

Sciurus griseus. By Leslie N. Carraway and B. J. Verts

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Sciurus griseus Ord, 1818

Western Gray Squirrel

Sciurus griseus Ord, 1818:152. Type locality "The Dalles of the Columbia [River, Wasco Co., Oregon]."

Sciurus leporinus Audubon and Bachman, 1841:101. Type locality "Northern parts of California."

Sciurus fossor Peale, 1848:55. Type locality "Southern parts of Oregon."

Sciurus heermanni Le Conte, 1852:149. Type locality "California." Tentatively restricted to "central Sierran foothills in vic. Calaveras River, Calaveras Co." (Hall, 1981:434).

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae, Subfamily Sciurinae, Genus *Sciurus*, Subgenus *Hesperosciurus* (Hall, 1981; McLaughlin, 1984; Nelson, 1999). Three subspecies are recognized as follows (Hall, 1981):

S. g. anthonyi Mearns, 1897:501. Type locality "Campbell's Ranch, at Laguna, San Diego County, California."

S. g. griseus Ord, 1818, see above.

S. g. nigripes Bryant, 1889:25. Type locality "San Mateo County, [California]."

DIAGNOSIS. *Sciurus griseus* (Fig. 1) is distinguishable as a sciurid by pointed, posteriorly directed postorbital processes; it is recognizable as a member of the genus by a strongly depressed braincase posteriorly, a broad squarish palate that extends only slightly beyond the toothrows, a canal-like infraorbital foramen, four transverse crests on M1 and M2 with the middle two more prominent, one transverse crest on M3 (Fig. 2), prominent ears, and a bushy tail (Hall, 1981). *S. griseus* may be distinguished from congeners and other tree squirrels by its large ears, bright uniformly silvery-gray dorsum, pure white venter, lack of tufts on the ears, and long, plumose tail (Fig. 1; Bailey, 1936). The only congeners with which *S. griseus* is sympatric are the introduced *S. niger* and *S. carolinensis*; the former is distinguishable from *S. griseus* by the pinkish or reddish bones (Levin and Flyger, 1971) and the latter by P4 usually being longer than wide (Hall, 1981).

GENERAL CHARACTERS. *Sciurus griseus* is the largest tree squirrel within its range. It has plantigrade, pentadactyl feet; the pollex is vestigial, has two phalanges, and is equipped with a flat nail but the remaining toes of the forefoot are long and slender, have three phalanges, and are equipped with heavy, strongly arched claws. Similarly, the hind feet have a phalangeal formula of 2, 3, 3, 3, 3, but all toes are equipped with claws (Bryant, 1945). The forefeet have five apical pads, three interdigital pads, and two metacarpal pads, whereas the hind feet have five apical pads, four interdigital pads, and no metatarsal pads (Bryant, 1945).

Reported ranges of external measurements (in mm) are: total length, 500-615; length of tail, 240-309; length of body, 265-323; length of hind foot, 67-83; and length of ear, 28-39 (Crace, 1973; Ingles, 1965; Nelson, 1899). Range in mass for 38 squirrels from El Dorado Co., California, was 520-942 g (Crace, 1973; Hall, 1981; Ingles, 1965).

Means of cranial measurements (in mm) for five topotypes of *S. g. griseus* (Nelson, 1899) were: basal length, 58.3; palatal length, 32.1; interorbital breadth, 20.8; zygomatic breadth, 38.7; length of upper molar row, 12.9. The same dimensions for five topotypes of *S. g. anthonyi* were: 56.3, 30.2, 20.9, 37.7, 11.7, respectively (Nelson, 1899). Skull length was 65-70 mm (Ingles, 1965).

DISTRIBUTION. The geographic distribution of *S. griseus* (Fig. 3) extends from Lake Chelan and Tacoma, Washington, southward through Oregon, Nevada, and California along the forested

eastern slopes of the Cascade, Sierra Nevada, Tehachapi, Little San Bernardino, Santa Rosa, and Laguna mountains then westward (except for the Central Valley, California) through the Coast Ranges of California and into the foothills of the Coast Range in Oregon (Hall, 1981). Western gray squirrels were reported to occur as high as 2,590 m in the San Bernardino Mts., California (Seton, 1929; Stephens, 1892).

FOSSIL RECORD. A specimen of Pleistocene age from Samwell Cave, Shasta Co., California, consisting of the anterior portion of the right mandible with p4 and a broken i1 was referred to *Sciurus griseus fossilis* (Kellogg, 1912).

FORM AND FUNCTION. The eye lens of *S. griseus* is yellow (Yolton et al., 1974). Western gray squirrels are considered to have eyes with duplex retinas, unlike the all-cone retinas reportedly possessed by ground squirrels (*Spermophilus*) and prairie dogs (*Cynomys*—Anderson and Fisher, 1975; Yolton et al., 1974). Conelike and rodlike cells occur at a ratio of 5:4 (Yolton, 1975). In *S. griseus*, rodlike and conelike photoreceptors that exhibit "a strictly diffuse pattern of protein renewal" shed outer-segment discs (Anderson and Fisher, 1975:954); previously, this process was believed to occur only in rods. Multiple invaginations are present at the base of outer segments of rodlike cells in adults, probably representing the development of new discs (Anderson and Fisher, 1976). In conelike cells, single partially formed invaginations occur in the same locations as in rodlike cells. Subsurface cisterns occur in retinal neurons and their processes, in amacrine, bipolar, and ganglion cells, and are connected with the rough endoplasmic reticulum (Fisher and Goldman, 1975).

