MAMMALIAN SPECIES No. 630, pp. 1–8, 3 figs.

Tamiasciurus douglasii.

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Published 3 December 1999 by the American Society of Mammalogists

Tamiasciurus Trouessart, 1880

Tamiasciurus, Trouessart, 1880:292. Type species [*Sciurus vulgaris*] *hudsonicus* Erxleben, 1777.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciurognathi, Family Sciuridae, Subfamily Sciurinae, Tribe Sciurini, Genus *Tamiasciurus.* The genus contains three species and is restricted to the Neartic Region. The following key is modified from Hall (1981) and Lindsay (1982).

1 Underparts nearly all white .... *T. hudsonicus*
Underparts yellowish or rust colored (but can be white) 2
2 Dark gray or blackish dorsally; yellow-orange on venter; tail reddish dorsally and light ventrally; interorbital breadth usually <14.5 mm .... *T. douglasii*
Pale gray dorsally with reddish-yellow dorsal band; venter light yellow; interorbital breadth usually >14.5 mm .... *T. mearnsi*

Tamiasciurus douglasii Bachman, 1839

Douglas' Squirrel

Sciurus douglasii Bachman, 1839:99. Type locality "shores of the Columbia River." Restricted by Allen (1898:284) to "mouth of Columbia River," Clatsop Co., Oregon.

Sciurus molli-pilosus Audubon and Bachman, 1841:102. Type locality "coast of northern California." According to Grinnel (1933:121) "somewhere in southern Oregon."

Sciurus belcheri Gray, 1842:263. Type locality "mouth of Columbia River."

Sciurus suckleyi Baird, 1855:33. Type locality from "Steilacoom, Puget Sound," Washington.

Sciurus hudsonicus Allen, 1890:165. Type locality from "Blue Canyon, Placer Co., California."

Tamiasciurus douglasii Hayman and Holt, 1940:347, first use of current name combination.

CONTEXT AND CONTENT. Context same as for genus. Three subspecies of *T. douglasii* are currently recognized (Hall, 1981).

T. d. albolimbatus Allen, 1890:165, see above (*hudsonicus* is synonym).

T. d. douglasii Bachman, 1839:99, see above (*belcheri* and *suckleyi* are synonyms).

T d. mollipilosus Audubon and Bachman, 1841:102, see above (*orarius* and *cascadensis* are synonyms).

DIAGNOSIS. Across most of its range, the Douglas' squirrel (Fig. 1) is easily distinguished from other tree squirrels by its smaller body size, its gray-brown dorsum and yellow-tinted underparts, as well as its conspicuous vocalizations and territorial behavior (Flyger and Gates, 1982; Gurnell, 1987). The tail of tamiasciurids is flatter and smaller in proportion to body size (<40%) and lacks the longitudinal bands typical of other tree squirrels (Flyger and Gates, 1982; Gurnell, 1987). Where its range borders that of *Tamiasciurus hudsonicus* (pine squirrel), *T. douglasii* can be distinguished on the basis of pelage. Douglas' squirrels are gray-brown to dusky olive dorsally with yellowish white to deep orange underparts, except in eastern Oregon where the venter is white. In contrast, *T. hudsonicus* is usually reddish above and white below. Tail hairs of *T. hudsonicus* are yellowish with black borders, and those of *T. douglasii* possess faint yellow or white tips with wider black bands (Flyger and Gates, 1982; Ingles, 1965). Although not sympatric with *T. douglasii, T. mearnsi* (formerly included in *douglasii*—Hoffmann et al., 1993; Lindsay, 1981), located in the Sierra San Pedro Martir of Baja California, is nearly indistinguishable from *T. douglasii* on the basis of external characteristics. However, multivariate comparisons of skull morphology (size and shape) have led to specific status for *T. mearnsi* (Hoffmann et al., 1993; Lindsay, 1981).

GENERAL CHARACTERS. *Tamiasciurus douglasii* is a diurnal squirrel easily recognized by its small size (<300 g); grayish, chestnut brown dorsum; reddish or yellow venter; dark lateral band; white eye ring; and white ear tufts (most evident in winter—Fig. 1). The dorsum varies from an olivaceous gray to gray brown often with a dark or chestnut, median band. Underparts vary from white or pale buff to a yellow tint or reddish orange, always with a gray or blackish wash. The pronounced lateral black stripe, separating dorsal pelage from that of the venter, is most pronounced in the summer and absent or faint in winter (Flyger and Gates, 1982). The tail is dark above and lighter or buff below, often with a white band on the edge (Ingles, 1965). In summer the pelage is often darker with blackish ear tufts and orangish feet. In contrast, in winter the pelage is often longer, more vellous, with grayer sides, a "reddish brown middorsal stripe," and lighter venter (Banfield, 1974:142). The distinct white eye rings and slight ear tufts are most evident in winter (Flyger and Gates, 1982). Pelage of Douglas' squirrels varies among individuals, geographic locale, and season (Hall, 1981).

Ranges of external measurements for *T. douglasii* (in mm) are as follows: total length, 270–348; length of tail, 102–156; length of hindfoot, 41–55; and ear length, 19–31 (Cowan and Guiguet, 1956; Flyger and Gates, 1982; Hall, 1981; Smith, 1965). Although Douglas' squirrels are not considered sexually dimorphic (Flyger and Gates, 1982), Smith (1965) reported males were significantly heavier, but not longer, in southwestern British Columbia.

