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Tamiasciurus hudsonicus.

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***Tamiasciurus hudsonicus* (Erxleben, 1777)**

Pine Squirrel

[Sciurus vulgaris] hudsonicus Erxleben, 1777:416. Type locality "mouth of Severn River, Hudson Bay, Ontario." Based on "Hudson Bay Squirrel" of Pennant (cited in Howell, 1936*b*).
Sciurus rubrolineatus Desmarest, 1822:333. Eastern United States.
Sciurus lanuginosus Bachman, 1839:101. Type locality Fort McLaughlin, Campbell Island, British Columbia.
Sciurus richardsoni Bachman, 1839:100. Type locality from head Big Lost River, Custer Co., Idaho.
Sciurus fremonti Audubon and Bachman, 1853:237. Type locality "Rocky Mountains," probably park region of central Colorado (Hall, 191).
Tamiasciurus hudsonicus Pocock, 1923:213, first use of current name combination.
Tamiasciurus regalis Howell, 1936*a*:1. Type locality "Belle Isle, Isle Royale, Michigan."

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciurognathi, Family Sciuridae, Subfamily Sciurinae, Tribe Sciurini, Genus *Tamiasciurus*. The genus contains two species (and possibly a third—Lindsay, 1981). Twenty five subspecies of *Tamiasciurus hudsonicus* are recognized (Hall, 1981):

T. h. abieticola Howell, 1929:75. Type locality "Highlands, North Carolina."
T. h. baileyi Allen, 1898:261. Type locality "Bighorn Mountains (alt. 8,400 ft.), [Washakie Co.], Wyoming."
T. h. columbiensis Howell, 1936*b*:135. Type locality "Raspberry Creek (about 30 mi SE of Telegraph Creek), northern British Columbia."
T. h. dakotensis Allen, 1894:325. Type locality "Squaw Creek, Black Hills, [Custer Co.], South Dakota."
T. h. dixiensis Hardy, 1942:87. Type locality "near Further Water, 9,500 ft., Dixie National Forest, Pine Valley Mts., Washington Co., Utah."
T. h. fremonti Audubon and Bachman, 1853:253, see above (*wasatchensis* is a synonym).
T. h. grahamensis Allen, 1894:350. Type locality "Graham Mountains, Graham Co., Arizona." Restricted entirely to Graham Mts. (Hall, 1981).
T. h. gymnicus Bangs, 1899:28. Type locality "Greenville near Moosehead Lake, [Piscataquis Co.], Maine."
T.h. hudsonicus Erxleben, 1777:416, see above (*rubrolineatus* is a synonym, but in view of its "type locality" may not belong here).
T. h. kenaiensis Howell, 1936*b*:136. Type locality "Hope, Cook Inlet, Alaska." Reported only from the Kenai Peninsula (Hall, 1981).
T. h. lanuginosus Bachman, 1839:101, see above (*vancouverensis* is a synonym).
T. h. laurentianus Anderson, 1942:31. Type locality Lac Marchant, near Moisie Bay, Saguenay Co., N shore Gulf of St Lawrence, Quebec.
T. h. loquax Bangs, 1896:161. Type locality "Liberty Hill, [New London Co.], Connecticut."
T. h. lychnuchus Stone and Rehn, 1903:18. Type locality "Forks of Ruidoso, Lincoln Co., New Mexico" (*ruidoso* is a synonym).
T. h. minnesota Allen, 1899:640. Type locality "Fort Snelling, [Hennepin Co.], Minnesota" (*murii* is a synonym).
T. h. mogollonensis Mearns, 1890*b*:277. Type locality "Quaking Asp Settlement, near summit of Mogollon Mts., [Coconino Co.], Central Arizona" (*neomexicanus* is a synonym). The often cited earlier reference (Mearns, 1890*a*:49) is of very dubious validity.
T. h. pallescens Howell, 1942:13. Type locality "8 mi E of Upham, McHenry Co., North Dakota."
T. h. petulans Osgood, 1900:27. Type locality "Glacier, White Pass, Alaska (alt. 1,870 feet)."
T. h. picatus Swarth, 1921:92. Type locality "Kupreanof Island, 25 mi S of Kake Village at southern end of Keku Straits, SE Alaska."
T. h. preblei Howell, 1936*b*:133. Type locality "Fort Simpson, Mckenzie District, Northwest Territories."
T. h. regalis Howell, 1936*a*:1, see above.
T. h. richardsoni Bachman, 1839:100, see above.
T. h. streatori Allen, 1898:267. Type locality "Ducks, British Columbia."
T. h. ungavensis Anderson, 1942:33. Type locality "Woswonaby Post" (Lake Waswanipi), Abitibi District, Quebec.
T. h. ventorum Allen, 1898:263. Type locality South Pass City, Wind River Mts., Fremont Co., Wyoming.

DIAGNOSIS. *Tamiasciurus hudsonicus* is easily distinguished from other tree squirrels by its smaller body size (<30% of that of the gray squirrel, *Sciurus carolinensis*), its deep reddish color, and its territorial behavior. Where its range borders that of *T. douglasii* (in the Pacific Northwest), it is distinguished by color of pelage. The venter of *T. hudsonicus* is all white or white with a faint yellowish wash, whereas that of *T. douglasii* is rust colored or reddish, often with a blackish wash (Gurnell, 1987; Hall, 1981; Ingles, 1965). Tail hairs have yellowish to rusty tips with black band, as compared with those of *T. douglasii,* which are white-tipped with a black band (Gurnell, 1987; Ingles, 1965).

GENERAL CHARACTERISTICS. *Tamiasciurus hudsonicus* is a diurnal tree squirrel that is easily recognized by its small size (200–250 g), reddish dorsum, and white venter (usually demarcated by dark lateral lines, especially in summer), slightly tufted ears (in winter), and a white eye ring (Fig. 1). Dorsal surface is reddish, feruginous brown, or olivaceous gray, usually with a distinctive reddish or brownish median band (Hall, 1981). The tail is smaller and flatter than that of other tree squirrels and varies in

FIG. 1. *Tamiasciurus hudsonicus* from Fairbanks, Alaska. Photograph by J. O. Wolff.

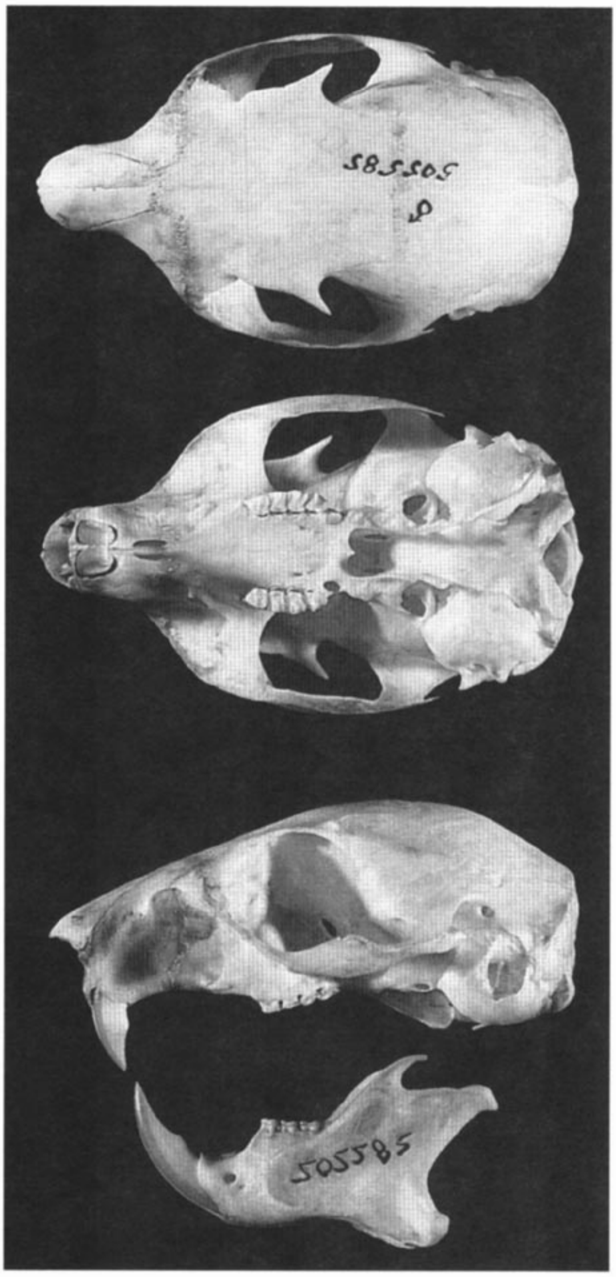

FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of mandible of *Tamiasciurus hudsonicus* (male, Frederick Co., Maryland, National Museum of Natural History, Smithsonian Institution 505580). Greatest length of cranium is 45.5 mm. Photographs courtesy of Smithsonian Institution.