Most light absorption by the eye lens occurs in the spectral region of 440-520 nm (Yolton et al., 1974). However, Jacobs (1976: 325) and Yolton (1975) reported that *S. griseus* has "dichromatic color vision with two spectral mechanisms peaking at about 450 and 540 nm." Relative preretinal absorbance was 0.54 at 440 nm (Yolton et al., 1974), about half the level recorded for ground squirrels. The cornea contributes negligibly to the total preretinal absorbance (Yolton et al., 1974). A background luminance of 0.006-0.02 cd/m² was sufficient for *S. griseus* to exhibit a cone-threshold effect (Jacobs and Birch, 1975; Jacobs et al., 1982). Below this level the threshold dropped and was associated with a shift in spectral sensitivity characteristic of that "in other mammalian duplex visual systems" (Jacobs and Birch, 1975:376). In a test of visual sensitivity, western gray squirrels exhibited spatial acuity that increased with



FIG. 1. Photograph of an adult *Sciurus griseus*.

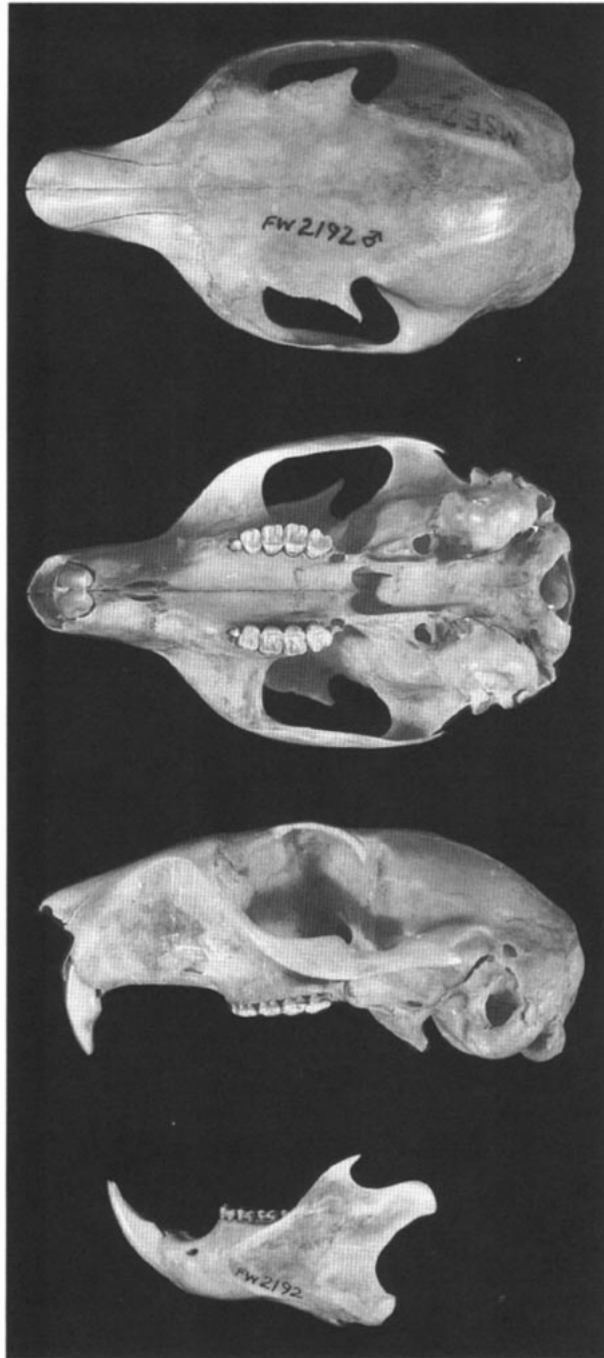


FIG. 2. Dorsal, ventral, and lateral views of cranium, and lateral view of the mandible of an adult male *Sciurus griseus* (OS-UFW [Oregon State University Department of Fisheries and Wildlife mammal collection] 2192; from 6 mi S, 2 mi W Philomath, Benton Co., Oregon). Occipitonasal length is 66.97 mm.

luminance level. Maximum visual sensitivity occurred at spatial frequencies of 0.5 c/d (cycles/degree) with a luminance level of 3.4 cd/m² (Jacobs et al., 1982). Nevertheless, maximum spatial resolution occurred at 2.2 c/d with 3.4 cd/m² and at 3.8 c/d with 340 cd/m².

The labial surfaces of the metaconids on the lower cheekteeth are dominated by detrital striations, the lingual surfaces of the protoconids exhibit markings resulting from striations and polish, and the centers of the metalophs are dominated by markings caused by polish (Rensberger, 1978). Differences in markings on portions of the lower and upper teeth are the result of the labial surfaces having minimal contact with food; the other two surfaces come into contact with large amounts of food (Rensberger, 1978).