The skull (Fig. 2) is relatively short with laterally expanded zygomata and a rostrum laterally compressed with a flattened frontal area. Auditory bullae are slightly inflated and the braincase is depressed posteriorly. Condylobasal length varies from 42 to 49 mm. Mean cranial measurements (in mm, ± *SD*) for 82 specimens from central and southern California (Lindsay, 1981) are as follows: greatest length of skull, 48.38 ± 0.81; zygomatic width, 27.94 ± 0.66; breadth of braincase, 20.68 ± 0.43; greatest height of skull, 17.31 ± 0.36; interorbital breadth, 14.07 ± 0.46; nasal length, 12.94 ± 0.65; temporal fossa diagonal, 16.64 ± 0.42; diastema

FIG. 1. *Tamiasciurus douglasii* (photograph by R. B. Forbes).

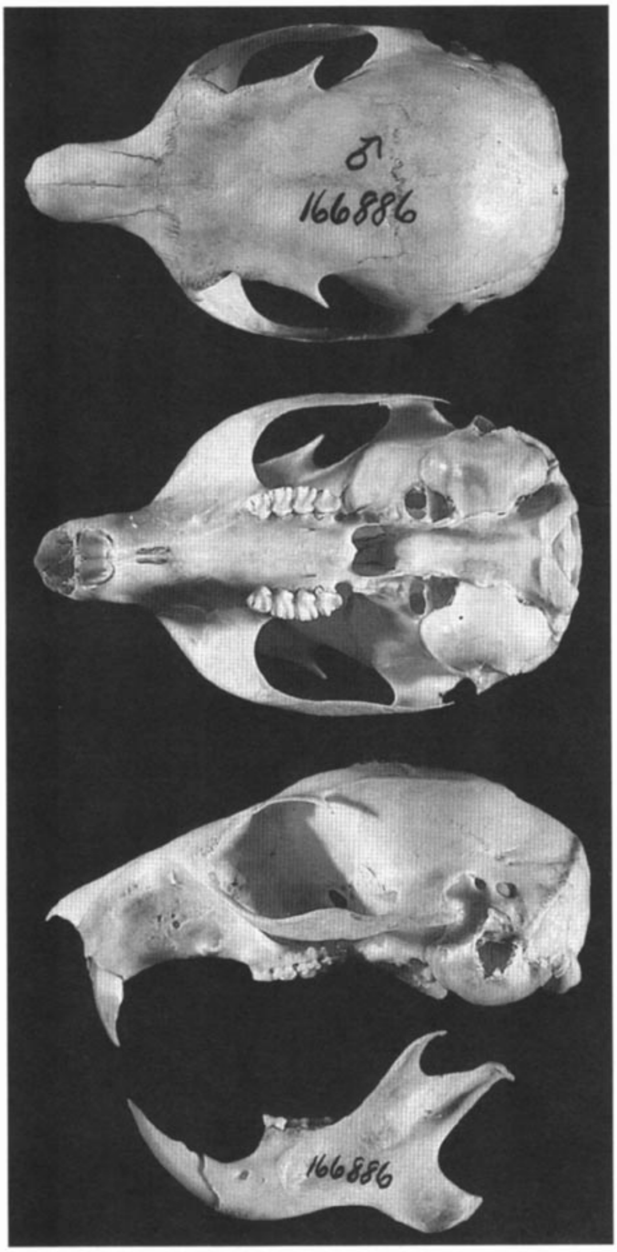

FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of mandible of *Tamiasciurus douglasii* (male from Empire, Oregon, National Museum of Natural History, USNM 166886). Greatest length of cranium is 44.5 mm. Photographs courtesy of Smithsonian Institution.

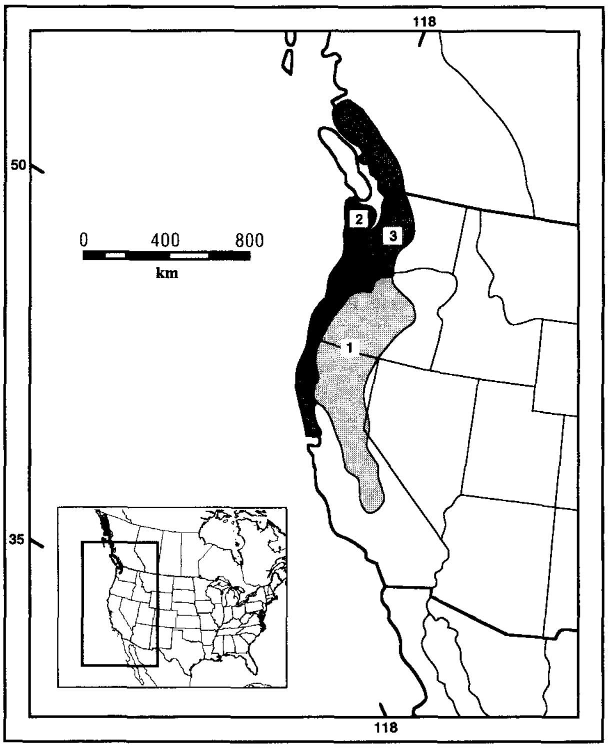

FIG. 3. Distribution of *Tamiasciurus douglasii* in North America: 1, *T. d. albolimbatus*; 2, *T. d. douglasii*; 3, *T. d. mollipilosus* (modified from Flyger and Gates, 1982 and Hall, 1981).

length, 12.73 ± 0.41; length of maxillary tooth row, 8.11 ± 0.22; width of M2, 2.56 ± 0.08; width of P, 2.22 ± 0.10; breadth at M3, 6.22 ± 0.26; pterygoid width, 3.93 ± 0.23; height of foramen magnum, 6.21 ± 0.26; width of foramen magnum, 7.54 ± 0.23; nasal width, 7.61 ± 0.31; and breadth of infraorbital foramen, 7.43 ± 0.39.

