatest change in the luminal epithelium within 2–3 days after implantation. Thus, failure of earlier attempts to induce implantation during embryonic diapause, and failure of blastocysts "to undergo continuous development and implant without a period of diapause" were not the result of absence of these receptors (Mead and Eroschenko 1995: 827).

Average serum-testosterone levels in male western spotted skunks ranged from 0.15 ng/ml ± 0.05 *SE* in January to 6.42 ± 1.79 ng/ml in October. Testosterone levels increased from February to May, declined to late July, then increased rapidly to the October peak (Kaplan and Mead 1993). Testes of males on which abalation of suprachiasmatic nuclei was preformed in January–March or in which capsules containing melatonin were inserted in March attained maximum size in June, 4 months before controls. However, testes of the former group remained fully enlarged during June–November, whereas regression of testes of the latter group commenced during July, the usual time for western spotted skunks suggesting the pineal gland is involved in regulation of this seasonal cycle (Berria et al. 1990).

ONTOGENY AND REPRODUCTION. In September, average mass of both testes in wild-caught skunks was 2.75 g and average volume of a testis was 266 mm^3. Testicular regression commenced in October and continued to February when testes weighed <0.6 g and had an average volume of 66 mm^3 (Mead 1968b). Spermatozoa were absent from ductus epididymis of most males in January–February and all males in March; the earliest that spermatozoa were found in the cauda epididymides was 22 April. Spermatozoa were present in testes and epididymides of essentially all adult male western spotted skunks by June and in those of most young-of-the-year (only 4–5 months old) by September (Mead 1968b). Semen was collected from captive males by electroejaculation during 104 (94.5%) of 110 attempts during a 15-month period; average ejaculates ranged from a nadir of 11 μl ± 3 *SE* ($n = 6$) in March to a peak of 129 ± 22 μl ($n = 31$) in October (Kaplan and Mead 1993). Volume of semen was >60 μl during October–December. Of 104 samples, 101 (97.1%) contained spermatozoa, but (mean) concentration (1.32 × 10^8/ml ± 0.16 × 10^8 *SE*, $n = 97$), motility of spermatozoa (56% ± 2.4 *SE*, $n = 93$), proportion of morphologically normal spermatozoa (70.3% ± 1.5 *SE*), and number of spermatozoa per ejaculate (8.14 × 10^6 ± 0.85 × 10^6 *SE*, $n = 97$) did not vary seasonally. Average semen pH was 7.76 ± 0.20 *SE* ($n = 6$) and osmolarity was 394 mmol/kg ± 13 *SE* ($n = 10$—Kaplan and Mead 1993). Postthawing (at 37°C) motility (mean) of cryopreserved spermatozoa was greatest (21% ± 3 *SE*) when semen was diluted with TEST (20% egg yolk, 0.4% D-glucose, 4.83% *N*-tris[hydroxymethyl]methyl-2-aminoethanesulfonic acid, 1.05% tris[hydroxymethyl]-aminomethane hydrochloride, 746 units/ml penicillin-G potassium salt, and 563 units/ml streptomycin sulfate), treated with 5% dimethyl sulfoxide, and frozen in 0.25-ml French straws in liquid nitrogen (Kaplan and Mead 1992). Average testis size (length × width) of captives measured through the scrotum ranged from 1.22 cm^2 ± 0.25 *SE* in February to 2.68 ± 0.08 cm^2 in October. Testis size was correlated positively with testosterone concentration (Kaplan and Mead 1993).

Ovulation in western spotted skunks occurs spontaneously and was detected from September to February in wild-caught or laboratory-reared females maintained in isolation. One individual appeared to ovulate twice within a 5-day interval. Ova require 6–7 days to reach the uterus (Greensides and Mead 1973).

Ovaries of anestrous females of western spotted skunks contain antral follicles that attain 0.5 mm in diameter before undergoing atresia, 0.2 mm less than the maximum attained in *S. putorius* (Mead 1968a, 1968b). Corpora albicantia are present in ovaries of postpartum females for ca. 10 months, but luteal cells degenerate by onset of estrus (Mead 1968b). Estrus likely is earlier in southern latitudes; estrus may recur if the female does not mate. Both adults and young-of-the-year usually breed in September (Mead 1968b; Mead and Eik-Nes 1969a). Evidence of mating was detected in 91% of females ($n = 45$) captured after 25 September (Mead 1968b).