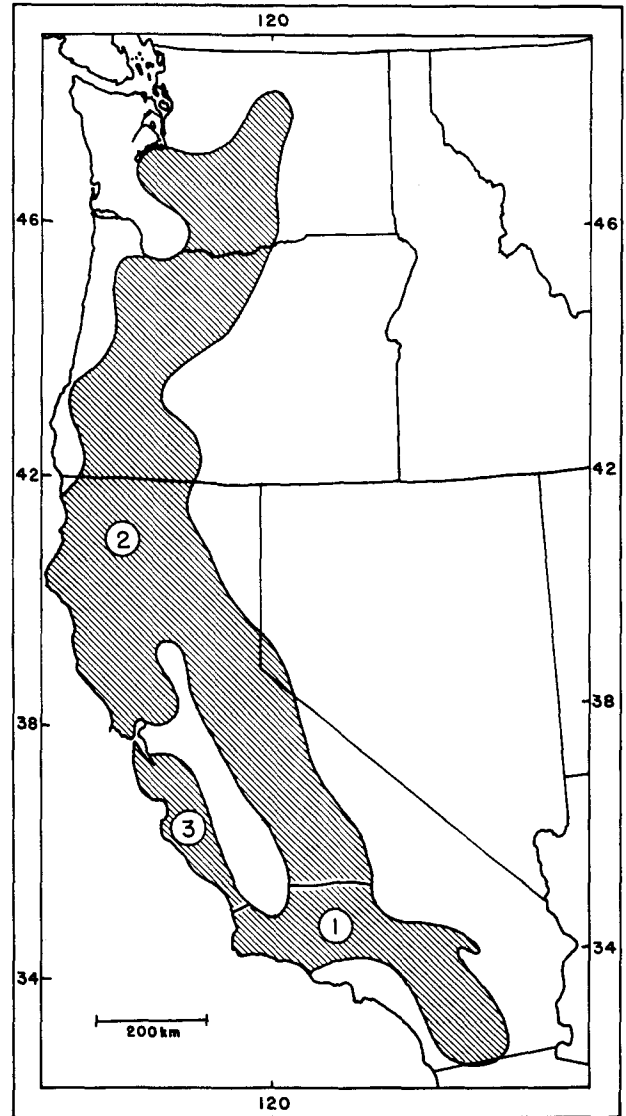


FIG. 3. Geographic distribution of *Sciurus griseus*. Subspecies are: 1, *S. g. anthonyi*; 2, *S. g. griseus*; 3, *S. g. nigripes* (redrawn after Hall, 1981).

In lateral view, the os clitoridis (Layne, 1954:364) "... has a curved shaft which is bent laterally at about its middle" (Fig. 4). It has a large, convex, laterally compressed head on the distal end; one large and one small rounded expansion adorn the ventral aspect. The length of the os clitoridis is 5.4 mm and the distal enlargement is 2.2 mm; the os clitoridis is the largest of those of any North American *Sciurus*. Generally, the os clitoridis is one-third the size of the baculum (Layne, 1954). The baculum (Fig. 4) has an enlarged bladeliike distal end "with a curved and slightly twisted edge" (Howell, 1938:49). The blade is blunt on the distal end, but forms a short, sharp hook on the proximal end. The shaft of the baculum averages 16.5 mm long and the blade 6.8 mm long. The baculum is more like that of *S. aberti* than those of other *Sciurus* (Howell, 1938).

In *S. griseus*, the zygomatic plate forms an angle of about 60° with the basicranial axis (Bryant, 1945). The zygomatic arches are not as appressed as in *Tamiasciurus*. The ventral tubercle on the caudal border of the atlas is bifid, but is a single projection in other sciurids. There are 54–55 vertebrae: 7 cervical, 12 thoracic, 7 lumbar, 3 sacral, and 25–26 caudal (Bryant, 1945). The sternum is composed of five sternebrae. The body of the manubrium is triangular; its apex and lateral edges are rounded. The fibula is rounded and skewerlike in *S. griseus* (Hill, 1937). Mammary are arranged one pair pectoral, two pairs abdominal, one pair inguinal (Bryant, 1945; Nelson, 1899).

In *S. griseus*, the medial flexor caudae has two slips; the thyrohyoideus is relatively large; the sternothyroideus is distinct from the sternohyoid; the insertion of the rhomboideus capitis is restricted to the vertebral border of the scapula; and the levator scapulae ventralis inserts on the acromion, but its origin is on the ventral arch of the atlas (Hill, 1937). The pectoralis minor inserts onto the lateral ridge of the humerus; the extensor indicis et pollicis originates from the ulna, crosses the dorsum of the forefoot above the extensor carpi radialis brevis, and inserts at the tendon of the common extensor of the second digit; the tenuissimus is large and functional; the rectus femoris has two distinct heads; the peroneus longus inserts on the first cuneiform and first metatarsal, and retains the primitive insertion on the tuberosity of the fifth metatarsal; and the adductor longus is large and partly fused with the adductor brevis (Hill, 1937). Only the portion of the circular external jugular vein deep to the clavicle is present in *S. griseus* (Hill, 1937).

The dental formula is $i\ 1/1$, $c\ 0/0$, $p\ 2/1$, $m\ 3/3$, total 22 (Bryant, 1945). In *S. griseus* and congeners, the crowns of P4-M3 are low compared with those of other Nearctic genera of Scuridae. The occlusal outlines of M1 and M2 are quadrate, the trigon is U-shaped on P4-M2, the metaloph joins the protocone on P4-M2, the mesostyle is present on P4-M2, and M2 and M3 are equal in size (Bryant, 1945).

In several studies of membrane transport systems in erythrocytes of hibernating and nonhibernating sciurids, *S. griseus* reportedly was used as an example of a nonhibernating species (Ellory and Willis, 1983; Hall and Willis, 1987; Willis et al., 1980). Specimens used were *S. carolinensis* misidentified as *S. griseus* (J. S. Willis, pers. comm.).