DISTRIBUTION. *Tamiasciurus douglasii* is found in coniferous forests of the Pacific Coast and the Sierra Nevada and Cascade ranges of North America (Ingles, 1965; Smith, 1965). Its range extends from southwestern British Columbia, through the Cascade Range of western and central Washington and Oregon, southward along the coast of northern California to San Francisco, and southward through the Sierra Nevada Mountains to southcentral California (Fig. 3; Flyger and Gates, 1982; Ingles, 1965). Formerly, the distribution extended to northern Baja California, Mexico, when *T. douglasii* included *T. d. mearnsi,* now recognized as a distinct species, *T. mearnsi* (Hoffmann et al., 1993; Lindsay, 1981—but see comments in Remarks section, below).

The distribution of Douglas' squirrel is nearly continuous along the southwestern coast of mainland Vancouver, British Columbia (from Fraser Delta north to Rivers Inlet, west of the Coast Range—Banfield, 1974), but it is absent from Vancouver island where it is replaced by *T. hudsonicus* (Cowen and Guiguet, 1956; Lindsay, 1981). Although *T. hudsonicus* and *T. douglasii* are generally allopatric, zones of sympatry occur along a parapatric border in southern British Columbia (Smith, 1965, 1970, 1981), northwestern Washington (Cowan and Guiguet, 1956; Dalquest, 1948), and eastern Oregon (Hatton and Hoffmann, 1979). Morphometric studies (Lindsay, 1982) have dismissed reports of hybridization that were based on vocalizations and fur color (Hall, 1981; Hatton and Hoffmann, 1979; Smith, 1965) and instead suggest that character convergence has occurred in transitional forests where both species are present.

FOSSIL RECORD. Despite marked differences in the bacula (Pocock, 1923) and skulls (Black, 1963; Moore, 1959) of *Tamiasciurus* and *Sciurus,* suggesting a distant relationship, the two are now grouped together in one tribe (Sciurini) based on comparisons of several osteological, myological (Bryant, 1945), immunological (Ellis and Maxon, 1980; Hight et al., 1974), and protein traits (Hafner et al., 1994). It is argued that *Tamiasciurus* diverged from *Sciurus* in the late Pliocene, 3×10^6 years ago (Hafner, 1984). *T. douglasii* is reported from only two Rancholabrean faunas in northern California: Potter Creek and Samuel caves, (Kurtén and Anderson, 1980). It is estimated that complete and final isolation between *T. douglasii* and *T. mearnsi* in Baja California occurred at the end of the last glaciation, ca. 15,000 years ago. Little else is known of the historical distribution of *T. douglasii,* possibly because of the limited number of faunal deposits recorded within its range (Graham and Lundelius, 1994; Kurtén and Anderson, 1980).

FORM AND FUNCTION. The dental formula of *T. douglasii* is i 1/1, c 0/0, p 1–2/1, m 3/3, total 20 or rarely 22 (Flyger and Gates, 1982; Hall, 1981). Incisors exhibit indeterminant growth, and malocclusion is likely when damage occurs and toothwear is prevented (Layne, 1954; Smith, 1984).

Tamiasciurus douglasii exhibits two annual molts (Flyger and Gates, 1982; Nelson, 1945), although the tail molt probably occurs only once during the year. In Canada, spring molt occurs in May and June; autumn molt takes place between late August and early October (Banfield, 1974). Detailed descriptions on molting patterns are not available for this species, although they probably parallel those of *T. hudsonicus* reported in detail by Layne (1954).

As in all sciurids, the stance is plantigrade and plantar tubercles are present (Gurnell, 1987). The species exhibits strong hind limbs, hind feet with five elongated digits, smaller forelimbs, and forefeet with four long digits and a reduced first digit. Sharp, recurved claws, present on all long digits, aid in climbing (Gurnell, 1987).

Although body size among tree squirrels tends to increase with latitude, pine and Douglas' squirrels are among the smallest species and occur at the highest latitudes (Heaney, 1984; Reynolds, 1985). Gurnell (1987) suggested that smaller size of these squirrels may result from selection for increased foraging ability and agility in the smaller branches of conifer trees, rather than competition for seed resources, as suggested by Heaney (1984) for other tree squirrels.