Greensides and Mead (1973) were unable to breed western spotted skunks in captivity; however, a wild-caught female that gave birth in captivity was placed with a male "the following winter" and gave birth to a litter on 12 April (Walker 1930:229). After conception and development to the blastula stage, "further development of the blastocyst is greatly retarded and the embryos float freely in the uterine lumen" for an extended period (Mead 1968b: 373). Blastocysts are randomly distributed and unequally spaced in the uterine horns from October to March. During the delay (October–November to February–March), average number of cells in the inner cell mass did not increase (actually averaged 14 less), but average number of cells in the trophoblast increased from 273 to 438 ($t = 6.944$, *d.f.* = 47, $P < 0.001$—Mead 1968b). Typically, development is arrested in blastocysts <1.1 mm in diameter, whereas those 1.2–1.6 mm are in early stages of activation, and those 1.7–2.1 mm are considered activated and likely will implant in ≤3 days (Enders et al. 1986; Mead and Rourke 1985). A few blastocysts as small as 1.05 mm in diameter may be in early activation (Mead and Rourke 1985).

An inhibitor of plasminogen activator, produced by the endometrium and present in uterine fluids but not plasma, increased during pregnancy from 1.7 units/μg protein 40–70 days before implantation to 3.2 units/μg in 20–25 days before implantation, declined to 1.2 units/μg 1–3 days before implantation, then to 0.6 units/μg 1–5 days after implantation, thereby protecting the uterus and blastocysts from damage by plasmin protease. During these same intervals, average protein content of uterine fluids was 12.9 μg ± 3.0 *SD*, 21.8 ± 6.4 μg, 99 ± 44.8 μg (at activation of blastocysts), and 256 ± 150 μg, respectively (Fazleabas et al. 1984).

In *S. gracilis*, epidermal growth factors may be involved in regulating embryonic development and the number and functional status of their receptors may be essential for blastocyst activation and implantation. These receptors are located in the uterine luminal and glandular epithelium, endometrial stroma, myocytes of the myometrium, and smooth muscles of the uterine blood vessels during diapause and peri-implantation (Paria et al. 1994). Transition from diapause to full activation of blastocysts is gradual for 12–20 days then rapid for 1–2 days with an abrupt increase in accumulation of RNA (Enders et al. 1986; Mead and Rourke 1985). During activation, "lipid in both inner cell mass and trophoblast diminishes, polyribosomes increase in number, and the endodermal layer differentiates as the blastocyst grows" (Enders et al. 1986: 423). Within 48 h of implantation, blastocysts expand rapidly, trophoblasts become cuboidal, and blastocysts become uniformly spaced within the uterus (Enders et al. 1986). Uterine concentration of glycoprotein leukemia inhibitory factor messenger RNA (mRNA) is low during delayed implantation, increases by 1.6 times during early embryonic activation, and remains elevated until implantation. Prolactin, progesterone, and estradiol did not increase leukemia inhibitory factor mRNA in the uterus, suggesting that delayed implantation is the result of insufficient expression of this factor and that it contributes to uterine preparation for implantation (Hirzel et al. 1999).

Just before implantation, the somewhat flaccid uterus increases in diameter (Enders and Mead 1996) and mass (Das et al. 1999; Hirzel et al. 1999). Leucocytes infiltrate the uterine epithelium, possibly in response to the proximity of the trophoblast or some antigenic material it produces. This is followed by adhesion of the trophoblast to the uterine epithelium and then by penetration of the trophoblast into the epithelium (Sinha and Mead 1976); however, the trophoblast does not invade or adhere to maternal capillaries (Enders and Mead 1996). At implantation, the myometrium constricts, causing a decrease in the diameter of the uterus except in the vicinity of the 2.0–2.1-mm blastocysts. The trophoblast does not invade or adhere to maternal capillaries (Enders and Mead 1996).

