**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 Sciuriini, 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*
2. Underparts yellowish or rust colored (but can be white) ............... 2
2. *T. douglasii*
   Pale gray dorsally with reddish-yellow dorsal band; ventor light yellow; interorbital breadth usually >14.5 mm .......................................................... *T. mearnsi*

**Tamiasciurus douglasii** Bachman, 1839

*Douglas’ Squirrel*


*Sciurus multi-pilosus* Audubon and Bachman, 1841:102. Type locality “east of northern California.” According to Grinnel (1933:121) “somewhere in southern Oregon.”

*Sciurus balcheri* Gray, 1842:263. Type locality “mouth of Columbia River.”


*Sciurus hudsonicus* Allen, 1890:165. Type locality from “Blue Lake, 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 (*balcheri* and *suckleyi* are synonyms).

*T. d. multifilosus* Audubon and Bachman, 1841:102, see above (*orarius* and *ecuadensis* 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, grayer dorsal and yellow-tinted underparts, as well as its conspicuous vocalizations and territorial behavior (Flyer and Gates, 1982; Gurnell, 1987). The tail of tamiwsciurids is flatter and smaller in proportion to body size (<40%) and lacks the longitudinal bands typical of other tree squirrels (Flyer 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 ventral 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 (Flyer and Gates, 1982; Ingles, 1965). Although not sympatric with *T. douglasii*, *T. mearnsi* (formerly included in *douglasii*)—Hoffmann et al., 1953; 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., 1953; 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 ventor, is most pronounced in the summer and absent or faint in winter (Flyer 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 vellos, 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 (Flyer 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 hind foot, 41–55; and ear length, 19–31 (Cowen and Guiguet, 1956; Flyer and Gates, 1982; Hall, 1981; Smith, 1965). Although Douglas’ squirrels are not considered sexually dimorphic (Flyer 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 zygoma and a rostrum laterally compressed with a flattened frontal area. Auditory bullae are slightly inflated and the braincase is depressed posteriorly. Condylar 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

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**FIG. 1. Tamiasciurus douglasii** (photograph by R. B. Forbes).
length, $12.73 \pm 0.41$; length of maxillary tooth row, $8.11 \pm 0.22$; width of M2, $2.56 \pm 0.08$; width of P, $2.22 \pm 0.10$; breadth at M3, $6.22 \pm 0.26$; pterygoid width, $3.93 \pm 0.23$; height of foramen magnum, $6.21 \pm 0.26$; width of foramen magnum, $7.54 \pm 0.23$; nasal width, $7.61 \pm 0.31$; and breadth of infraorbital foramen, $7.43 \pm 0.39$.

**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, southwest along the coast of northern California to San Francisco, and southward through the Sierra Nevada Mountains to southercentral California (Fig. 3; Flyer 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 Guignard, 1936; 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 (Cowen and Guignard, 1936; Dakquest, 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 (Poeck, 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 $\times$ 10 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 Lendelius, 1994; Kurtén and Anderson, 1980).

**FORM AND FUNCTION.** The dental formula of *T. douglasii* is 1/1, c 0-0, p 1-2/1, m 3/3, total 20 or rarely 22 (Flyer and Gates, 1982; Hall, 1981). Incisors exhibit indeterminant growth, and malocclusion is likely when damage occurs and toothwear is prevented (Layne, 1954; Smith, 1984).
Tammiasciurus douglasi is exhibited 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 mid-May to late-June, and the autumn molt takes place in early October (Banfield, 1974). Detailed descriptions on molt 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, 1967).

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, and for juveniles, 514, 602, and 505, 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 arctic and 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 (Machiski and Shump, 1979). Sclerocytes, 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 Tammiasciurus 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 Scandaler, 1971; Kemp and Keith, 1970), closure of the epiphyses (Davis and Scandaler, 1971), and possibly tooth wear, cementum annuli (Fog and Mosby, 1978; Smith, 1981), and suspensorial tuberosities (Colburn, 1986). An epiphyseal notch at the distal end of the femur is evident up to 8 months of age (Davis and Scandaler, 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. douglasi 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 ± 0.061 for T. douglasi 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 midlateral 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 their 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. douglasi 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 tammiasciurids differ significantly from those of other tree squirrels (Mossman, 1940). In contrast to that of Sciurus, both the baculum and os clitoris are vestigial (Flyger and Gates, 1982). The coiled vagina, unique to Tammiasciurus (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 ± 0.1 and 5.7 ± 1.2. Individual females also may produce two litters per year, especially when food is abundant (Cowan and Guignet, 1956; Koford, 1982; Smith, 1968, 1981); however, in most years it is unlikely that Douglas' squirrels fully realize their reproductive potential (Smith, 1981). Smith (1981) has reported a number of southern Cascade Range of Washington (Carey, 1995). Densities are most directly related to abundance of food and territoriality (Carey, 1995, 1996; Smith, 1965, 1968; Sullivan and Sullivan, 1982).

Throughout their range, and especially in coniferous forests, all species of Tammiasciurus 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 midden with cones. Territories are typically centered around food larderbanks (primarily cones) and the nest (Smith, 1960). The primary proximate factors influencing territoriality (and territory size and shape) are the availability, type, and distribution of food (Gurnell, 1987; Smith, 1965, 1981). Range overlap and breakdown in territoriality may occur when defensive 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, 1965; 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 (Dalbeattie, 1973; Kemp and Keith, 1970; Smith, 1968).