Although little is known about the physiology of this species, several inferences can be made from studies on *T. hudsonicus*. Metabolic rate follows patterns of body temperature and, for adult squirrels, likely ranges from 143 to 168 kcal/kg (Grodinski, 1971). Estimates of energy budgets (in kcal kg^{-1} day^{-1}) for free-ranging, adult (ca. 240 g) and subadults (ca. 160 g), respectively, are as follows: consumption, 514, 620; assimilation, 369, 448; and metabolic waste, 146, 260. Total energy requirements for lactating females may be >175% of that of males (Smith, 1965, 1968). The small body size and low insulative ability of Douglas' squirrels may necessitate several adaptations for colder climate, including an elevated body temperature, the ability for heterothermy (Pauls, 1979), and adipose tissue in the thoracic and cervical regions, as reported for pine squirrels (Aleksiuk, 1970, 1971). Vascular bundles involved in countercurrent heat exchange may be present in the base of the tail (Muchlinski and Shump, 1979). Sebaceous, sudoriferous, and mucous glands present in the oral region (Quay, 1965) most likely function in scent marking (Flyger and Gates, 1982).

In the wild, adults of *Tamiasciurus* can be distinguished from juveniles by differences in pelage and tail hairs (Kemp and Keith, 1970). Adults can be distinguished from subadults by the presence of a pigmented scrotum of the male or pigmented teats on parous females (Flyger and Gates, 1982). In the laboratory, age determinations can be made by mass of the eye lens (Davis and Sealander, 1971; Kemp and Keith, 1970), closure of the epiphyses (Davis and Sealander, 1971), and possibly toothwear, cementum annuli (Fogl and Mosby, 1978; Smith, 1981), and suspensory tuberosities (Colburn, 1986). An epiphyseal notch at the distal end of the femur is evident up to 8 months of age (Davis and Sealander, 1971).

Comparisons of the anatomical structure of the mandible and skull reveal four characteristics that together strongly suggest that the temporal jaw musculature of *T. douglasii* is significantly less powerful than that of *T. hudsonicus* (Smith, 1981). These include a lower ratio of temporal muscle mass to body mass (mean ± *SE* = 4.18 ± 0.091 for *T. douglasii* vs. 4.78 ± 0.386 to 6.30 ± 0.269 for *T. hudsonicus*); a smaller coronoid process of the dentary bone; frequently absent sagittal crest (<37.5% vs. >85.7% of *T. hudsonicus*) indicating that the temporal muscle does not reach the middorsal line of the skull; and a lower mechanical advantage of the moment arm between the coronoid process and the articular process of the dentary (Smith, 1981). These differences, the first two of which are likely to involve both a genetic and acquired basis, and the entire temporal complex, which in part involves an ontogenetic component, may reflect adaptations of Douglas' squirrels to the smaller, softer foods within its range and adaptations of *T. hudsonicus* to the harder, serotinous cones of lodgepole pine (*Pinus contorta*—Smith, 1981). However, it should be noted that in Oregon and Washington, *T. douglasii* consumes the same hard seeds as *T. hudsonicus*.

REPRODUCTION AND ONTOGENY. Douglas' squirrels are spontaneous ovulators (Gurnell, 1987; Millar, 1970; Smith, 1965). Estrous females, which remain so for only one day, are easily recognized by their enlarged, pink genitalia (Koford, 1982). During this period, males converge on the territory of the female where she eventually mates with one or more males.

The structure of the male and female reproductive tracts of tamiasciurids differ significantly from those of other tree squirrels (Mossman, 1940). In contrast to that of *Sciurus*, both the baculum and os clitoridis are vestigial (Flyger and Gates, 1982). The coiled vagina, unique to *Tamiasciurus* (Mossman, 1940), may function to produce secretions at the time of breeding (Smith, 1968). Likewise, the reduced size of the baculum, Cowper's gland, and bulbourethral gland (nearly absent), as well as the enlarged seminal vesicles and elongated penis, likely represent counteradaptations of the male to allow efficient penetration and transfer of sperm (Smith, 1968). The testes descend into the scrotum at 3–4 months of age (Layne, 1954) and are pigmented and nearly hairless by 10 months (Flyger and Gates, 1982). The eight mammae become pigmented with the first pregnancy and remain so for life (Flyger and Gates, 1982).

The breeding season lasts from 4 to 5 months (Koford, 1982; Smith, 1965). The limited information available on litter sizes of Douglas' squirrels indicates that the species typically has 4–8 young/litter (Smith, 1965, 1981). Mean (± *SE*) litter sizes for 2 and 3 litters, in Manning Provincial Park, British Columbia, in 1962 and 1963, respectively, was 4.0 ± 0.0 and 5.7 ± 1.2. Individual females also may produce two litters per year, especially when food is abundant (Cowan and Guiget, 1956; Koford, 1982; Smith, 1968, 1981); however, in most years it is unlikely that Douglas' squirrels fully realize their reproductive potential (Smith, 1981). Smith (1965) reported a year in which failure of cone crops in all conifers except lodgepole pine resulted in 100% of 35 *T. douglasii* failing to breed, as well as a positive relationship between earlier breeding and the use of cones stored from the previous year. No information is available on growth and development.

ECOLOGY. Douglas' squirrels typically are associated with forests of fir (*Pseudotsuga, Abies*), spruce (*Picea*), and hemlock (*Tsuga*) from the Transition to the Hudsonian life zones. Analyses of habitat use in old-growth and younger, managed forests fail to identify any significant predictors of microhabitat requirements (Carey, 1995), although squirrels are three times more abundant in old-growth forests, which is considered higher quality habitat because of the greater abundance and reliability of conifer cones (Buchanan et al., 1990). Densities also may be high in other habitats in which food supply is elevated (Sullivan and Sullivan, 1982).