color from yellowish-gray to rusty red and is often grizzled (Flyger and Gates, 1982; Hall, 1981); a dorsal median band of black often extends the entire length of tail.

Ranges of external measurements (in mm) for *T. hudsonicus* (Fig. 1) are as follows: total length, 270–385; length of tail, 92–158; length of hind foot, 35–57; length of ear, 19–31 (Cowan and Guiguet, 1956; Flyger and Gates, 1982; Hall, 1981; Smith, 1965). Adult body mass ranges from 197.3 to 282.2 g (Smith, 1965). Significantly larger males are reported from southwestern British Columbia (Flyger and Gates, 1982; Smith, 1965).

The skull (Fig. 2) is relatively short with laterally expanded zygomata, and the rostrum is laterally compressed with a flattened frontal area. Auditory bullae are slightly inflated and the braincase is depressed posteriorly. Condylobasal length is 42–50 mm. Cranial measurements for 102 specimens are reported by Lindsay (1981).

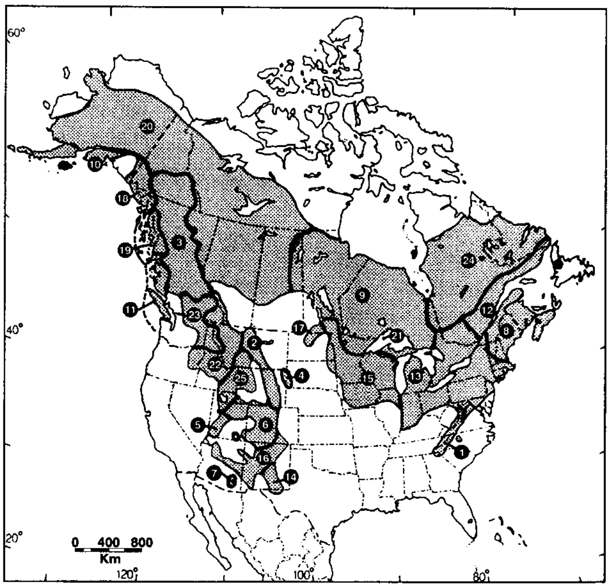

FIG. 3. Distribution of *Tamiasciurus hudsonicus* in North America: 1, *T. h. abietcola*; 2, *T. h. baileyi*; 3, *T. h. columbiensis*; 4, *T. h. dakotensis*; 5, *T. h. dixiensis*; 6, *T. h. fremonti*; 7, *T. h. grahamensis*; 8, *T. h. gymnicus*; 9, *T. h. hudsonicus*; 10, *T. h. kenaiensis*; 11, *T. h. lanuginosus*; 12, *T. h. laurentianus*; 13, *T. h. loquax*; 14, *T. h. lychnuchus*; 15, *T. h. minnesota*; 16, *T. h. mogollonensis*; 17, *T. h. pallescens*; 18, *T. h. petulans*; 19, *T. h. picatus*; 20, *T. h. preblei*; 21, *T. h. regalis*; 22, *T. h. richardsoni*; 23, *T. h. streatori*; 24, *T. h. ungavensis*; 25, *T. h. ventorum* (modified from Flyger and Gates, 1982; Hall, 1981).

Pelage aberrations are relatively rare in the pine squirrel, although melanism (Allen, 1898; Linzey and Linzey, 1971; Mengel and Jenkinson, 1971), albinism (Wood, 1965), and white spotting are recorded (Layne, 1954). A completely melanistic population is reported from New Brunswick (Adams, 1873).

Although body size among tree squirrels tends to increase with latitude, the pine squirrel is the smallest species, yet occurs at the highest latitudes (Heaney, 1984; Reynolds, 1985). Gurnell (1987) suggests that their smaller size may result from selection for increased foraging agility in the smaller branches of conifer trees, rather than for competition for seed resources, as suggested by Heaney (1984) for other tree squirrels. Few studies have examined intraspecific variation in body size, although clinal variation is reported in the Lake Superior region. Skull and mandibular dimensions increase with increasing distance from the lake, possibly in response to harsher climates (Kramm et al., 1975).

DISTRIBUTION. *Tamiasciurus hudsonicus* occurs across much of boreal Canada and the northern United States from Alaska to the Atlantic Ocean in the north, and southward into western, southwestern, and southeastern USA in the Cascade, Rocky, and Appalachian Mountains, respectively (Fig. 3—Armstrong, 1972; Hall, 1981; Ingles, 1965; Linzey and Linzey, 1971). Its affinity for northern boreal vegetation contributes to a distribution that is considerably more fragmented than indicated by most range maps. In the southern Appalachians populations are isolated primarily on mountaintops >500 m, although a few disjunct populations do occur at lower elevations (Linzey and Linzey, 1971), at least one as far east as Winston-Salem, North Carolina (Webster et al., 1985). In the western USA the species reaches its southern range limit in Arizona and New Mexico, where it is restricted to subalpine and mixed coniferous forests on mountains >2,500 m (Brown, 1984).

In the Pacific northwest the species occurs on most coastal islands, including all of Vancouver Island where it is separated from mainland populations by those of *T. douglasii*. (Cowan and Guiguet, 1956; Lindsay, 1982). Although *T. hudsonicus* and *T. douglasii* are generally allopatric, zones of sympatry occur along a parapatric border in southeastern British Columbia (Smith, 1965, 1970, 1981), northwestern Washington (Cowan and Guiguet, 1956; Dalquest, 1948), and eastern Oregon (Hatton and Hoffmann, 1979). Recent studies (Lindsay, 1982) have dismissed suggestions of hybridization in these areas (Hatton and Hoffmann, 1979; C. C.

Smith, 1968) and instead implicate character convergence in transitional forests containing habitat suitable for both species. The species was introduced to Newfoundland in 1963 and has since expanded its range (Hall, 1981).

FOSSIL RECORD. *Tamiasciurus* likely diverged from *Sciurus* in the late Pliocene (Hafner, 1984). *T. hudsonicus* is first reported from the Irvingtonian (Conard Fissure, Cumberland, Trout) and now is recorded from more than 30 late Rancholabrean faunas from the central and eastern United States (Graham and Lundelius, 1994; Kurtén and Anderson, 1980). A larger extinct subspecies, *T. h. tenuidens* (Hay), is reported from Cavetown, Cumberland, Natural Chimneys, New Paris No. 4, and Whitesburg (Guilday et al., 1964). Records of the species in a fauna are indicative of boreal vegetation, cooler climates (Guilday et al., 1964), and a more southerly historical distribution (Blair, 1971).

FORM AND FUNCTION. The dental formula of *T. hudsonicus* is i 1/1, c 0/0, p 1 or 2/1, m 3/3, total 20 or rarely 22 (Flyger and Gates, 1982; Hall, 1981). Incisor growth is indeterminate and malocclusions are reported (Layne, 1954; Smith, 1984).