Cyclooxygenase, an enzyme that converts arachidonic acid to prostaglandins, occurs in 2 isoforms (cyclooxygenase 1 and cyclooxygenase 2) encoded by separate genes. Cyclooxygenase 1 mRNA occurs in the trophoblast and uterine glands only after blastocyst attachment; it cannot be detected in the trophoblast 48–72 h after attachment, but is present in the neck of uterine glands. Little or no cyclooxygenase 2 mRNA was detected in uteri of western spotted skunks during delayed implantation, but was present in uteri and trophoblasts during early activation of blastocysts; it remained detectable for 5–6 days after implantation (Das et al. 1999). The increase in cyclooxygenase 2 mRNA is correlated temporally with increase in serum proteins in the uterus and other uterine changes related to implantation (Das et al. 1999).

Implantation occurs in April and most litters of *S. gracilis* are born in May after a gestation period 1st reported as 210–230 days (Mead 1968b), then revised to 230–250 days, with a delay period of 200–220 days (Foresman and Mead 1973). The average preimplantation period was shortened from 218 to 169 days by increasing day length and prolonged from 218 to 265 days by bilateral orbital enucleation (blinding). Blastocysts of several blind skunks did not implant, but remained alive, for ≥316 days (Mead 1971).

Mead (1971:219) believed that "light, acting via the hypothalamus, is the proximate factor in timing nidation in the spotted skunk." Length of the preimplantation period was not affected by pinealectomy, thus the observed effect of daylength was not believed to be mediated through the pineal gland (Mead 1972). Subsequently, May and Mead (1986) reported that denervation of the pineal gland had no significant effect on average duration of the preimplantation period, but that surgery reversed the prolonging effect of blinding on the rate of nidation and the period of delay. Also, both daily injections of the pineal hormone melatonin and implanted Silastic capsules containing melatonin lengthened the preimplantation period. These results support the contention that the pineal gland is involved in timing of nidation in western spotted skunks (May and Mead 1986). Removal of suprachiasmatic nuclei, a possible site of action of melatonin, did not prevent the significant lengthening of the preimplantation period, thus they likely are not required for melatonin to influence timing of implantation in *S. gracilis.* However, lesions to the anterior hypothalamic area reversed the effect of melatonin on implantation (Berria et al. 1988, 1989a). Western spotted skunks given radiolabeled melatonin accumulated relatively high amounts (mean) in the pineal gland (367 disintegrations per minute [dpm]/mg ± 304 *SD*), ovary (69 ± 38 dpm/mg), pituitary (89 ± 56 dpm/mg), liver (107 ± 29 dpm/mg), and kidney (63 ± 15 dpm/mg—Berria and Mead 1990). Autoradiograms revealed that 2-[^{125}I]-iodomelatonin accumulated in the pars tuberalis, but not in any other hypophyseal region, hypothalamus, or thalamus, in both pregnant and nonpregnant females; thus, this region may mediate photoperiodic responses in *S. gracilis* (Duncan and Mead 1992).

Embryos 60–66 mm long (crown–rump) may require 2 weeks of development before birth (Mead 1968b). However, Foresman and Mead (1973) reported a linear relationship ($Y = 1.94 + 0.92X$) between diameter of uterine swellings (mm) and interval to parturition (days).

Average and range (in parentheses) of litter size based on number of corpora lutea ($n = 44$) was 5.2 (3–9), on number of unimplanted blastocysts ($n = 36$) was 3.7 (2–5), on number of pigmented sites of implantation ($n = 23$) was 4.1 (3–6), on implanted embryos ($n = 3$) was 4.7 (4–6), and on young at birth ($n = 7$) was 3.8 (2–5—Mead 1968b). Sex ratio at birth ($n = 33$) was 2.3:1 in favor of males (Mead 1968b).

At birth, neonates are blind and almost hairless, although areas on the skin that will bear white fur are demarcated (Walker 1930). A female neonate weighed 11.4 g (Constantine 1961).

Southern populations of the eastern spotted skunk may produce a 2nd litter after breeding in July or August (Mead 1967). Thus, overlap in the estrous cycles of the eastern and western spotted skunks cannot be discounted (Mead 1968b).