Mean (±2*SE*) densities (per ha) of Douglas' squirrels are 0.2 (±0.0) in Douglas-fir (*Pseudotsuga menziesii*) forests of southern Oregon, <0.01 (±0.00) in western hemlock (*Tsuga heterophylla*) of the western Olympic Peninsula, Washington, and 0.5 (± 0.6) in western hemlock of the northern Cascade Range of Washington (Carey, 1995). Densities are most directly related to abundance of food and territoriality (Carey, 1995; Smith, 1965, 1968; Sullivan and Sullivan, 1982).

Throughout their range, and especially in coniferous forests, all species of *Tamiasciurus* vigorously defend exclusive territories against conspecifics and other competitors (Gurnell, 1984; Kemp and Keith, 1970; Rusch and Reeder, 1978; Smith, 1968, 1981). Defense of these territories occurs year-round but is most obvious in the autumn when squirrels are provisioning middens with cones. Territories are typically centered around food larderhoards (primarily cones) and the nest (Smith, 1968). The primary proximate factors influencing territoriality (and territory size and shape) are the availability, type, and distribution of food (Gurnell, 1987; Smith, 1968, 1981). Range overlap and breakdown in territoriality may occur when defensible foods are not available, especially in the spring (Gurnell, 1987; Smith, 1968). Territorial conflicts have been described by Smith (1965, 1968), and detailed accounts of territory establishment following the death or removal of a territory holder is described for *T. hudsonicus* by Gurnell (1984, 1987) and Price et al. (1986).

While territoriality of Douglas' squirrels is likely to limit densities through the spacing of individuals, population densities are likely to vary with availability of food, especially cone crops (Smith, 1968; Sullivan and Sullivan, 1982). Sullivan and Sullivan (1982) report a 5–10-fold increase in density following a two-year food supplement (442 kg of sunflower seeds and oats), primarily as a result of immigration, higher reproduction by females, and increased juvenile survival rates.

Minimum survival rates of Douglas' squirrels (expressed as the number of juveniles captured per total number of resident lactating females) during the first 4 weeks of life varies between 1.00 and 2.00, well below that reported for *T. hudsonicus* (Dolbeer, 1973; Kemp and Keith, 1970; Smith, 1968).

The diet of Douglas' squirrels consists almost entirely of reproductive structures of fungi, conifers, and angiosperms, and the cambium of pine (Flyger and Gates, 1982; Gurnell, 1987; McKeever, 1964; Smith, 1965, 1968). Other occasional items include the stalks and fronds of ferns, leaves, flowers, arthropods, and bone (McKeever, 1964; Smith, 1965). Consumption of bone is performed most frequently (1.4–1.9% of observation time) by juveniles and pregnant and lactating females; adult males spend <0.05% of their time eating bone (Smith, 1968). Other animal material, including young birds or nestlings, also may be taken on occasion (Adams, 1939).

A volumetric analysis of stomach contents of 206 animals in Lassen County, California, revealed that tree seeds and fungi are the most common foods in the diet (total mean of diet = 91.9%). Mean stomach volumes by month range from 3% (spring) to 60% (February) for tree seeds and from 33% (February) to 91% (June) for fungi; an inverse relationship between volume of seeds and fungi throughout the year is evident. Cambium, obtained from shoots cut from the tips of pine branches, is a major dietary component in winter and spring (January–May) and accounts for 40–63% of the volume of stomachs at that time (McKeever, 1964). Specific items reported in the diet of *T. douglasii* include true truffles (Ascomycetes); the Basidiomycetes *Chroogomphus rutilus, Gomphidius subroseus, Cortinarius, Pholiota lenta, Russula brevipes, Suillus granulatus, S. tomentosa, Hydnum fuliginineo-violaceum, H. imbricatum, Gautieria graveolens, Rhyzopogon pachyphloeus, R. rubescens,* and *Peridermium harknessii* (hyphae in *Pinus contorta* bark); seeds of lodgepole pine (*P. contorta*), western white pine (*P. monticola*), ponderosa pine (*P. ponderosa*), western hemlock (*Tsuga heterophylla*), Engelmann spruce (*Picea engelmannii*), Douglas-fir (*P. menziesii*), Pacific silver fir (*Abies amabilis*), subalpine fir (*A. lasiocarpa*), grand fir (*A. grandis*), and mountain hemlock (*T. mertensiana*); seeds of cottonwood (*Populus trichocarpa*), vine maple (*Acer circinatum*), dwarf maple (*A. glabrum*), and alder (*Alnus*); pollen of lodgepole pine, Pacific silver fir, and Douglas-fir; and fruit or seeds of larger twisted stalk (*Streptopus amplexifolius*) and highbush blueberry (*Vaccinium*—Smith, 1968). Douglas' squirrels also consume and store hazel nuts (*Corylus cornuta* var. *californica*), often rejecting nuts infested with insects (Mailliard, 1931). The species also is reported to readily consume conifer seeds infested with *Caloscypha fulgens*, as well as sporocarps of the seed pathogen. Free water often is not available to *T. douglasii* and may be obtained from fungi, which often contain 90–95% water by mass (Smith, 1965).