The species exhibits two annual molts (Flyger and Gates, 1982; Layne, 1954; Nelson, 1945), although the tail molts only once annually (Layne, 1954). The spring molt, occurring from late March through August, starts on the nose and front feet, and continues posteriorly, ending on the rump and rear edge of the hind limbs (Layne, 1954). The fall molt (late August-early December) begins on the tail and then progresses to the rump and the head before the legs and flank. The length of juvenile molt is variable, beginning after 12 weeks of age, between late June and early September (Layne, 1954).

The baculum and os clitoris are vestigial (Layne, 1952), in contrast to that of *Sciurus* (Flyger and Gates, 1982). The penis is long, slender, and symmetrical, the Cowper's gland reduced, and the bulbar gland absent (Flyger and Gates, 1982; Mossman, 1940). The testes descend into the scrotum at 3–4 months of age (Layne, 1954), and the scrotum is pigmented and nearly hairless by 10 months (Flyger and Gates, 1982). A coiled vagina is unique to *Tamiasciurus* (Mossman, 1940). The eight mammae become pigmented with the first pregnancy and remain so for life (Flyger and Gates, 1982). Seasonal changes in the structure of male and female reproductive tracts in New York are detailed by Layne (1954).

Metabolic rate for adult squirrels ranges from 143 to 168 kcal/kg (Grodinski, 1971). Estimates of energy budgets (kcal kg^{-1} day^{-1}) for free-ranging adult (ca. 240 g) and subadult squirrels (ca. 160 g), respectively, are as follows: consumption, 514, 620; assimilation, 369, 448; metabolic waste, 146, 260. Total energy requirements for lactating females may exceed 75% that of males (C. C. Smith, 1968).

Irving et al. (1955) reported a basal metabolism of 1.50 cm^3 O_2 g^{-1} hr^{-1} (80% higher than that predicted by body weight, possibly due to hyperactivity of animals), a lower critical temperature of 20°C, and a thermal conductance of 0.085 cm^3 O_2 g^{-1} hr^{-1}. Oxygen consumption of 12 pine squirrels (mean ± 1 *SE*, 35 measurements) at 10°C was 2.16 ± 0.05 for animals at rest, and 1.4–2.8 times higher when running. Velocity of running (V = km/hr), angle of inclination (G = sine of the angle of incline), and ambient temperature T_A) all significantly affect metabolic rate (M) according to the equation, $M = \text{alpha}\ [1.50 + 0.085(20 - T_A)] + 0.77V + 1.67VG$, although metabolic estimates based on this equation are less accurate below thermoneutrality (Wunder and Morrison, 1974).

While body size of pine squirrels is small and insulative ability low (Irving et al., 1955), body temperature is high for mammals (Grodinski, 1971; Irving and Krog, 1954), suggesting adaptations for extreme cold. Abdominal temperature (T_B) for two captive squirrels in Manitoba was 35.9–41.4°C (<39.0°C inside the nest; >39.0°C outside), indicating the potential for heterothermy (Pauls, 1979). Inside the nest T_B is positively correlated with T_A; outside the nest (above 15°C) T_B is negatively correlated with T_A. A rapid decline in T_B occurs during subnivean activity (Pauls, 1979). Pine squirrels have brown adipose tissue in the thoracic and cervical regions, especially during autumn and winter (Aleksiuk, 1970, 1971).

Seasonal variation in water balance was measured by Bakko (1975). Osmotic urine concentrations are lowest in July (<500 mOsM/l) and highest in autumn (>1,000 mOsM/l). Maximum ratios of urine to plasma (± 1 *SE*), which measure the ability of the kidney to concentrate urine, are 4.74 ± 0.64 (*n* = 12) for field-collected squirrels and 4.16 ± 0.80 (*n* = 6) for captive squirrels. Although pine squirrels may drink water or eat snow (Klugh, 1927; Layne, 1954), C. C. Smith (1968) reported that free water is rarely available to them and seldom drunk when present. The mean (± 1 *SE*) relative medullary thickness of the kidney (5.79 ± 0.08) is significantly larger than that of gray squirrels and may reflect an adaptation to withstand water deprivation and account for the use of a wide variety of arboreal habitats. The relative medullary thickness of the kidney is also reported to be significantly lower for pine squirrels from river bottoms than for those from upland forests (Bakko, 1975).

Mean mass of the brain is 4.42 g (Meier, 1983). Mean organ masses (in g) for males and females, respectively, are as follows: kidneys, 1.39, 1.37; heart, 1.63, 1.54; lungs, 2.62, 2.45; liver, 5.94, 6.54; spleen, 0.45, 0.50; and adrenals, 0.091, 0.087 (Layne, 1954). Sebaceous, sudoriferous, and mucous glands present in the oral region (Quay, 1965) may function in scent marking (Flyger and Gates, 1982). The eyes are well adapted to daytime vision (Flyger and Gates, 1982), and reasonably capable of night vision (Dippner and Armington, 1971).

In the field adults 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 in males and pigmented teats on females that have reproduced (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) and closure of the epiphyses (Davis and Sealander, 1971).

REPRODUCTION AND ONTOGENY. Pine squirrels are spontaneous ovulators (Layne, 1954; Millar, 1970). Females are in estrus only 1 day and conception usually occurs within a few hours of mating (C. C. Smith, 1968).

Precise calculations of gestation period are limited. Mean gestation time is 33 days (range of 31 days, 20 h to 35 days, 3 h, for five litters—Ferron and Prescott, 1977; Lair, 1985). The estimated gestation time of 40 days reported by Hamilton (1939) is questionable and may render other calculations (Layne, 1954; C. C. Smith, 1968) inaccurate.

Mean litter sizes (derived from counts of corpora lutea, placental scars, embryos, and/or nest young) from seven localities throughout the range (Davis, 1969; Ferron and Prescott, 1977; Kemp and Keith, 1970; Layne, 1954; Millar, 1970; C. C. Smith, 1968; Wood, 1967) vary from 3.2 to 5.4. Pine squirrels typically produce one litter a year, especially in the western and northwestestern portion of their range (Davis, 1969; Dolbeer, 1973; Hatt, 1943; Kemp and Keith, 1970; C. C. Smith, 1968). Two litters a year occur frequently in the eastern United States, one in spring (March–May) and a second in summer (late July–early September—Layne, 1954; Linzey and Linzey, 1971). Two breeding seasons may occur in southern Quebec (Wrigley, 1969) and occurred in a single, mild year in British Columbia (Millar, 1970). Harsher conditions at northern latitudes and higher elevations most likely limit reproduction to a single breeding season (Ferron and Prescott, 1977; Millar, 1970). Yearly variation in female reproduction is also common; a 51% decrease in number of breeding females over 2 years occurred in British Columbia (C. C. Smith, 1968), and 30% and 20% increases in successive years were recorded in Colorado (Dolbeer, 1973) and Alberta (Kemp and Keith, 1970), respectively.

Seasonal variation in reproductive patterns in New York is reported for 440 specimens and 116 live animals (Layne, 1954). Frequency of female estrus is highest February–March and June–July, pregnancy peaks March–April and July–August, and lactation occurs primarily April–May and August–September. External condition of the female genitalia and teats correspond well with stage of reproductive cycle (Layne, 1954). In Colorado conception is estimated to occur April–June (Dolbeer, 1973). In New York enlargement of testes occurs in November and December, further development of the prostate and seminal vesicles in January, and fully developed gonads from February to August (Layne, 1954); gravid and lactating individuals are reported as late as 29 September and 19 October, respectively (Hamilton, 1939). With few exceptions (4 of 116 specimens), sperm are present in the cauda epididymis of all testes >15 mm in length and 1,000 mg in weight. Partial regression of the prostate and vesicles occurs in April and May when females are reproductively inactive. Testes, prostate, and vesicles are fully regressed between September and November (Layne, 1954).