ONTOGENY AND REPRODUCTION. In Alameda Co., California, females with developing ovarian follicles were collected in November, estrus occurred in most individuals by late December or January, and parturition and lactation occurred in February-May. Follicles mature at a minimum diameter of 1.21 mm and seem to inhibit development of smaller follicles (Fletcher, 1963). During June and July, young postpartum females became anestrous, whereas the oldest adults often began a second period of ovarian activity; a few pregnant females were taken in March, June, July, August, and September (Fletcher, 1963; Stephens, 1892). During pregnancy and lactation, developing follicles were present continuously; mature follicles became atretic. Corpora lutea attained maximum size about mid-gestation, then commenced to degenerate; degeneration usually was completed near the end of lactation or shortly thereafter (Fletcher, 1963). In Butte Co., California, corpora lutea began to degenerate after the first quarter of gestation and disappeared three-quarters through gestation (Swift, 1977). Pregnant females were collected January-June; however, the breeding season (first copulation to last parturition) was considered to extend from 1 month before to 1 month after this period (Swift, 1977).

In Butte Co., California, mean weight of testes, prostate gland- seminal vesicles combined, and bulbo-urethral (Cowper's) glands increased substantially from January to February and reached a peak in May (Swift, 1977). Adult males with black, sparsely furred scrota were collected February-May, but those collected June-July had pinkish or grayish scrota; males with black scrota were considered to be sexually active (Swift, 1977).

Mean litter size in California, based on counts of embryos, was 2.2 ($n = 13$) in Alameda Co. (Fletcher, 1963), 2.67 ($n = 9$ —Ingles, 1947a) and 2.8 ($n = 10$ —Swift, 1977) in Butte Co., and 3.0 ($n = 25$) in Kern Co. (W. C. Asserson III, in litt.); the range was two-three in the first study, two-four in the latter three. Other investigators placed the range at one-four (Seton, 1929; Stephens, 1892), two-five (Maser et al., 1981), and two-six (Jameson and Peeters, 1988). Mean litter size for younger females was smaller than that for older females (Swift, 1977). Intrauterine losses accounted for 31% of implanted embryos in Butte Co., California (Swift, 1977).

In Butte and Kern counties, California, young usually are born from February to mid-June or July, after a gestation period of >43 days (W. C. Asserson III, in litt.; Ingles, 1947a; Swift, 1977). Two peaks of breeding are evident (W. C. Asserson III, in litt.; Fletcher, 1963; Swift, 1977), but these may be artifacts related to different age classes breeding at different times (Bailey, 1936; Fletcher, 1963). The presence of lactating females as late as October in California suggests two litters may be produced in the same calendar year although no definite records of multiple pregnancies not attributable to intrauterine loss of the first litter are available (W. C.

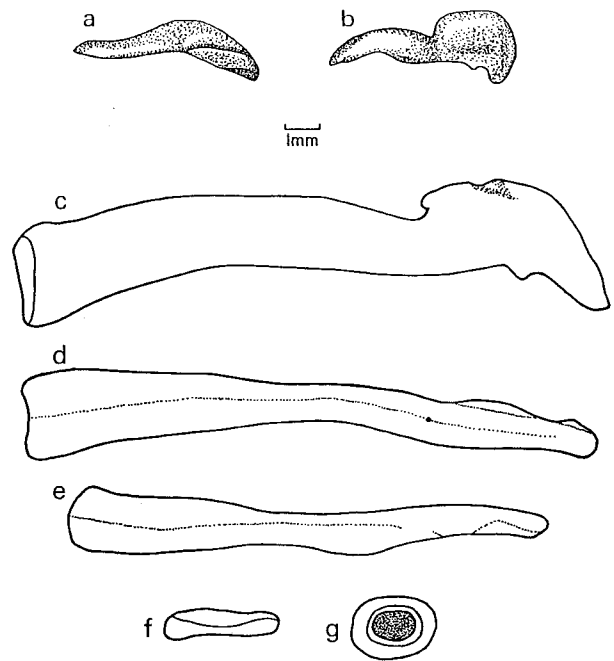


FIG. 4. a, Dorsal and b, right lateral views of the os clitoridis of *Sciurus griseus*. Os clitoridis redrawn after Layne (1954:363, fig. 2). Camera lucida tracings of c, right lateral; d, dorsal; e, ventral; f, distal; and g, proximal views of the baculum of *Sciurus griseus* (OSUFW 2742; from 5 mi N, 4 mi W Corvallis, Benton Co., Oregon). Distal is at right for dorsal, ventral, and lateral views.

Asserson III, in litt.; Bailey, 1936; Fletcher, 1963; Jameson and Peeters, 1988; Swift, 1977). Young begin to leave the nest about mid-March, but most leave about mid-April. Sexual maturity is attained at about 10-11 months of age (Fletcher, 1963; Swift, 1977).

Young are thought to be born in tree-hole nests but are moved to dreys (sometimes spelled "drays") constructed of sticks and bark when cavities become too small for growing young or when external parasites become intolerable (Ingles, 1947a). A male and a female, thought to be about a week old, taken from a drey and weighed within 48 h of collection, were 74.6 and 80.4 g, respectively (Storer, 1922); their external measurements (in mm) were (male first): total length, 205 and 225; length of tail, 93 and 100; length of hind foot, 34 and 35; length of ear, 8 (both). Their eyes were not open. The skin of the week-old pair was loose and wrinkled at capture; a slight growth of hair was present only on the dorsum. Within 3 days the skin was no longer wrinkled and the pelage had grown rapidly; the white-tipped hairs of the tail, black-tipped hairs of the dorsum, and brown spot at the base of the ear were discernible (Storer, 1922). Another week-old male weighing 55 g had closed eyes and ears and was sparsely furred with hairs <1 mm long on the dorsum and <3 mm long on the head and tail (Swift, 1977). A female estimated to be 3 weeks old when captured weighed 126 g; in captivity, it gained 227 g in 34 days (Ingles, 1947a). The feet and head of nestlings are disproportionately large (Ingles, 1947a; Storer, 1922).