The diet of Douglas' squirrels consists almost entirely of reproductively structures of fungi, conifers, and angiosperms, and the chestnut of pine (Phytophthora, 1962; Gurnell, 1967; McKeever, 1964; Smith, 1965, 1968). Other occasional items include the stalks and fronds of ferns, leaves, flowers, arthropods, and algae (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, 1969). 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 = 49.7%). 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 (Aescopyctes); the Basidiomycetes Rhizopogon patellatus, Geomyces subrubescens, and Pseudoloma betulina granulatus, S. tomentosa, Hydmus fuliginosus-violaceus, H. imbricatum, Gasteria graveolens, Rhizopogon 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), and Jeffrey's pine (P. jeffreyi); Acer heterophyllus, 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 (Maillard, 1931). The species also is reported to readily consume conifer seeds infested with Calocypis fulgens, as well as sporecarps 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, 1968).

Both species of Tasmiaclaria 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 cones (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 seed for food by Douglas' squirrels is summarized by Smith (1970, 1981).

Predation of Douglas' squirrels is considered relatively rare (Flyer and Gates, 1982; Gurnell, 1967; 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 Douglas' squirrel nests in winter (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 predation avoidance (Smith, 1968).

Little information is available on the parasites of Tasmiaclaria douglasii; these include the nematode Baylisascaris procyonis (golus, 1955); the ticks, Dermacentor variabilis (Mason, 1958) and Rhipicephalus sanguineus (Ansell, 1962); the mites, Chitinotus cuniculi (Goff and Brennan, 1980), Baylisascaris procyonis, and Rhipicephalus sanguineus (Ansell, 1962). Prevalence and distribution of barrellial spirochetes harbored by ticks (D. variabilis) of T. douglasii has been reported (Mason, 1993), and a single case of encephalitic nematodiasis is reported that resulted from infection by Baylisascaris procyonis (Coates et al., 1993). Tasmiaclaria douglasii is likely to compete with its congeners T. hudsonicus in the Blue Mountains of eastern Oregon and the Cascade and Coastal ranges of north-central 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 forest of lodgepole pine. However, the generally parapatic ranges of the two species suggest competitive exclusion, possibly due to the prohibitive energetic costs of partitioning of communal 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 characteristics 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 castkims; 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 coexisted without competition with each other (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 (Flyer and Gates, 1966) include heavy loss to crop 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, 1966; Walters and Soos, 1961). Damage appears to be most influential of stands of moist 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 Galoscypha 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 (Flyer and Gates, 1982; Oblad 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 landings of also are effective techniques (Gurnell, 1984, 1987). Ability to track 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 Sittman, 1982). Squirrels can be restrained in a cloth or mesh wire cone to reduce stress and facilitate handling (Yahner and Mahan, 1992). The fur-infrared thermography 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 census (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 daily activity is hibernal 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 precipitation, and strong winds (Gurnell, 1987; Smith, 1965).

Douglas’ squirrels are promiscuous (Gurnell, 1987) and their breeding cycle is distinct 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 (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, 1968). Males and females engage in grooming of the genitals with the mouth and forefoot 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 4–8 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; groargs (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 (5.6–5.5 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 dancing 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 12 m, usually lasts about 1–10 s, although longer calls are given in response to perceived 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 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).

Speeak (1–2 kHz) and buzz calls of Douglas’ squirrels also are used by young to call 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 territories (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 pillaging by other rodents or birds (Smith, 1968; Vander Wall, 1990). Douglas’ squirrels will occasionally 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 allele distributions, based on electron microscopy of several loci, shows that T. douglasii is more closely related to the Sciurini-Microtus clade than is Sciurillus, thus supporting previous arguments (Bryant, 1945; Ellis and Mason, 1980; Hight et al., 1974) that Tamiasciurus be included with the New World tree squirrels (Sciurini—
Hafner et al., 1994). Previous suggestions of hybridization between *T. Hudsonicus* and *T. douglassii* in a zone of sympathy in areas of British Columbia, Washington, and Oregon (Hail, 1961; 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. douglassii* and *T. mexicanus* (Hoffmann et al., 1995; Lindsay, 1981).

**REMARKS.** It is not clear at the present whether *T. mexicanus* is a full species, as the most recent studies of Lindsay (1981) indicate, or whether it is a subspecies of *T. douglassii*, as indicated by genetic comparisons (B. S. Arborgast, in litt.). The name *Tamiasciurus* is derived from the Greek words *Tamias*, meaning animal which catches food, *skia*, meaning shadow, and *oura*, meaning tail (Gurnell, 1987). Alternative vernacular names of this species include pine squirrel or chipmunk (Cowen and Guignet, 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.

**LITERATURE CITED**

**ADAMS, L. 1939.** Sierra chickaree eats young blue-fronted jays. Yosemite Nature Notes, 18:93.


Sullivan, T. P., and D. S. Sullivan. 1982. Barking damage by snowshoe hares and red squirrels in lodgepole pine stands in


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M. A. STEELE, DEPARTMENT OF BIOLOGY, WILKES UNIVERSITY, WILKES-BARRE, PENNSYLVANIA 18766.