Growth and development of young are reported by Svihla (1930) for two litters and by Layne (1954) for 23 litters; Layne (1954) detailed ontogenetic changes in body mass and external and skeletal dimensions up to 19 weeks of age. Young are born pink and hairless except for vibrissae and fine chin hairs. The external auditory meatus is patent at 18 days, eyes open at 26–35 days, and pelage is fully developed by 40 days. Dentition is complete and external and skeletal measurements reach adult size by 125 days; full body mass is attained some time thereafter (Layne, 1954). Young are active outside the nest by 7 weeks, weaned by 8 weeks, and fully independent a few weeks after weaning (Layne, 1954; Nice et al., 1954).

Maximum longevity for pine squirrels is 10 years in the wild (Walton, 1903) and 9 years in captivity (Klugh, 1927), although most squirrels rarely live >5 years (Halvorson and Engeman, 1983; Gurnell, 1987). Differential mortality between the sexes has been inferred (Hurly, 1987) from the male-biased adult sex ratios (Davis and Sealander, 1971; Hurly, 1987; Rusch and Reeder, 1978; C. C. Smith, 1968).

ECOLOGY. Pine squirrels prefer boreal coniferous forests that provide abundant conifer seeds, fungi, and interlocking canopies for efficient foraging and escape from predators (Flyger and Gates, 1982; Rusch and Reeder, 1978; C. C. Smith, 1968; Vahle and Patton, 1983). Cool, moist conditions in these forests may aid in the preservation of middens and promote fungal growth (Rusch and Reeder, 1978; C. C. Smith, 1968). Suboptimal habitats occupied by pine squirrels include planted stands of Norway spruce (*Picea abies*) and red pine (*Pinus resinosa*) in Colorado (Gurnell, 1984), aspen (*Populus*), and mixed coniferous-deciduous stands in Pennsylvania and New York (Mahan and Yahner, 1992; Yahner, 1986, 1987), as well as hedgerows throughout the range (Layne, 1954; Yahner, 1980). The species occurs in seven distinct habitat types in New York (beech-maple-hemlock, mixed hardwoods with scattered conifers, old orchards, hedgerows, parks, building sites), suggesting that it may be more versatile in its requirements than gray squirrels (Layne, 1954). Herbaceous density, canopy cover, and proximity to tree cavities, underground burrows, and logs were the most significant proximate factors determining trap success in marginal habitat in Pennsylvania (Mahan and Yahner, 1992).

Nest site selection by pine squirrels has been examined in detail in white spruce (*Picea glauca*) forests of Alaska (Dice, 1921), lodgepole pine (*Pinus contorta*) forests of Wyoming (Rothwell, 1979), whitepine (*P. strobus*) and spruce-hemlock (*Tsuga canadensis*) forests of New York (Hatt, 1929), and mixed coniferous forests of British Columbia (Fancy, 1980). Nest site selection in *Tamiasciurus hudsonicus* is most critical for winter survival and thermoregulation (Irving et al., 1955; C. C. Smith, 1968), efficient winter use and protection of food caches (Finley, 1969; Hatt, 1929, 1943; Layne, 1954; C. C. Smith, 1968), and avoidance of predators (Fancy, 1980; Hatt, 1929, 1943; Rothwell, 1979; C. C. Smith, 1968). Most nests are constructed within 30 m of cone caches (Hatt, 1929, 1943; Layne, 1954; C. C. Smith, 1968). Where available, *T. hudsonicus* prefers natural cavities (Hamilton, 1939; Layne, 1954), but due to the lack of such resources in coniferous forests, it constructs leaf nests or occasionally underground nests in subterranean cavities (Fancy, 1980; Hatt, 1929; Klugh, 1927; Yahner, 1980). A single ground nest has been reported by Mayfield (1948). Tree diameter, branching structure, and especially the availability of canopy escape routes are the most important proximate factors influencing nest-tree selection (Fancy, 1980; Rothwell, 1979; Vahle and Patton, 1983). Nests are found at heights of 2–20 m (Hatt, 1929). Nest material varies with habitat but typically includes grasses, mosses, inner cambium, shredded bark, leaves, feather, and fur (Fancy, 1980).

Densities range between 0.3 and 2.0 squirrels/ha (Gurnell, 1987), and populations may be limited by the availability of food (Erlien and Tester, 1984). Long-term experiments with food supplements resulted in a 3–4 fold increase in density (Sullivan, 1990; Sullivan and Klenner, 1992); however, Koford (1992) argues that these estimates may be inflated by movement of non-resident squirrels onto sites with food supplements. A significant drop from densities of 1.2–1.5 squirrels/ha has been reported following selective and clear cutting of commercial forests in Alaska (J. O. Wolff, in litt.).

Sex ratios (male : female), based on animals that were trapped or shot, vary from 0.71:1 to 1.12:1 in embryos (Davis and Sealander, 1971; Layne, 1954), from 1.12:1 to 1.30:1 in nestlings (Davis and Sealander, 1971; Layne, 1954), from 1.06:1 to 2.40:1 in juveniles (Davis and Sealander, 1971; Erlien and Tester, 1984; Kemp and Keith, 1970; Rusch and Reeder, 1978; C. C. Smith, 1968), and from 1.08:1 to 1.33:1 in adults (Davis and Sealander, 1971; Kemp and Keith, 1970; Rusch and Reeder, 1978). Greater numbers of juvenile males may reflect greater activity or increased mobility as a result of fewer territory acquisitions by males (Gurnell, 1987; C. C. Smith, 1968), rather than a male bias at birth (Davis and Sealander, 1971). Male-skewed ratios of adults peak during autumn (1.63:1—Davis and Sealander, 1971) and the breeding season (1.57:1—Kemp and Keith, 1970).

Measures of age-specific survivorship (Halvorson and Engeman, 1983), time-specific survivorship (Kemp and Keith, 1970; Rusch and Reeder, 1978), and other estimates based on pooled age classes (Davis and Sealander, 1971; Erlien and Tester, 1984) reveal a Type III survivorship curve, with >60% mortality occurring in the first year of life, >80% by the second, and a plateau in mortality (>90% mortality) by the third. Mortality rates of >60% are reported for nestlings (70 days) in Yukon and Alberta (Boutin and Larsen, 1993). Pine squirrels born in a year of high seed crops may show higher survivorship (Halvorson and Engeman, 1983), although food supplementation experiments generally do not result in increased survival rates (Boutin and Larsen, 1993; Sullivan, 1990). Females tend to exhibit higher survivorship than males (Boutin and Larsen, 1993; Erlien and Tester, 1984; Halvorson and Engeman, 1983). The annual population cycle is characterized by a peak in density during summer following recruitment of young and a gradual decline through autumn and winter (Gurnell, 1987; Rusch and Reeder, 1978).

Extensive reviews of the diet of pine squirrels are provided by Gurnell (1987), Hatt (1929), Layne (1954), and C. C. Smith (1968). Pine squirrels are primarily granivorous, but they are also opportunistic in the absence of mast foods. Primary diet items vary with habitat and include the seeds of conifers, oak (*Quercus*), hickory (*Carya*), beech (*Fagus*), walnut (*Juglans*), yellow poplar (*Liriodendron tulipifera*), sycamores (*Platanus*), and maple (*Acer*—Hatt, 1929; Layne, 1954; C. C. Smith, 1968). Both epigeous and hypogeous mycorrhizal fungi are also important during summer and other periods of food shortage (Gurnell, 1987; C. C. Smith, 1968; M.C. Smith, 1968). Pine squirrels consume at least 45 species of fungi in the Cascade Mountains (C. C. Smith, 1968). Secondary food items in approximate order of relative importance include tree buds and flowers, fleshy fruits, tree sap, bark, insects, and other animal material (Hamilton, 1939; Hatt, 1929; Layne, 1954; Linzey and Linzey, 1971). Pine squirrels prey on bird eggs, hatchlings, adult birds (Layne, 1954; Rathcke and Poole, 1974; Reitsma et al., 1990), eastern cottontails (*Sylvilagus floridanus*), and gray squirrels (Hamilton, 1934). During winter, spring, and early summer, bark stripping and tree girdling for consumption of phloem and cambial tissues is common (Hosley, 1928; Linzey and Linzey, 1971; Pike, 1934). Pine squirrels also eat the bark of rust galls (Salt and Roth, 1980) as well as sap from sugar maple trees (*Acer saccharum*) in the northeast (Hamilton, 1939; Hatt, 1929; Heinrich, 1992; Kilham, 1958; Klugh, 1927; Layne, 1954) and yellow birch (*Betula alleghaniensis*) in the Great Smoky Mountains (Linzey and Linzey, 1971). Widespread, systematic sugar tapping by pine squirrels occurs in New England (Heinrich, 1992).