ECOLOGY. In Washington, the western gray squirrel is considered a species of "... the oak woods rather than the coniferous forest"; its geographic range "... is largely regulated by the distribution of oaks, especially garry [Oregon white] oak (*Quercus garryana*)" (Dalquest, 1948:285). In western Oregon, these squirrels are associated with Transition Zone forests on both sides of the Cascade Mountains; they are "... more common in the interior valleys with the oaks, maples, yellow pines, and sugar pines" (Bailey, 1936:117). In California, "... at low elevations it is common in groves of native walnuts (*Juglans* spp.) and at higher elevations it is associated with Black Oak" (Jameson and Peeters, 1988:244). The habitat at lower elevations of Bidwell Park, Butte Co., California, where Ingles (1947a:139) studied the ecology and life history of *S. griseus*, was in the Lower Sonoran Life Zone and was "... char-

acterized by virginal growths of such trees as western sycamore (*Platanus racemosa*), Fremont cottonwood (*Populus fremontii*), valley oak (*Quercus lobata*), and California black walnut (*Juglans hindsii*). Foothill portions of the park were Upper Sonoran and included digger pine (*Pinus sabiniana*), blue oak (*Quercus douglasii*), interior live oak (*Q. wislizenii*), and scrub oak (*Q. dumosa*). In the same study, other observations of *S. griseus* were conducted in the Transition Life Zone in which ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*P. lambertiana*), redwoods (*Sequoia gigantea* and *S. sempervirens*), and California black oak (*Q. kelloggii*) were common (Ingles, 1947a).

In Oregon, *S. griseus* feeds on seeds of conifers (*Pseudotsuga menziesii*, *Abies balsamea*, *Picea sitchensis*, *Tsuga* sp., and *Pinus* sp.) in autumn; some cones are cached for use in winter. When available, seeds, berries, buds, bark, sap, nuts, acorns, and fungi are eaten (Bailey, 1936; Maser et al., 1978). In Washington, "the principal food is acorns, although the seeds of the Douglas fir and probably other conifers are eaten" (Dalquest, 1948:285). In Butte Co., California, western gray squirrels were observed to feed on acorns (*Quercus lobata*, *Q. kelloggii*), catkins (*Q. lobata*), nuts (*Juglans hindsii*, *Carya pecan*, *Amygdalus communis*, *Pinus ponderosa*, *P. sabiniana*, *Cupressus macrocarpa*), berries (*Morus rubra*, *Phoradendron flavescens*), samaras (*Acer saccharinum*, *Ulmus americana*), leaves (*Montia perfoliata*), aphids (*Aphis* sp.) causing leaf roll in Oregon ash (*Fraxinus oregona*), and flower buds and leaves of chickweed (*Stellaria media*—Ingles, 1947a). *S. griseus* reportedly also feeds on the seeds of eucalyptus (*Eucalyptus globulus*) in California (Little, 1934). In the Willamette Valley, Oregon, failure of the Oregon white oak to produce acorns in 1978 was speculated to have affected populations of *S. griseus* seriously (Coblentz, 1980). However, in a quantitative study of dietary habits of 310 *S. griseus* collected in a 5-year period in California (mostly in Trinity, Tehama, and Monterey counties), hypogeous fungi ranked first by volume and frequency of occurrence (Stienecker and Browning, 1970). Seasonal consumption of fungi ranged from 56 to 60% in Trinity Co., 30–73% in Tehama Co., and 14–58% in Monterey Co.; greatest use of fungi was in spring and summer. The "most important" fungus was *Rhizopogon* (Stienecker and Browning, 1970:39). Nevertheless, mast was considered the critical food for western gray squirrels; pine nuts and acorns ranked second and third, respectively, by both volume consumed and frequency of occurrence in both Trinity and Tehama counties. Fruits of California bay (*Umbellularia californica*) and unidentified vegetable material ranked second and third, respectively, by both volume consumed and frequency of occurrence in Monterey Co. (Stienecker and Browning, 1970). Subsequent analysis of contents of an additional 320 stomachs (mostly from Kern and Mendocino counties) tended to corroborate earlier findings and to extend them to a wider area in California (Stienecker, 1977). The extensive use of fungi in spring and summer and use of pine and oak mast throughout the year also were corroborated by analysis of stomach contents ($n = 59$) in southern Oregon (Cross, 1969). Other items in the diet of *S. griseus* in Oregon included green vegetation, insect larvae, thistle (*Cirsium* sp.), fescue seeds (*Festuca* sp.), oat seeds (*Avena* sp.), club moss (Lycopodiaceae), and pollen grains (*Pinus* sp.). Western gray squirrels frequently cause serious depredations in almond (*Prunus amygdalus*), filbert (*Corylus auellana*), and walnut (*Juglans* sp.) orchards (Cross, 1969; Flyger and Gates, 1982; Ingles, 1947a, 1947b; Jackson, 1983). In early spring, bark is stripped from near the tops of second-growth redwood and Douglas-fir trees and the cambium is eaten, causing some damage (Bowles, 1920; Fritz, 1932; Mitchell, 1950). Bone and antlers are gnawed by *S. griseus* possibly to obtain required mineral nutrients (Cross, 1969; Sumner and Dixon, 1953). Amounts of food eaten during a single foraging bout for each of two *S. griseus* were estimated at 43.6 and 51.6 g (Ingles, 1947a). Reports by the lay public of *S. griseus* preying on bird eggs or nestlings are relatively common (Ingles, 1947a), but no published anecdotal accounts or quantitative reports of the role of the species as a predator are available.