ECOLOGY. In Idaho, western spotted skunks occur most commonly "along streams, especially in the vicinity of basaltic outcroppings and rock piles" (Davis 1939:140). In southeastern Washington, *S. gracilis* occurs in rocky places and riparian thickets of willow (*Salix*) and cottonwood (*Populus*), whereas west of the Cascade Range it occurs in all stages of the forest sere (Carey and Kershner 1996; Dalquest 1948). In eastern Oregon, *S. gracilis* commonly uses canyons, cliffs, rimrocks, lava fields, and arid valleys (Bailey 1936), whereas in coastal regions it is common in alder (*Alnus rubra*)–salmonberry (*Rubus spectabilis*), riparian alder, riparian hardwood, and tanoak (*Lithocarpus densiflorus*) habitats (Maser et al. 1981). In the latter region, *S. gracilis* commonly uses tunnel systems constructed by mountain beavers (*Aplodontia rufa*—Hooven et al. 1979; Lovejoy 1972; Pfeiffer 1953) and runways and stick houses of woodrats (*Neotoma*—Bailey 1936). Along the Pacific Coast, *S. gracilis* is "known to frequent ocean beaches" (Howell 1906:8). In Durango, Mexico, spotted skunks were taken in a rimrock bordering a "mixed pine–oak forest . . . [with] a sparse growth of pine, oak, madroño, and manzanita on the grassy slopes below" (Baker and Baker 1975:672). Another was taken in "oak–pine woodland dominated by *Quercus eduardii, Pinus cooperi* and *Arbutus* spp." (Servín et al. 1995:228). In Sinaloa, Mexico, a specimen was collected "in an arroyo in tropical deciduous forest" (Armstrong et al. 1972:53). Western spotted skunks commonly reside in or under old buildings (Bailey 1936; Hall 1946; Howell 1906; Ingles 1954; Maser et al. 1981); sometimes use dens constructed by ground squirrels (*Spermophilus*—Ingles 1954) or other mammals (Howell 1906); or make use of man-made crevices, such as, at the base of dams, "shielded by a heavy growth of vegetation" (Patton 1974:51).

On Santa Cruz Island, California, of 47 dens used by *S. gracilis,* 29.8% were under shrubs, 21.3% in open grassland, 21.3% in cavities in rocks, 10.6% in road cuts, 10.6% under human structures, and 6.4% in cavities in roots and trunks of trees. Entrances to dens ($n = 13$) averaged 10.7 cm ± 2.95 *SD* wide by 10.6 ± 3.93 cm high (Crooks 1994a). Some dens were used by >1 skunk (e.g., 34.6% of 26 dens used by 6 radio-collared skunks) and some skunks used >1 den (e.g., 2 skunks each used 12 different dens in 3- to 6-month periods—Crooks 1994a). Because no other burrowing animals occur on Santa Cruz Island, Crooks (1994a) suggested that spotted skunks excavated their own dens and that burrowing owls (*Athene cunicularia*) on the island were dependent upon skunk-excavated dens.

In forests on the Olympic Peninsula, Washington, rates of capture for western spotted skunks were 0.9/1,000 trap nights in old-growth stands (>200 years old), 0.3/1,000 trap nights in naturally regenerated stands (90–120 years old), and 0.9/1,000 trap nights in 2nd-growth stands (40–70 years old). In Coast Range forests of Oregon, rates of capture in the 3 types of stands were 1.2/1,000, 0.4/1,000, and 0.2/1,000 trap nights, respectively (Carey and Kershner 1996). On Santa Cruz Island, California, the rate of capture was 5.7/1,000 trap nights (Crooks 1994b).

Spilogale gracilis is an omnivore with long, trenchant carnassials that feeds primarily on insects and small mammals (Ewer 1973; Kurtén and Anderson 1980) as well as carrion, berries, fruits, and trap bait for small rodents on occasion (Bailey 1936; Clark and Stromberg 1987; Maser et al. 1981). In Durango, Mexico, of 25 fecal samples, both larvae and adults of Scarabaeidae and Lucanidae each occurred in 100%, Silphidae adults in 4%, Lepidoptera larvae in 20% and pupae in 4%, centipedes (Chilopoda) in 4%, unidentified lizards in 12%, and unidentified seeds in 8% (Baker and Baker 1975). Stomachs of 6 taken in California contained "insects, *Peromyscus,* fruits of Comarostaphylis, and grapes" (Pearson 1951:366). In Texas, western spotted skunks were observed to feed on red-spotted toads (*Bufo punctatus*) after a rainstorm (Patton 1974). Other than records of items consumed by a few individuals (Dalquest 1948; Maser et al. 1981; Servín et al. 1995), general diet information presented in regional works on mammals or used in ecological treatments (e.g., Crooks and Van Vuren 1995) seemingly is extrapolated from reports of foods consumed by *S. putorius* (Crabb 1941; Selko 1937; Verts and Carraway 1998).