Both species of *Tamiasciurus* selectively harvest cones from species of tree with the highest seed-energy per cone, then concentrate on the species of tree with the next highest energy value. In mixed stands, cones are harvested first from Pacific silver fir, then Douglas-fir, Engelmann spruce, and western hemlock. Selection between individual trees of a species begins when squirrels are feeding on the species with the least energy per cone (Smith, 1965, 1968, 1970). For *T. hudsonicus*, and probably *T. douglasii* as well, cone selection is based on number of seeds per cone, ratio of seed weight to cone weight, cone hardness, the arrangement of cones on the branch (Elliot, 1974), and the distance from the midden where cones are harvested (Elliot, 1988). Such foraging patterns are predicted to exert strong selective pressures on the evolution of cone morphology and suggests coevolutionary interactions between squirrels and conifers (Elliot, 1974; Lindsay, 1986; Smith, 1965, 1970). The energetic value (energy per seed kernel, number of seeds per fruiting body, and energy of squirrel food per fruiting body) of several species of conifer and angiosperm used for food by Douglas' squirrels is summarized by Smith (1970, 1981).

Predation of Douglas' squirrels is considered relatively rare (Flyger and Gates, 1982; Gurnell, 1987; Layne, 1954; Smith, 1965) and no direct reports of predation are available. Pine martens (*Martes americana*) are known to rely on subnivean cavities associated with cone caches of Douglas' squirrels for winter resting sites (Spencer, 1987), and the northern spotted owl (*Strix occidentalis caurina*), a common inhabitant of forests of Douglas-fir and western hemlock, may also prey on Douglas' squirrels (Carey, 1995). Alarm calls are frequently given in the presence of many of these species (Smith, 1978), and its smaller body size may aid in agility and predator avoidance (Smith, 1965).

Little information is available on the parasites of *Tamiasciurus douglasii*, probably owing to the limited nuumber of surveys. Only 1 helminth and 10 species of ectoparasites are reported from *T. douglasii*. These include the nematode *Baylisascaris procyonis* (Coates et al., 1995); the ticks, *Dermacentor variabilis* (Monsen, 1993) and *Ixodes angustus* (Easton and Goulding, 1974); the mites, *Chatia cunninghamae* (Goff and Brennan, 1980), *Dermacarus* (Pence and Webb, 1977), *Euschoengasta* (chigger stage—Easton, 1975), and *Hirstionyssus affinis* (Herrin, 1970); the lice, *Enderleinellus tamiasciurini* (Kim, 1966) and *Hoplopleura sciuricola* (Spencer, 1966); and the flea, *Monopsyllus ciliatus* (Holland, 1963). Prevalence and detection of borrelial spirochetes harbored by ticks (*D. variabilis*) of *T. douglasii* has been reported (Monsen, 1993), and a single case of encephalitic nematodiasis is reported that resulted from infection by *Baylisascaris procyonis* (Coates et al., 1995).

Tamiasciurus douglasii is likely to compete with its congener *T. hudsonicus* in the Blue Mountains of eastern Oregon and the Cascade and Coastal ranges of northcentral Washington and southwestern British Columbia, where individuals of both species are found together in a zone of overlap of 15 to >30 km. Several areas of sympatry represent the transition between dense, moist coastal forests of conifers and the dry interior forests of lodgepole pine. However, the generally parapatric ranges of the two species suggest competitive exclusion, possibly due to the prohibitive energetic costs required for the partitioning of habitat and food resources resulting from their territorial social system and the variability in their food supply (Smith, 1968, 1981). Smith (1981) reported that the two species differed in at least five characters that provided each with a competitive edge within its respective habitat. Two characters relate to predator avoidance (alarm calls and pelage color) and three involve efficiency of resource acquisition (jaw strength, body size, and reproductive rate). Smith (1981) argued that the smaller body size and reduced jaw musculature of Douglas' squirrels may provide this species with an advantage in exploiting the smaller, softer cones and catkins; however, *T. douglasii* is known to feed on harder cones in several parts of its range. Densities of Douglas' squirrels are observed to be higher where those of northern flying squirrels (*Glaucomys sabrinus*) and Townsend's chipmunks (*Tamias townsendii*) are lowest (Carey, 1995), suggesting a strong potential for competition with these two species.

In the Cascade Range of southern British Columbia, where *T. douglasii* occurs on the west side of the range and *T. hudsonicus* in the rain shadow on the eastern side of the range, it was argued that both species coevolved with the conifers on which they feed (Smith, 1970). To the west in the damp forests of the Pacific Coast and Sierra Nevada and southern Cascade Ranges where *T. douglasii* is found, lodgepole pine is less abundant, possesses softer cones, and exhibits greater fluctuations in cone crops with frequent crop failures, compared with the east where lodgepole pine produces hard, serotinous cones and a nearly year-round food source for *T. hudsonicus* (Smith, 1965, 1970). Smith (1970) suggested that the weaker jaw musculature, greater population fluctuations, and greater overall reproductive potential of *T. douglasii* result from these contrasting conifer and habitat characteristics. Multivariate analysis of 30 cranial characters of Douglas' squirrels ($n = 791$) from sites from the opposite ends of the species range reveal a strong relationship between cranial morphology and the morphology of conifer cones in associated habitats (Lindsay, 1986), suggesting local adaptation to food resources. The smallest squirrels were reported from forests of spruce, hemlock, and redwood, where cones are smallest and possess the least amount of energy per cone. In contrast, larger squirrels and squirrels with larger cranial features were associated with forests with larger cones containing more energy (Lindsay, 1986). It should be noted, however, that such conclusions may be in part due to other factors related to the sites selected for this comparison.