California ground squirrels (*Spermophilus beecheyi*) and introduced tree squirrels (*Sciurus niger* and *S. carolinensis*) compete with the western gray squirrel for food in California (Ingles, 1947a). Northern flying squirrels (*Glaucomys sabrinus*) and Douglas' squirrels (*Tamiasciurus douglasii*) may compete for the same food resources and for tree-hole nesting sites (Cross, 1969). Competition

with *T. douglasii* was suggested as a factor "... limiting the upward extension of the Gray Squirrel's range" (Grinnell and Storer, 1924:196), although elsewhere in the same publication an overlap in elevational ranges of nearly 1,000 m was indicated for the two species. In southern Oregon, direct competition between western gray squirrels and California ground squirrels was observed; when the density of the population of the former declined, that of the latter increased (Cross, 1969). Other mammalian associates of *S. griseus* include dusky-footed woodrats (*Neotoma fuscipes*), piñon mice (*Peromyscus truei*), striped skunks (*Mephitis mephitis*), spotted skunks (*Spilogale gracilis*), black-tailed jackrabbits (*Lepus californicus*), porcupines (*Erethizon dorsatum*), and black-tailed deer (*Odocoileus hemionus*—Cross, 1969). Other syntopic, seed- and fungi-eating small mammals likely compete or otherwise associate with *S. griseus* to a lesser extent.

Accounts of aggressive interactions between western gray squirrels and acorn woodpeckers (*Balanosphyra formicivora*), scrub jays (*Aphelocoma coerulescens*), and Steller's jays (*Cyanocitta stelleri*) are recorded; squirrels commonly are driven away from feeders or caches of acorns by acorn woodpeckers (Cross, 1969; Ingles, 1947a). White-breasted nuthatches (*Sitta carolinensis*) glean nut fragments dropped by *S. griseus* and rufous-sided towhees (*Pipilo erythrophthalmus*), dark-eyed juncos (*Junco hyemalis*), and plain titmice (*Parus inornatus*) enter live traps set for western gray squirrels (Cross, 1969).

House cats (*Felis silvestris*—Murie, 1936), red-tailed hawks (*Buteo jamaicensis*—Fitch et al., 1946), golden eagles (*Aquila chrysaetos*—Connolly et al., 1976), and coyotes (*Canis latrans*—Sperry, 1941) are known predators of *S. griseus*. Stomachs of seven of 537 coyotes and nine of 324 bobcats (*Felis rufus*) collected on game refuges in California contained remains of western gray squirrels (McLean, 1934). Other suspected predators include goshawks (*Accipiter gentilis*), great horned owls (*Bubo virginianus*), gray foxes (*Urocyon cinereoargenteus*), martens (*Martes americana*), and fishers (*M. pennanti*—Ingles, 1947a, 1947b). Although an increase in abundance of *S. griseus* in the Yosemite Valley, California, was attributed to removal of coyotes, bobcats, and other predators (Grinnell and Storer, 1924), predation was considered to play a negligible role in regulation of density of populations of the western gray squirrel (Ingles, 1947a). Other mortality factors include sport harvest, diseases, and being hit by automobiles; mortality related to the latter factor was considered to be several times that related to predation (Ingles, 1947a). The estimated annual sport harvest averaged 214,000 (range, 152,700–253,400) in California from 1965 to 1971 (W. C. Asserson III, in litt.). Longevity in captivity may exceed 11 years (Ross, 1930).

Estimates of density for populations of *S. griseus* were 0.25/ha in the foothills of the Sierra Nevada Range in California and 2.5/ha in the Yosemite Valley, California (Grinnell and Storer, 1924). In Lake Co., California, estimates (Schnabel model) were 1.8 and 2.5/ha in spring and 2.0 and 2.8/ha in autumn in pine and mixed coniferous forest, respectively (D. J. Hall, in litt.). In Bidwell Park, Butte Co., California, the density was estimated at 4.3/ha; the area contained introduced nut-bearing trees that may have supported a density in excess of that possible by the native vegetation (Ingles, 1947a). Although no estimates of density are recorded, populations apparently erupted at several localities in the Sierra Nevada Range several times in the 20th century, but soon declined in response to epizootics (Bryant, 1921; Fritz, 1932; Ingles, 1947a; Payne, 1940; Stanley, 1916; Sumner and Dixon, 1953). For 2 years in southern Oregon, 12–13 western gray squirrels were captured on a 1.8-ha area repeatedly sampled; however, during the 3rd year only eight individuals were captured, four of which used the area irregularly (Cross, 1969). Roadside counts of *S. griseus* on deer-census routes in Jackson and Josephine counties, Oregon, produced indices of ca. 0.21/km driven in 1960, <0.08/km in 1961–1964, >0.30/km in 1965–1967, and ca. 0.13/km in 1968, suggesting a multiannual cycle in density. The peak index in 1965 (ca. 0.44/km) was almost 9 times greater than the lowest index (ca. 0.05/km) in 1963 (Cross, 1969:32, fig. 8).