On the 250-km^2 Santa Cruz Island, California, *S. g. amphiala* (ca. 500 g) and the island gray fox (*Urocyon littoralis*; ca. 2,000 g) coexist with "substantial overlap . . . in spatial, dietary, and temporal dimensions," suggesting competition between the species (Crooks and Van Vuren 1995:301). At 1 site, skunks used ravines more than expected and grasslands less than expected, whereas for foxes the reverse was true; at another site, 1 skunk used open grasslands more than expected, but foxes did not select among available types. Average adaptive-kernel home-ranges (Worton 1989) during the wet season (December–April) were 29.6 ha ± 12.2 *SD* for skunks ($n = 7$) and 25.4 ± 12.0 ha for foxes ($n = 12$); values for the dry season (May–November) were 61.1 ha ($n = 1$) for skunks and 23.5 ± 7.5 ha for foxes ($n = 12$). Average overlap ("geometric mean of the product of the ratios of overlap size to seasonal home range size") of home ranges was 0.21 (37 skunk–fox pairs) during the wet season and 0.28 (6 skunk–fox pairs) during the dry season (Crooks and Van Vuren 1995:303). Also, both skunks and foxes consumed mostly deer mice (*Peromyscus maniculatus*) and insects, especially Jerusalem crickets (*Stenopelmatus fuscus*), but skunks also consumed lizards (no taxon provided), whereas foxes did not; foxes also consumed fruits and berries, whereas skunks did not. Skunks were never observed to be active during daylight hours, but foxes were active throughout the 24-h period. These differences in habitat use, home ranges, and activity "may be sufficient to permit long-term coexistence" between the skunks and foxes (Crooks and Van Vuren 1995:305).

Western spotted skunks have been preyed upon by golden eagles *(Aquila chrysaetos*—von Bloeker 1937). They also fall victim to automobile traffic (Maser et al. 1981; Sperry 1933). In the San Luis Potosi–Zacatecas Plateau of Mexico, western spotted skunks are captured by shooting for medicinal use (Mellink et al. 1987). Recorded longevity in captivity is 9 years and 10 months (Egoscue et al. 1970).

Western spotted skunks are infested by bots (presumably *Cuterebra*—Cahalane 1939). Fleas (Siphonaptera) infesting *S. gracilis* in declining frequency of occurrence in California were *Echinophaga gallinacea, Pulex simulans, Oropsylla* (*Diamanus*) *montanus, Hoplopsyllus anomalus, Ctenosephalides felis,* and *Foxella ignota* (Mead 1963). Fleas from *Spilogale* also include *Hystrichapsylla dippiei* (Svihla 1941) and *Orchopeas sexdentatus nev-*

adensis (Lewis et al. 1988). The skunk louse (Mallophaga) *Neotrichodectes mephitidis* and the tick (Acarina: Metastigmata) *Demacentor variabilis* also were found on western spotted skunks in California (Mead 1963). The Lone Star tick (*Amblyomma americanum*) was found on 1 individual in Texas (Patton 1974). Mites (Acari, excluding chiggers) identified from *S. gracilis* in Oregon included *Androlaelaps fahrenholzi, Eulaelaps stabularis, Haemogamasus reidi, Xenoryctes latiporus, Echinonyssus staffordi, Pygmephorus designatus, Eucheyletia bishoppi,* and *Euryparasitus* (Whitaker and Maser 1985).

The tapeworm (Cestoda) *Oochoristica pedunculata* occurred more frequently in the anterior intestine, whereas *Mesocestoides corti* was scattered throughout the intestine (Mead 1963). The roundworm (Nematoda) *Physaloptera maxillaris* was reported from the vicera of *S. gracilis* in Texas (Tiner 1946).