Pine squirrels are likely prey for snakes, owls, hawks, and a number of carnivorous mammals (e.g., martens and fishers, *Martes*; weasels, *Mustela*, various canids and felids—Gurnell, 1987), although specific reports of predation are few (Flyger and Gates, 1982; Gurnell, 1987; Hatt, 1929; Layne, 1954; Smith, 1965). Significant predation on *T. hudsonicus* are reported for the following: Cooper's hawks (*Accipiter cooperii*; 4% of 853 animals brought to 34 nests); goshawks (*A. gentilis*; 31% of 185 animals brought to 14 nests—Meng, 1959); pine martens (*Martes americana*; 12–20% of the total diet—Bursick and MacDonald, 1984; Sherburne and Bissonette, 1993). Other known predators of *T. hudsonicus* include lynx (*Lynx lynx*), mink (*Mustela vison*), red fox (*Vulpes vulpes*), bald eagle (*Haliaeetus leucocephalus*), great gray owl (*Strix nebulosa*), great horned owl (*Bubo virginianus*), American kestrel (*Falco sparverius*), red-shouldered hawk (*Buteo lineatus*), northern harrier (*Circus cyaneus*), red-tailed hawk (*B. jamaicensis*), sharp-shinned hawk (*A. striatus*—Flyger and Gates, 1982; Luttich et al., 1970; Nellis and Keith, 1968; Smith, 1965), and timber rattlesnake (*Crotalus horridus*— Linzey and Linzey, 1971).

Comprehensive surveys of the parasites of pine squirrels are provided for animals in New York (Layne, 1954), Alberta (Mahrt and Chai, 1972), and Manitoba (Rausch and Tiner, 1948). Incidence of botfly (*Cuterebra emasculator*) infection (Dorney, 1965), quantitative data on four species of *Eimeria* (Dorney, 1966), and incidence of trypanosomes (Dorney, 1967) reveal potential for host regulation by parasites. Parasite species reported from the pine squirrel, compiled from Flyger and Gates (1982) and additional sources, include 4 protozoans, 9 nematodes, 9 cestodes, 31 mites and ticks, 8 lice, 25 fleas, and 1 dipteran larva.

The potential for interspecific competition is probably most intense between the pine squirrel and its congener *Tamiasciurus douglasii*; their parapatric ranges suggest competitive exclusion, possibly due to the prohibitive energetic costs required for the partitioning of food resources (C. C. Smith, 1968). Pine squirrels in Colorado are absent from ponderosa pine forests, where they may be excluded by Abert's squirrels (*Sciurus aberti*; Ferner, 1974) by exploitative competition (Gurnell, 1987). Across most of the east, pine squirrels are likely to compete with gray squirrels (*S. carolinensis*), especially for nest cavities, although it is unlikely the two species are especially aggressive towards each other (Ackerman and Weigl, 1970). Habitat specialization in relation to food resources, rather than competition, best explains the local distribution of these two species (Riege, 1991).

Economic losses due to pine squirrels are often extensive. Specific causes of damage, reviewed in detail by Flyger and Gates (1982), include interference with reforestation of conifers (e.g.,white pine, jack pines, ponderosa pine; table mountain pine, *Pinus pungens*) resulting from consumption of 60–100% of cone crops and direct damage to trees as a result of bud consumption and bark stripping. Bark stripping and tree girdling for consumption of phloem and cambial tissues, most common during periods of food shortage (Hosley, 1928; Linzey and Linzey, 1971; Pike, 1934; Stilliger, 1944), result in up to 37% damage to conifer stands (Sullivan and Sullivan, 1982; Sullivan and Vyse, 1987; Sullivan et al., 1993). Use of diversionary food during food shortages, however, significantly reduces damage to lodgepole pine (Sullivan and Klenner, 1993). Damage is most influenced by proximity of stands to mature forests, frequency of cone crops, and availability of shrub cover for protection from predators (Sullivan et al., 1994). Next to muskrat (*Ondatra zibethica*) and beaver (*Castor canadensis*), the pine squirrel is the most commonly harvested furbearer in Canada (Kemp and Keith, 1970; Obbard, 1987).

BEHAVIOR. Pine squirrels are diurnal (Gurnell, 1987), but on occasion they exhibit nocturnal activity (references in Layne, 1954). Diel activity is bimodal (with peaks in morning and afternoon) in spring and summer, equally distributed throughout the day during fall, and unimodal in winter, usually peaking in midday (Deutch, 1978; Pauls, 1978; Pruitt and Lucier, 1958).

Heavy rains, snow, and high winds may result in reduced activity (Gurnell, 1987; Layne, 1954; Pauls, 1978), although pine squirrels are unlikely to remain in the nest for more than 1 day without foraging (Pauls, 1978). For captive animals in Winnipeg, intensity of activity, locomotor activity, and time spent out of the nest are all positively correlated with air temperature (Pauls, 1978). Nevertheless, a negative relationship between activity and temperature is reported for temperatures of 10–35°C (Clarkson and Ferguson, 1969). Complete inactivity below −31.6°C (Pruitt and Lucier, 1958) is probably due to increased use of subnivean tunnels for winter foraging (Pruitt and Lucier, 1958; C. C. Smith, 1968; Zirul and Fuller, 1970). Food supplementation also results in reduced activity outside the nest, less time spent foraging, and an earlier shutdown in daily activity (Deutch, 1978). Ferron et al. (1986) report that reproductive constraints do not affect the activity of males and females differently.

Although mate pairings may occur, both during and outside the breeding season (references in Layne, 1954), pine squirrels are generally characterized as promiscuous (Hamilton, 1939; Layne, 1954; C. C. Smith, 1968). Males typically invade the territory of estrous females and actively pursue females in obvious mate chases (C. C. Smith, 1968). Females may mate with more than one male (Smith, 1965).

During mate chasing a single dominant male actively pursues a female, while driving off approaching subordinate males with low aggressive calls, territorial calls, or direct chases. Mounting and copulation, lasting several minutes, usually occurs several times in the afternoon of the only day the female is receptive (Smith, 1965). Copulation, most often observed on the ground or in the lower branches of trees, is frequently initiated by the female and terminated by the male. During copulation the male holds the female around the posterior abdomen while resting his head on her back, and both males and females engage in grooming of the genitals before and after copulation (Gurnell, 1987; Smith, 1965).

Pine squirrels are larderhoarders (Smith and Reichman, 1984). Beginning in late summer and continuing through autumn, squirrels cut female conifer cones and store them in one or a few central middens (Finley, 1969; C. C. Smith, 1968; Yeager, 1937). Middens serve as a central larder that is economically defensible against competitors and provides a moist, cool environment that prevents cones from opening and making seed available to competitors (C. C. Smith, 1968). Middens vary in size and number depending on habitat, food availability, and individual squirrel (Gurnell, 1984), contain enough food to last one to two seasons (Gurnell, 1984; M. C. Smith, 1968), and are often used by several generations of squirrels (Gurnell, 1987). In the eastern USA and Canada pine squirrels also frequently engage in scatterhoarding, which may account for 85% of all hoards and >50% of all cones stored (Hurly and Robertson, 1986), but provides enough cones to last <37 days (Dempsey and Keppie, 1993). Middens of *T. h. grahamnensis* exhibit significantly greater foliage volume, canopy closure, basal area, volume of downed logs, and density of snags than random sites in spruce-fir and transitional forests of Graham Mt., Arizona (Smith and Mannan, 1994).