In autumn in Lake Co., California, adults composed 64, 51, and 27% of trapped samples in ponderosa pine, mixed coniferous, and knobcone pine (*Pinus attenuata*) forests, respectively (D. J. Hall, in litt.). In trapped samples in ponderosa pine forest in Kern Co., California, sex ratios were 1.9:1 ($n = 102$) and 1.5:1 ($n = 32$) in favor of males in spring and summer, respectively (W. C. Asserson

III, in litt.). In southern Oregon, the sex ratio of a sample ($n = 63$) of *S. griseus* obtained at various times throughout the year was 1.6:1 in favor of males (Cross, 1969).

Ectoparasites of *S. griseus* include fleas (Siphonaptera): *Orchopeas nepos*, *O. latens*, *O. dieteri*, *O. howardi*, *Opisodasys enoplus*, *O. keeni*, *Diamanus montanus*, *Monopsyllus fornacis*, *Ceratophyllus (Amonopsyllus) ciliatus protinus*, and *Eumolpianus cyrturus* (Eads et al., 1985; Easton, 1983; Hubbard, 1943, 1947; Lewis et al., 1988); ticks (Acarina): *Dermacentor occidentalis* and *Ixodes pacificus* (Cross, 1969; Kohls, 1937); mites (Acarina): *Haemogamasus ambulans*, *H. reidi*, *Hirstionyssus cyonomys*, *Notoedres douglasi* (Bryant, 1921; Cross, 1969; Keegan, 1951; Lavoipierre, 1964); and lice (Anoplura): *Hoplopleura sciuricola* (Emerson et al., 1984). Infestations by scabies or mange mites (*Notoedres*) sufficient to cause rapid declines in abundance of western gray squirrels were reported periodically in California in the first half of the 20th century (Bryant, 1921; Ingles, 1947a; Sumner and Dixon, 1953). Nevertheless, in Kern Co., California in 1968–1971 mange was evident in <3% of 425 squirrels examined (W. C. Asserson III, in litt.).

Endoparasites include roundworms (Nematoda): *Cistellinema grisei* (Lichtenfels, 1971) and undescribed species of *Citellinema* (Cross, 1969; Lichtenfels, 1971); coccidia (Apicomplexa): *Eimeria* (apparently a new species—Henry, 1932) and *E. tamiasciuri* (Hill and Duszynski, 1986). Coccidiosis (etiologic agent not specified) apparently was responsible for a die-off of western gray squirrels in Los Angeles and Santa Barbara counties, California in January–April 1930 (Moffitt, 1930).

Ringworm, probably caused by the fungus *Trichophyton rubrum*, was diagnosed in western gray squirrels in southern Oregon (Cross, 1969). The virus responsible for western equine encephalomyelitis was isolated from three naturally infected *S. griseus* in California (Lennette et al., 1956).

BEHAVIOR. Western gray squirrels are largely arboreal; they are wary and secretive (Cross, 1969). They are curious and investigate new objects placed in their environment; they sometimes shake or invert live traps. After capture and release, some become trap-shy, but some learn to pilfer nuts from trigger mechanisms of live traps without causing the trap doors to fall, requiring that at least one thick-shelled nut be attached to each trigger mechanism with a sheet-metal screw (W. C. Asserson III, pers. comm.).

Western gray squirrels nest in cavities created by woodpeckers (Picidae) or they build stick nests or dreys. The latter usually are used for rearing young, but cavities are used for sleeping at other times (Ingles, 1947a). Dreys consist of three or four concentric layers with the largest and heaviest sticks forming the outside and base and the inner chamber insulated and lined with progressively finer materials (Cross, 1969; Merriam, 1930). Dreys usually are constructed in both conifer and hardwood trees in California (Grinnell and Storer, 1924; Ingles, 1947a; Merriam, 1930; Sumner and Dixon, 1953), but in southern Oregon they were observed only in conifers (Cross, 1969). Two dreys examined by Cross (1969) were lined with burlap pilfered from a blind for observing squirrels constructed about 100 m away, indicating that nesting materials may be transported considerable distances.

Western gray squirrels are active throughout the year; they tend to be slightly more active on cloudy days when wind velocity is low, but rain does not cause them to reduce their activity (Ingles, 1947a). They may remain in their nests on stormy days (Grinnell and Storer, 1924). Onset of daily activity usually is near civil sunrise even though the sun may be obscured by mountains (Cross, 1969). Activity peaks about 1–2 h after civil sunrise with some variation with season and locale. By midday, about 40% of individuals in an area are in their nests, a proportion maintained until about 3 h before civil sunset when more individuals begin to enter nests. By civil sunset, >90% are in nests (Cross, 1969). During the interval that individuals are out of their nests, they commonly rest for long periods. While resting out of nests, they commonly sprawl on a limb with chin on the limb and legs and tail hanging alongside the limb (Cross, 1969; Ingles, 1947a).

Upon emergence from a nest at onset of activity, western gray squirrels commonly engaged in grooming behavior for 3–5 min, but sometimes as long as 15 min (Cross, 1969). Most grooming was concentrated on the head and neck; the face and nape were cleaned by wiping with the forefeet and forearms, which, in turn, were licked;

the ears and lower neck were scratched with a hind foot; and the vibrissae were wiped on a tree branch (possibly in combination with scent marking). The hind feet were held, one at a time, with both forefeet and cleaned with biting movements. The remainder of the body was groomed with the mouth, hind foot (scratching), or both. The tail was held with the forefeet and “nibbled” in several locations, then the entire tail was drawn through the mouth once or twice.