The nematode *Skrjabingylus chitwoodorum* infests the frontal sinuses of *S. gracilis* and causes dilation and erosion of the surrounding bone (Fig. 2); 3 (42.9%) of 7 western spotted skunks in California exhibited eroded sinuses characteristic of the nematode (Mead 1963). In the United States and Canada, 716 (85.0%) of 842 *S. gracilis* exhibited characteristic sinusoidal erosion (Kirkland and Kirkland 1983). In British Columbia and coastal states, 573 (92.7%) of 618 spotted skunks had eroded sinuses, whereas in inland states sinuses of only 143 (63.8%) of 224 were eroded, supporting the conclusion that skrjabingyliasis was more common in mesic regions. Although differences in rates of sinusoidal erosion between sexes and among age classes were demonstrated for *Spilogale,* Kirkland and Kirkland (1983) did not present data in a manner that rates for *S. gracilis* and *S. putorius* could be distinguished. In Mexico, skrjabingyliasis was detected in 90.5% (n = 84) of adult males and in 84.6% (n = 39) of adult females; rates of sinusoidal erosion were 58.3% (n = 12) and 33.3% (n = 3) in younger age classes of the 2 sexes, respectively. The extent of sinusoidal erosion in Mexico was not related to precipitation (Kirkland and Maldonado 1988).

Powassan virus was isolated from kidney tissue of *S. gracilis* in California. This was the only record of isolation of the virus from west of the Rocky Mountains (Johnson 1987). Rabies is relatively uncommon in *Spilogale* (Krebs et al. 1995).

BEHAVIOR. Western spotted skunks are strictly nocturnal (Bailey 1936; Dalquest 1948; Howell 1906) and highly secretive. In a live-trapping study in Texas, *S. gracilis* was not captured before midnight (Patton 1974). They do not hibernate, but tend to be less active during periods of cold weather (Dalquest 1948). Despite being secretive, several workers who have spent the night in a building occupied by spotted skunks remarked about the amount of noise they made while going about their activities (Dalquest 1948; Grinnell et al. 1937; Maser et al. 1981). Some workers claimed that spotted skunks "do not like water" (Clark and Stromberg 1987:237), whereas Dalquest (1948) reported to have captured 1 in a leg-hold trap set beneath 5 cm of water, suggesting that it was either swimming or wading. In some areas, live traps set for small mammals are sprung or animals captured therein are eaten by *S. gracilis* (Hooven et al. 1979).

Captive *S. gracilis* given eggs of domestic chickens grasped "the egg with its forefeet, drawing it back to the stomach, and with its hind feet kicking it across the cage or into some object. This was repeated until the egg was broken" (Patton 1974:168).

Despite having an excellent system of defense in its ability to eject musk, *S. gracilis* often uses this ability only as a last resort (Bailey 1936; Maser et al. 1981). Often it warns an intruder by stamping its forefeet or makes a series of hops toward the intruder (Dalquest 1948), then stands on its forefeet for ≤5 s (Walker 1930) with tail hairs flared and sometimes with anus everted. If pressed by the intruder, it can eject musk from the handstand position (Maser et al. 1981; Seton 1929). More commonly, the western spotted skunk, with all 4 feet on the ground, bends its body with both head and rear directed toward the intruder before ejecting musk (Walker 1930). *S. gracilis* is an expert climber (Bailey 1936; Dalquest 1948) and can eject musk on an intruder from the vantage point of a post or tree.

In 8.7% of 92 in-den locations of radio-collared skunks, 2 or 3 individuals occupied the same den simultaneously; only females were involved (Crooks 1994a). A captive individual performed "handstands" when its 2-year-old littermates scampered about the pen (Walker 1930). Also, 2 individuals made threatening gestures toward each other as they tugged on the same piece of meat. The odor of musk was present when the 2 engaged in such activities, but the release of musk was probably accidental and not an aimed discharge (Walker 1930). Spotted skunks may make high-pitched vocalizations (mostly squeals and bird-like twitters) and nip at individuals of the same or different species of skunks that approach too closely (Patton 1974). An encounter between a western spotted skunk and an island gray fox consisted of a series of approaches and withdrawals by both individuals until the skunk performed a handstand, whereupon the fox retreated (Crooks and Van Vuren 1995).