Pine squirrels are highly selective in their foraging behavior, first harvesting cones from the tree species with the highest seed energy per cone, and then concentrating on the tree species with the next highest energy value. Discrimination between individual trees begins when they feed on the species with the least energy per cone (Smith, 1970). Cone selection is based on the number of seeds/cone, ratio of seed weight to cone weight, cone hardness, arrangement of cones on the branch (Elliot, 1974), and the distance from the midden to where cones are harvested (Elliot, 1988).

Throughout most of their range, and especially in coniferous forests, both male and female pine squirrels vigorously defend exclusive territories against conspecifics and other competitors (Gurnell, 1984; Kemp and Keith, 1970; Rusch and Reeder, 1978; C. C. Smith, 1968, 1981). Defense of these territories occurs year-round, but it is most obvious in the autumn when squirrels are stockpiling cones and when competition from subordinate animals is often intense. In mixed forests pine squirrels often hold both permanent (prime) and transient territories. Transient territories are established in winter by subordinate animals in mostly deciduous stands (Kemp and Keith, 1970). Similarly, in New York forests dominated by deciduous trees, pine squirrels exhibit overlapping home ranges and occasionally defend only nests and caches from intruders (Layne, 1954). Intraspecific interactions other than those involved in maintaining a territory may occur when ranges overlap, especially in the spring when animals are feeding on male cones (Gurnell, 1987; C. C. Smith, 1968). The primary proximate factors influencing territoriality (and territory size and shape) are the availability, type, and distribution of food (Gurnell, 1984, 1987; C. C. Smith, 1968, 1981).

Territories, typically centered on the midden, are circular in shape (Rothwell, 1977), which may minimize time and energy to provision the larderhoard (C. C. Smith, 1968, 1981). Mean territory sizes vary with habitat and location but are usually 0.24–0.98 ha (Fancy, 1980; Hatt, 1929; Klugh, 1927; Rothwell, 1977; Rusch and Reeder, 1978; C. C. Smith, 1968) although M. C. Smith (1968) reports larger territories (1.6–4.8 ha) in Alaska during and after mast failure, and Sullivan (1990) observed a reduction in territory sizes of 24–50% in response to supplemental food. Mean estimates (±1 *SD*) of territory size (in ha), as reviewed by Gurnell (1987), are as follows: 0.66 (±0.45) in jack pine (*Pinus banksiana*), 0.35 (±0.7) in mixed spruce (*Picea*), and 0.24 (±0.07) in white spruce of Alberta (Rusch and Reeder, 1978); 0.51 (±0.18) in western hemlock (*Tsuga heterophylla*) and 0.91 (±0.20) in lodgepole pine of British Columbia (C. C. Smith, 1968); 0.60 (±0.13) in lodgepole pine of Colorado (Gurnell, 1984); 0.28 (±0.09) in mixed conifer and 0.48 (±0.16) in lodgepole pine of Wyoming (Rothwell, 1977). Territory sizes typically required to sustain a pine squirrel in Alberta through an entire year are estimated to be <1 ha (Rusch and Reeder, 1978).

Territorial conflicts have been described by Kilham (1954) and C. C. Smith (1968); detailed accounts of territory establishment, following the death or removal of a territory holder, are provided by Gurnell (1984, 1987) and Price et al. (1986). Young and subordinate squirrels quickly identify vacant territory space, move to the center of the range, and then circle the periphery to ward off competitors. Control of the territory is usually established within a few hours (Gurnell, 1987; Price et al., 1986; C. C. Smith, 1968), although territory holders must regularly patrol boundaries to maintain control (Ferron, 1979; Gurnell, 1987; Kilham, 1954). Territory overturn is relatively common and some squirrels may occupy a different territory each year (Rothwell, 1977). Removal experiments indicate high site and boundary tenacity following takeover of a territory (Price et al., 1986). Prior to dispersal and territory establishment, young make forays up to 900 m (mean of 126 m), but eventually they settle adjacent to or near (<323 m) their mothers' territories (Larsen and Boutin, 1994). Offspring that settle farther from the natal territories experience greater predation risks but often secure larger territories and experience higher overwintering survival (Larsen and Boutin, 1994).

Although juveniles frequently disperse from natal territories (Boutin et al., 1993; Price et al., 1986), post-breeding dispersal by adult females and juvenile philopatry appear common in this species (Boutin et al., 1993; Price et al., 1986). Females may expand their territory to include additional resources prior to dispersal (Boutin and Schweiger, 1988), then "bequeath" part or all of their territory to the young (Price, 1992; Price and Boutin, 1993) and disperse to neighboring territories (Boutin et al., 1993; Price et al., 1986). This strategy appears to increase juvenile survival (Boutin et al., 1993), as predation risks significantly increase when young move off natal territories (Larsen and Boutin, 1994).

Pine squirrels depend on vocalizations for maintenance of territories and for courtship (Lair, 1990; Gurnell, 1987; Smith, 1978). Five calls are considered important in adult behavior: the chirp (1–2 kHz; an alarm call given in the presence of potential predators); a rattle call (0.5–2 kHz; a threat call involved in territorial defense); a variable screech call (used alone or in sequence with rattles); a growl (0.5–2 kHz; used during aggressive defense or by a female during an approach by a male, or by any adult); and a buzz call (5–6.5 kHz; used by males in approach to females—Smith, 1978). A contextual, field analysis of calls suggests that an additional threat call is used as an honest signal of the territory holder's intention to chase intruders and that the rattle call is a "signature" often used by courting males in approach to females (Lair, 1990). Alarm calls to predators may function to announce an animal's presence and thereby reduce chance of attack (Smith, 1978). Squeak (1–2 kHz) and buzz calls, used by young to call to the mother, are the first vocalizations to develop (Gurnell, 1987; C. C. Smith, 1968). Scent marking, usually performed when the animal is feeding, resting, and grooming, takes the form of cheek-rubbing, which results in deposition of saliva and secretions from sebaceous glands (Ferron, 1983).

Homing experiments indicate that pine squirrels possess information on direction but not distance when displaced (600–2,000 m—Bovet, 1984). Route-based visual information enhances homing ability (Bovet, 1991).

Two phases in the development of behavior are identified. Early ontogeny involves the emergence of simple reflexes, vocalizations, and sleeping, resting and stretching postures (Ferron, 1981, 1984; Gurnell, 1987; Nice et al., 1954). Late ontogeny, characterized by the learning of adult behaviors, occurs after 4–5 weeks of age and involves the development of grooming behavior (30–51 days), play behavior (37–43 days), agonistic interactions (e.g., biting, foot stamping, tooth chattering, jumping, crouch posture; 31–36 days), and adult activities (consumption of solid food, digging, nest building, and cheek rubbing; 37–45 days—Ferron, 1981). Play behavior involves object play, play-locomotion, mock attacks (Ferron, 1975), and sexual play and pseudo-copulatory behavior (C. C. Smith, 1968). Young pine squirrels improve feeding efficiency and feeding technique by observing adults (i.e., observational learning—Weigl and Hanson, 1980).

GENETICS. The diploid chromosome number is 46 (Nadler and Hoffmann, 1970). A probability analysis of allelic distribution (based on electrophoretic studies of *T. hudsonicus* and five species of *Sciurus*—Hafner et al., 1994) indicates that *Tamiasciurus* is closely related to the *Sciurus-Microsciurus* clade and should be grouped with the new world tree squirrels as suggested previously (Ellis and Maxon, 1980; Hight et al., 1974).