Exploratory behavior, commonly initiated upon leaving the vicinity of the nest, may consist of searching for food by moving in short hops with nose held close to the ground with occasional digging at the surface. Alternatively, the squirrels traveled rapidly through the trees, then descended to the ground and continued rapid travel; occasionally, they stopped and sat upright or jumped onto a tree trunk ≥ 1 m above the ground seemingly to survey the surroundings. The latter more extensive explorations graded into the short-hop phase when food was encountered (Cross, 1969).

In California, home-range areas based on unstated numbers of observations and delineated as polygons with both concave and convex sides ranged from 0.12 to 0.34 ha for three males and from 0.47 to 0.62 ha for five females (Ingles, 1947a). In southern Oregon, home-range areas based on locations obtained by trapping, direct observation, and radiotracking, and delineated by convex polygons, ranged from 0.79 to 3.49 ha for four individuals of each sex in February–April and from 1.75 to 5.56 ha for 12 individuals of mixed sex and age in July and August (Cross, 1969). Differences in home-range areas by sex and age were claimed, but data for different age classes within sex groups were combined and vice versa. Individuals followed through several seasons commonly extended their home ranges in late summer apparently to take advantage of some particularly abundant food resource (Cross, 1969). Mass migrations similar to those of eastern congeners (Flyger, 1969; Schorger, 1949) have not been reported for *S. griseus*.

While active, western gray squirrels commonly forage on the ground; they travel by quadrupedal hopping, sometimes for >2 m/hop (Ingles, 1947a). Between hops, they sit in an alert posture with all four feet on the ground and the tail curled over the back; the curled tail also is used as an umbrella (Cross, 1969; Ingles, 1947a). While inactive but alert, individuals may lie on a limb with head elevated slightly and tail held over the back, or they may sit on a limb with tail held over the back in an S-curve (Cross, 1969).

When disturbed by noise or movement, western gray squirrels may “freeze” (often in awkward positions) or, if danger does not seem imminent, they may produce a series of barks combined with foot-stamping and tail-flicking (Cross, 1969; Ingles, 1947a). The scolding barks have been described phonetically as “cha-cha-cha—cha—cha—cha” (Ingles, 1947a) or as “chewnnk-chewnnk-chewnnk” (Cross, 1969); the sounds may be repeated for ≤ 1 h and may be heard for ≥ 180 m (Ingles, 1947a). The squirrels seem unaware of animals or people that remain motionless (Cross, 1969).

Cones commonly are cut and allowed to fall to the ground, collected one at a time, and carried to a log or tree branch where seeds are removed by holding the cones with the forefeet and cutting the scales at their points of attachment (Grinnell and Storer, 1924). Cones too large for the squirrels to carry are opened on the ground where they fall. Acorns not eaten where collected are scatter-hoarded; buried acorns are relocated by olfaction (Cross, 1969; Ingles, 1947a). There is some evidence that empty or wormy walnuts are detected kinesthetically (Cross, 1969).

Western gray squirrel populations tend to exhibit linear-right social hierarchies (not absolutely fixed or stable straight-line pecking orders) with few reversals; within age groups, males are dominant to females (Cross, 1969). Chasing is the most common overt agonistic behavior. Threat postures characterized by an extended head and neck, elevated rump, raised dorsal pelage, and the tail held parallel to the dorsum were observed; foot-stamping, tail-flicking, and teeth-chattering may occur occasionally, but boxing, reported in congeners, was not observed (Cross, 1969). Body contact (biting and scratching accompanied by growling) is rare, but when it occurs, it may be sufficiently violent to cause injuries (Cross, 1969; Ingles, 1947a). Signs of submission include running, resumption of eating, and alteration of travel routes. In southern Oregon, social rank and size of the home range were correlated positively in winter and spring, but not in summer (Cross, 1969). Social structure also may have affected activity as subordinate individuals were required to wait to feed at good sources of food until dominant individuals had fed, thereby extending periods of activity (Cross, 1969).

GENETICS. The karyotype for the one specimen examined (a male) had FN = 76, 2n = 40, with 14 metacentric and 24 submetacentric autosomes and 2 submetacentric sex chromosomes (Nadler and Sutton, 1967). The karyotype depicted (Nadler and Sutton, 1967:250, fig. 4) shows sex chromosomes of approximately equal size. *S. griseus* differs from *S. carolinensis*, *S. niger*, and *S. aberti* "by the absence of an acrocentric Y and the consistent presence of secondary constrictions in the second largest pair of metacentric and largest pair of submetacentric autosomes" (Nadler and Sutton, 1967:251).

REMARKS. The generic name *Sciurus* was derived from the Greek prefix *skia* meaning a shadow, and *oura* meaning the tail, apparently alluding to the habit of members of the genus carrying the tail over the back in sun-shade fashion. The specific name *griseus* was derived from the modern Latin *griseis* meaning gray (Jaeger, 1978). The species also is known by the vernacular names silver-gray squirrel and Columbian gray squirrel (Bailey, 1936).

The photograph used in Fig. 1 was provided by M. S. Eltzroth. T. E. Lawlor and J. S. Willis commented on an earlier draft of this manuscript. This is Technical Paper No. 9988, Oregon Agricultural Experiment Station.

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