Copulatory behavior by a pair of skunks in Texas included "squeals, bites, and an occasional burst of musk" as the male grasped the female by the nape and attempted to mount (Patton 1974:171). The female, apparently unreceptive, repeatedly fought free; after 10 min, the pair entered a crevice in rocks, but continued to vocalize. Young skunks only 10 weeks old included copulatory behavior in their play; the female was the aggressor and grasped the male by the nape and attempted to mount. The young skunks rolled onto their sides whereupon the female made thrusting motions (Patton 1974).

GENETICS. *Spilogale g. latifrons* has a diploid chromosome number (2n) of 58 autosomes, with 9 pairs of large, 9 pairs of medium, and 5 pairs of minute acrocentric, 2 pairs of large submetacentric, and 4 pairs of medium metacentric chromosomes (Hsu and Mead 1969). *S. g. phenax* has 2n = 62 autosomes, with 9 pairs of medium, 9 pairs of small, and 7 pairs of minute acrocentric, 2 pairs of medium submetacentric, and 4 pairs of small metacentric chromosomes. *S. g. leucoparia* has 2n = 56 autosomes, with 9 pairs of large, 9 pairs of medium, and 3 pairs of small acrocentric, 4 pairs of large submetacentric, and 2 pairs of large and 1 pair of minute metacentric chromosomes (Lee and Modi 1983). A specimen of *S. g. leucoparia* from Arizona karyotyped by T. C. Hsu had 2n = 60 (R. A. Mead, in litt.). For *latifrons* and *leucoparia* the X chromosome is a large metacentric (Hsu and Mead 1969; Lee and Modi 1983); the X chromosome of *phenax* is a medium metacentric (Hsu and Mead 1969). The Y chromosome for all 3 subspecies is a minute acrocentric (Hsu and Mead 1969).

Spilogale and *Mephitis* are sister taxa descended from a common ancestor with *Conepatus* (Dragoo et al. 1993). Analysis of a 760-basepair (bp) section of the conserved central domain and the more variable left domain of the mtDNA D-loop and the mtDNA cytochrome *b* regions resulted in a single most-parsimonious tree (length = 341, consistency index [CI] = 0.795, retention index [RI] = 0.741) that indicated *S. gracilis* and *S. putorius* are as distinct from one another as *M. mephitis* is from *M. macroura.* An expanded analysis of 451 bp of D-loop and 309 bp of cytochrome *b*, resulted in a single most-parsimonious tree of length 153, CI = 0.752, and RI = 0.716. Percentage sequence divergence, based on this analysis, showed divergence values for *S. gracilis* from *S. putorius* of 4.03–5.36, from *Mephitis* of 9.48–16.43, and from *Conepatus* of 16.99–18.28. Bootstrap analysis, based on an 80% majority-rule consensus tree, strongly supported the sister-taxa relationship between *Spilogale* and *Mephitis* at the 97.25% level (Dragoo et al. 1993).

CONSERVATION. *Spilogale g. amphialus* is considered to be a subspecies of special concern by the state of California (Crooks 1994b).

REMARKS. *Spilogale gracilis* commonly is referred to as the "civet cat," but it is neither a civet (Viverridae) nor a cat (Felidae). In some regions, the species is called the "polecat" (a name also applied to some Mustelidae and other skunks), possibly because pioneers confused them with some foul-smelling Old World mustelids referred to by that name (Lowery 1974). Although sometimes referred to as the "hydrophobia cat," or "phoby cat," relatively few individuals are reported to be infected with rabies virus (Cahalane 1947). The etymological origin of *Spilogale* is the Greek *spilos* meaning "spot" and the Greek *galeë* meaning "an animal of the weasel kind" (Jaeger 1978:107, 244). The specific name *gracilis* is from the Latin meaning "slender, thin, simple" (Jaeger 1978: 112).

Captive specimens used in the analysis that revealed autumn breeding and delayed implantation in spotted skunks were collected in Washington, Oregon, California, Nevada, New Mexico, and Texas, whereas those that breed in spring were collected in Iowa, Minnesota, South Dakota, and Florida (Mead 1968b:387, figure 8). All were exposed to northern-latitude photoperiods in captivity. Broad regions remain for which the breeding biology and molecular genetics (consequently, the species involved) of spotted skunks are uncertain.

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