REMARKS. *Tamiasciurus* is derived from the Greek words *Tamias,* meaning animal who caches food, *Skia,* meaning shadow, and *oura,* meaning tail (Gurnell, 1987). Use of the name pine squirrel, rather than red squirrel, distinguishes this species from the European red squirrel (*Sciurus vulgaris*), which is often referred to as red squirrel in the literature. I thank K. Munroe and G. Turner for their assistance, and J. N. Layne and an anonymous reviewer for improving the manuscript. B. J. Sefchik completed the figures.

LITERATURE CITED

Ackerman, R., and P. D. Weigl. 1970. Dominance relations of red and gray squirrels. Ecology, 51:332–334.

Adams, A. L. 1873. Field and forest rambles. Henry S. King Company, London, 333 pp. (not seen, cited in Layne, 1954).

Aleksiuk, M. 1970. The occurrence of brown adipose tissue in the adult red squirrel (*Tamiasciurus hudsonicus*). Canadian Journal of Zoology, 48:188–189.

———. 1971. Seasonal dynamics of brown adipose tissue function in the red squirrel (*Tamiasciurus hudsonicus*). Comparative Biochemistry, 38:723–731.

Allen, J. A. 1894. Description of ten new North American mammals, and remarks on others. Bulletin of the American Museum of Natural History, 6:317–332.

———. 1898. Revision of the chickarees, or North American red squirrels (Subgenus *Tamiasciurus*). Bulletin of the American Museum of Natural History, 10:249–298.

———. 1899. The North American arboreal squirrels. The American Naturalist, 33:635–642.

Anderson, R. M. 1942. Six additions to the list of Quebec mammals with descriptions of four new forms. Annual Report 1941 of the Provacher Society: 31–43.

Armstrong, D. M. 1972. Distribution of mammals in Colorado. University of Kansas, Lawrence, 415 pp.

Audubon, J. J., and J. Bachman. 1853. The viviparous quadrupeds of North America. V. G. Audubon, New York, 3:1–349.

Bachman, J. 1839. Monograph of the species of squirrel inhabiting North America. Proceedings of the Zoological Society of London for 1838:85–103.

Bakko, E. B. 1975. A field water balance study of gray squirrels (*Sciurus carolinensis*) and red squirrels (*Tamiasciurus hudsonicus*). Comparative Biochemistry and Physiology, 51A:759–768.

Bangs, O. 1896. A review of the squirrels of eastern North America. Proceedings of the Biological Society of Washington, 10: 145–167.

———. 1899. A new race of chickaree. Proceedings of the New England Zoology Club, 1:28.

Blair, W. F. 1971. Distributional patterns of vertebrates in the southern United States in relation to past and present environments. Pp. 433–468, *in* The distributional history of the biota of the southern Appalachians. Part III. Vertebrates (P. C. Holt, R. A. Paterson, and J. P. Hubbard, eds.). Virginia Polytechnic Institute and State University, Research Division Monograph 4, Blacksburg, 306 pp.

Boutin, S., and K. W. Larsen. 1993. Does food availability affect growth and survival of males and females differently in a promiscuous small mammal, *Tamiasciurus hudsonicus*? Journal of Animal Ecology, 62:364–370.

Boutin, S., and S. Schweiger. 1988. Manipulation of intruder pressure in red squirrels (*Tamiasciurus hudsonicus*): effects on territory size and acquisition. Canadian Journal of Zoology, 66:2270–2274.

Boutin, S., Z. Tooze, and K. Price. 1993. Post-breeding dispersal by female red squirrels (*Tamiasciurus hudsonicus*): the effect of local vacancies. Behavioral Ecology, 4:151–155.

Bovet, J. 1984. Strategies of homing behavior in the red squirrel, *Tamiasciurus hudsonicus*. Behavioral Ecology and Sociobiology, 16:81–88.

———. 1991. Route-based visual information has limited effect on the homing performance of red squirrels, *Tamiasciurus hudsonicus*. Ethology, 87:59–65.

Brown, D. E. 1984. Arizona's tree squirrels. Arizona Game and Fish Commisson, Phoenix, 114 pp.

Buckner, C. H. 1964. Weasel versus squirrel in Sequoia National Park. Journal of Mammalogy, 24:99–100.

Bursick, S. W., and S. O. MacDonald. 1984. Seasonal food habits of marten in south-central Alaska. Canadian Journal of Zoology, 62:944–950.

Clarkson, D. P., and H. J. Ferguson. 1969. Effect of temperature upon activity in the red squirrel. American Zoologist, 9: 1110.

Cowan, I. McT., and C. J. Guiguet. 1956. The mammals of British Columbia. British Columbia Provincial Museum of Natural History and Anthropology Handbook No. 11, Victoria, British Columbia, 413 pp.

Dalquest, W. W. 1948. Mammals of Washington. University of Kansas Museum of Natural History Publications, 2:1–444.

Davis, D. W. 1969. The behavior and population dynamics of the red squirrel, *Tamiasciurus hudsonicus,* in Saskatchewan. Ph.D. dissertation, University of Arkansas, Fayetteville, 222 pp.

Davis, D., and J. A. Sealander. 1971. Sex ratio and age structure in two red squirrel populations in northern Saskatchewan. The Canadian Field-Naturalist, 85:303–308.

Dempsey, J. A., and D. M. Keppie. 1993. Foraging patterns of eastern red squirrels. Journal of Mammalogy, 74:1007–1013.

Desmarest, A. G. 1822. Mammalogie ou description des espèce de mammifères. *In* Encyclopédie méthodique, part 2:277–555. Agasse, Paris.

Deutch, R. S. 1978. Seasonal activity budget of the red squirrel (*Tamiasciurus hudsonicus*) in a southern Ohio deciduous forest. M.S. thesis, University of Dayton, Ohio, 84 pp.

Dice, L. R. 1921. Notes on the mammals of interior Alaska. Journal of Mammalogy, 2:20–28.

Dippner, R., and J. Armington. 1971. A behavioral measure of dark adaptation in the American red squirrel. Psychonomic Science (Section on Animal Physiology and Psychology), 24: 43–45.

Dolbeer, R. A. 1973. Reproduction in the red squirrel (*Tamiasciurus hudsonicus*) in Colorado. Journal of Mammalogy, 54: 536–540.

Dorney, R. S. 1965. Incidence of botfly larva (*Cuterebra emasculator*) in the chipmunk (*Tamias striatus*) and red squirrel (*Tamiasciurus hudsonicus*) in northern Wisconsin. Journal of Parasitology, 51:893–894.

———. 1966. Quantitative data on four species of *Eimeria* in eastern chipmunks and red squirrels. Journal of Protozoology, 13:549–550.

———. 1967. Incidence, taxonomic relationships and development of *lewisi*-like trypanosomes in Wisconsin Sciuridae. Journal of Protozoology, 14:425–428.

Elliot, P. F. 1974. Evolutionary responses of plants to seed eaters: pine squirrel predation on lodgepole pine. Evolution, 28: 221–231.

———. 1988. Foraging behavior of a central-place forager: field tests of theoretical predictions. American Naturalist, 131:19–174.

Ellis, L. S., and L. R. Maxson. 1980. Albumin evolution within new world squirrels (Sciuridae). American Midland Naturalist, 104:57–61.

Erlien, D. A., and J. R. Tester. 1984. Population ecology of sciurids in northwestern Minnesota. Canadian Field-Naturalist, 98:1–6.

Erxleben, J. C. P. 1777. Systema regni animalis per classes, ordines, genera, species, varietates: cvm synonymia et historia animalivm. Impensis Weygandianis, Lipsiae, 416 pp. (not seen, cited in Hall, 1981).

Fancy, S. G. 1980. Nest-tree selection by red squirrels in a boreal forest. Canadian Field-Naturalist, 94:198.