Feeding activity of Douglas' squirrels can result in significant damage and economic loss to forests. Primary causes of damage (Flyger and Gates, 1982) include heavy loss to cone crops (Adams, 1955; Franklin, 1964; Shellhammer, 1966; Smith, 1965, 1968) and direct damage to trees as a result of consumption of buds and shoots, and bark stripping for consumption of phloem and cambial tissues (Fisch and Dimock, 1978; Hosley, 1928; McKeever, 1964; Smith, 1968; Walters and Soos, 1961). Damage appears to be most influenced by proximity of stands to mature forests (Fisch and Dimock, 1978) and may be more common during periods of low cone production (Fisch and Dimock, 1978; Smith, 1968; Walters and Soos, 1961). Damage, due to clipping of terminal shoots by Douglas' squirrels, is reported for red fir *(Abies magnifica)* and Douglas-fir and may be more extensive than realized, as such activity is often attributed to other species (Fisch and Dimock, 1978). Shoot clipping in sapling stands of Douglas-fir, recorded at 16 locations across western Washington and Oregon over several years, resulted in ≤38% damage to planted stands, suggesting strong interference with regeneration (Fisch and Dimock, 1978). Use of diversionary food during food shortages may be an effective method to reduce stand damage (Sullivan and Klenner, 1993). The seed-pathogenic fungus *Caloscypha fulgens*, found in the cone caches of Douglas' squirrels, is thought to be dispersed by the species (Sullivan et al., 1984). Douglas' squirrel is harvested for its fur in Canada (Flyger and Gates, 1982; Obbard et al., 1987).

Because of its vocalizations and territoriality, Douglas' squirrel is easily studied by direct observations (Smith, 1968); however, live-trapping, radiotelemetry, nest counts, and signs of feeding and larderhoarding also are effective techniques (Gurnell, 1984, 1987). Ability to trap Douglas' squirrels is reported to be lowest during the summer months (<40%), and higher on trapping grids than on a trap line (McKeever, 1961; Sullivan and Sullivan, 1982). Squirrels can be restrained in a cloth or mesh wire cone to reduce stress and mortality during handling (Yahner and Mahan, 1992). The Kania trap is recommended over pole snares for humane kill-trapping of this species (Proulx et al., 1993). Smoked aluminum track plates may be used to determine presence of Douglas' squirrels but are generally ineffective for estimating actual indices of density or abundance (Carey and Witt, 1991). Far-infrared thermal imaging has been shown to be an effective method for detecting free-ranging pine squirrels and may prove to be more cost-effective than traditional methods of censusing (Boonstra et al., 1994). Mahan et al. (1994) reported two methods of remote tagging (with fluorescent-colored, cable-tie collars), which allows members of the genus to be tagged without handling.

BEHAVIOR. Douglas' squirrels are diurnal (Gurnell, 1987). Direct observations on activity are restricted to those of Smith (1965, 1968) in which it was reported that diel activity is bimodal in spring through autumn (with peaks in morning and late afternoon) and unimodal in winter, with a midday peak (Gurnell, 1987; Smith, 1968). Activity likely is limited by extreme cold, heavy preciptation, and strong winds (Gurnell, 1987; Smith, 1965)

Douglas' squirrels are promiscuous (Gurnell, 1987) and their breeding behavior is nearly indistinguishable from that of *T. hudsonicus* (Koford, 1979, 1982; Smith, 1965, 1968). The mating system involves both intrasexual competition among males (Koford, 1982; Smith, 1965, 1968) as well as epigamic selection by females, usually by means of avoidance of dominant males (Koford, 1979, 1982).

Males congregate in or near the territory of an estrous female (Smith, 1965); but unlike many other species of tree squirrels, subordinate Douglas' squirrels are less likely to pursue the female. However, whereas estrous females spend >95% of their time in association with dominant males and <5% with subordinates, they frequently mate with subordinates (6 of 11 mountings—Koford, 1982).

Breeding activity has been observed as early as 0900 h, 4.5 h after the initiation of normal activity, and as late as 30 min prior to sunset. During the mate chase a single dominant male actively pursues a female, while displaying to subordinate males with low aggressive calls, territorial calls, or chases. Chases may occur as often as once every 2 min, last from a few seconds to 5 min, and take place over distances up to 17 m. During chases, females feed and wait for the dominant male to return (Smith, 1965).

Mounting and copulation usually occur several times in the afternoon of the one day the female is receptive (Koford, 1982; Smith, 1965). Copulation, most often observed on the ground or in the lower branches of trees, lasts between a few seconds and 25 min (Koford, 1982; Smith, 1965). It is suggested that initiation of copulation is controlled more by the female and cessation of the behavior by the male (Smith, 1965). During copulation the male holds the female around the posterior abdomen while resting his head on her back (Gurnell, 1987; Smith, 1965). The copulating pair then orients towards attacking males which may interrupt copulation (Smith, 1965). Both males and females engage in grooming of the genitals with the mouth and forefeet before and after copulation (Smith, 1965).

Little is known about the dispersal of young. However, detailed studies on dispersal of *T. hudsonicus* (Larsen and Boutin, 1994) suggest that establishment of territories close to that of the mother may be important for survival.

Both Douglas' and pine squirrels produce complex vocalizations that are critical for the maintenance of territories, courtship, and other aspects of social behavior (Gurnell, 1987; Smith, 1978). Five calls of similar structure and function are produced by the two species (Smith, 1965, 1968). In approximate order of the frequency of use, these include the chirp (with acoustic frequency of 1–8 kHz), an alarm call given in the presence of potential predators; the rattle call (0.5–2 kHz), a threat call involved in territorial defense; a variable screech call, used often in conjunction with rattles; growls (0.5–2 kHz), used during aggressive defense or by a female during an approach by a male or by any adult; and buzz calls (5–6.5 kHz), used by males in approach to females.

Chirp calls of *T. douglasii* are comprised of longer notes, are lower and less variable in frequency (1–2 kHz), and are more difficult to localize than those of *T. hudsonicus* (Smith, 1978). Additionally, note duration of rattle calls and buzz calls and the internote interval of rattle calls are significantly longer for *T. douglasii* (Smith, 1978). Smith (1965, 1978) suggested that these differences may reflect selection for reduced echoing due to thicker canopy cover in the habitat of *T. douglasii.*

The chirp call, the most common vocalization, consists of 1–100 notes, may last as long as 1 h and can be detected up to 100 m. The rattle call, detectable up to 130 m, usually lasts about 1–10 s, although longer calls are given in response to territory violators (Smith, 1968). Rattle calls are considered to function primarily to regulate spacing of squirrels in relation to limited resources such as food, habitat, or an estrous female (Smith, 1968). However, a functional analysis of calls of *T. hudsonicus* suggested that the rattle is associated primarily with courting of the female and is produced significantly more often in conjunction with screeches; aggression of the caller is only associated with the rattle call when given together with the screech (Lair, 1990).

The growl is interpreted as a signal used in motivational conflicts to elicit change in the receiver's behavior, and the buzz, a signal used in nonaggressive approaches by the caller (Lair, 1990). Growls and buzzes are only audible for short distances (up to 3 and 30 m, respectively—Smith, 1978).

Squeak (1–2 kHz) and buzz calls of Douglas' squirrels also are used by young to call to the mother (Gurnell, 1987; Smith, 1968) and are the first vocalizations to develop. All other threat and distress calls first appear when the young leave the nest at weaning (Prescott, 1979). Significant individual variation in structure and patterns of vocalization is evident. While it is not known whether such differences are used for individual recognition by squirrels, strong selection for individual recognition is likely for a species such as the Douglas' squirrel which maintains permanent territiories (Smith, 1978). Scent marking by cheek rubbing, usually while feeding, resting, and grooming, results in deposition of saliva and secretions from sebaceous glands (Ferron, 1983).

Douglas' squirrels are larderhoarders, stockpiling cones and seeds of conifer in one or a few middens located near the center of the territory (Smith, 1965; Vander Wall, 1990). Middens are economically defensible against competitors and may contain enough food to last one or more seasons. It is critical that middens be moist enough to maintain viability of conifer seeds and prevent cones from opening (Shaw, 1936), which also may prevent pilfering by other rodents or birds (Smith, 1968; Vander Wall, 1990). Douglas' squirrels will on occasion position middens near springs or bogs to maintain moisture levels (Vander Wall, 1990).

GENETICS. The chromosome number is 2n = 46 (Nadler and Hoffmann, 1970). A parsimony analysis of allelic distributions, based on electrophoretic studies, suggested that *Tamiasciurus* is more closely related to the *Sciurus-Microsciurus* clade than is *Sciurillus,* thus supporting previous arguments (Bryant, 1945; Ellis and Maxon, 1980; Hight et al., 1974) that *Tamiasciurus* be included with the New World tree squrrels (Sciurini—

Hafner et al., 1994). Previous suggestions of hybridization between *T. hudsonicus* and *T. douglasii* in a zone of sympatry in areas of British Columbia, Washington, and Oregon (Hall, 1981; Hatton and Hoffmann, 1979; Smith, 1965) were questioned on the basis of the morphological distinctiveness of the two (Lindsay, 1982). Lindsay (1982) concluded that reproductive isolation between the two species is complete. Similar conclusions are advanced for the relationship between *T. douglasii* and *T. mearnsi* (Hoffmann et al., 1993; Lindsay, 1981).

REMARKS. It is not clear at the present whether *T. mearnsi* is a full species, as the morphometric studies of Lindsay (1981) indicate, or whether it is a subspecies of *T. douglasii,* as indicated by genetic comparisons (B. S. Arbogast, in litt.). The name *Tamiasciurus* is derived from the Greek words *Tamias,* meaning animal who caches food, *skia,* meaning shadow, and *oura,* meaning tail (Gurnell, 1987). Alternative vernacular names of this species include pine squirrel or chickaree (Cowan and Guiguet, 1956), although pine squirrel usually refers to *T. hudsonicus.* I thank K. Munroe, B. Sacolic, and G. Turner for their assistance. K. Klemow produced the final map.

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Editors for this account were LESLIE N. CARRAWAY, KARL F. KOOPMAN, AND ELAINE ANDERSON. Managing editor was BARBARA H. BLAKE.

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