Ferner, J. W. 1974. Habitat relationship of *Tamiasciurus hudsonicus* and *Sciurus aberti* in the Rocky Mountains. Southwestern Naturalist, 18:470–473.

Ferron, J. 1975. Solitary play of the red squirrel (*Tamiasciurus hudsonicus*). Canadian Journal of Zoology, 53:1495–1499.

———. 1979. Le comportement agonistique de l'écureuil roux (*Tamiasciurus hudsonicus*). Biology of Behaviour, 4:269–285.

———. 1981. Comparative ontogeny of behaviour in four species of squirrels (Sciuridae). Zeitschrift für Tierpsychologie, 55: 193–216.

———. 1983. Scent marking by cheek rubbing in the northern flying squirrel (*Glaucomys sabrinus*). Canadian Journal of Zoology, 61:2377–2380.

———. 1984. Behavioral ontology analysis of sciurid rodents with emphasis on the social behavior of ground squirrels. Pp. 24–42, *in* The biology of ground-dwelling squirrels (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln, 459 pp.

Ferron, J., and J. Prescott. 1977. Gestation, litter size, and number of litters of the red squirrel (*Tamiasciurus hudsonicus*) in Quebec. The Canadian Field-Naturalist, 91:83–84.

Ferron, J., J. P. Ouellet, and Y. Lemay. 1986. Spring and summer time budgets and feeding behaviour of the red squirrel (*Tamiasciurus hudsonicus*). Canadian Journal of Zoology, 64:385–391.

Finley, R. B., Jr. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain region. Miscellaneous Publications of the University of Kansas Museum Natural History, 51:233–273.

Flyger, V., and J. E. Gates. 1982. Pine squirrels: *Tamiasciurus hudsonicus, T. douglasii.* Pp. 230–237, *in* Wild mammals of North America (J. A. Chapman and G. A. Feldhamer, eds.). John Hopkins University Press, Baltimore, 1147 pp.

Graham, R. W., and E. L. Lundelius, Jr. 1994. Faunmap: A database documenting late Quaternary distributions of mammal species in the United States. Illinois State Museum Science Papers, 25:289–690.

Grodinski, W. 1971. Food consumption of small mammals in the Alaskan taiga forest. Acta Zoologica Fennica, 8:133–136.

Guilday, J. G., P. S. Martin, and A. D. McCrady. 1964. A Pleistocene cave deposit in Bedford County, Pennsylvania. The Bulletin of the National Speleological Society, 26:121–194.

Gurnell, J. C. 1984. Home range, territoriality, caching behaviour and food supply of the red squirrel (*Tamiasciurus hudsonicus fremonti*) in a subalpine forest. Animal Behaviour, 32: 1119–1131.

———. 1987. The natural history of squirrels. Facts on File, New York, 201 pp.

Hafner, D. J. 1984. Evolutionary relationships of the nearctic Sciuridae. Pp. 3–23, *in* The biology of ground dwelling squirrels (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln, 459 pp.

Hafner, M. S., L. J. Barkley, and J. M. Chupasko. 1994. Evolutionary genetics of new world tree squirrels (Tribe Sciurini). Journal of Mammalogy, 75:102–109.

Hall, E. R. 1981. The mammals of North America. Second ed. John Wiley and Sons, New York, 1:1–600 + *90.*

Halvorson, C. H., and R. M. Engeman. 1983. Survival analysis for a red squirrel population. Journal of Mammalogy, 64:332–336.

Hamilton, W. J., Jr. 1934. Red squirrel killing young cottontail and young gray squirrel. Journal of Mammalogy, 15:322.

———. 1939. Observations of the life history of the red squirrel in New York. American Midland Naturalist, 22:732–745.

Hardy, R. 1942. Three new rodents from southern Utah. Proceedings of the Biological Society of Washington, 55:87–92.

Hatt, R. T. 1929. The red squirrel: its life history and habits, with special reference to the Adirondacks of New York and the Harvard Forest. Roosevelt Wild Life Annals, 2:10–146.

———. 1943. The pine squirrel in Colorado. Journal of Mammalogy, 24:311–345.

Hatton, L. E., Jr., and R. S. Hoffmann. 1979. The distribution of red squirrels (*Tamiasciurus*) in eastern Oregon. The Murrelet, 60:23–25.

Heaney, L. R. 1984. Climatic influences on the life-history tactics and behavior of the North American tree squirrels. Pp. 43–78, *in* The biology of ground-dwelling squirrels (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln, 459 pp.

Heinrich, B. 1992. Maple sugaring by red squirrels. Journal of Mammalogy, 73:51–54.

Herrin, C. S. 1970. A systematic revision of the genus Hirtionyssus (Acari: Mesostigmata) of the Neartic region. Journal of Medical Entomology, 7:391–437.

Hight, M. E., M. Goodman, and W. Prychodko. 1974. Immunological studies of the Sciuridae. Systematic Zoology, 23:12–25.

Hosley, N. W. 1928. Red squirrel damage to coniferous plantations and its relation to changing food habits. Ecology, 9:43–49.

Howell, A. H. 1929. Description of a red squirrel from North Carolina. Journal of Mammalogy, 10:75–76.

———. 1936*a*. Description of a new red squirrel from Isle Royale, Michigan. Occasional Papers of the Museum of Zoology, University of Michigan, 338:1–2.

———. 1936*b*. Descriptions of three new red squirrels (*Tamiasciurus*) from North America. Proceedings of the Biological Society of Washington, 49:133–136.

———. 1942. A new red squirrel from North Dakota. Proceedings of the Biological Society of Washington, 55:13–14.

Hurly, T. A. 1987. Male biased adult sex ratios in a red squirrel population. Canadian Journal of Zoology, 65:1284–1286.

Hurly, T. A., and R. J. Robertson. 1986. Scatter-hoarding by territorial red squirrels: a test of the optimal density model. Canadian Journal of Zoology, 65:1247–1252.

Ingles, L. G. 1965. Mammals of the Pacific states, California, Oregon and Washington. Stanford University Press, California, 506 pp.

Irving, L., and J. Krog. 1954. The body temperature of arctic and subarctic birds and mammals. Journal of Applied Physiology, 6:667–680.

Irving, L., J. Krog, and M. Monson. 1955. The metabolism of some Alaskan animals in winter and summer. Physiological Zoology, 28:173–185.

Kemp, G. A., and L. B. Keith. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. Ecology, 51:763–779.

Kilham, L. 1954. Territorial behavior of red squirrel. Journal of Mammalogy, 35:252–253.

———. 1958. Red squirrel feeding at sapsucker holes. Journal of Mammalogy, 39:596–597.

Klugh, A. B. 1927. Ecology of the red squirrel. Journal of Mammalogy, 8:1–32.

Koford, R. R. 1992. Does supplemental feeding of red squirrels change population density, movements, or both? Journal of Mammalogy, 73:930–932.

Kramm, K. R., D. E. Maki, and J. M. Glime. 1975. Variation within and among populations of red squirrel in the Lake Superior region. Journal of Mammalogy, 56:258–262.

Kurtén, B., and E. Anderson. 1980. Pleistocene mammals of North America. Columbia University Press, New York, 442 pp.

Lair, H. 1985. Length of gestation in the red squirrel, *Tamiasciurus hudsonicus*. Journal of Mammalogy, 66:809–810.

———. 1990. The calls of the red squirrel: a contextual analysis of function. Behaviour, 115:254–282.

Larsen, K. W., and S. Boutin. 1994. Movements, survival and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. Ecology, 75:214–223.

Layne, J. N. 1952. The os genitale of the red squirrel, *Tamiasciurus*. Journal of Mammalogy, 33:457–459.

———. 1954. The biology of the red squirrel *Tamiasciurus hudsonicus loquax* in central New York. Ecological Monographs, 24:227–267.

Lindsay, S. L. 1981. Taxonomic and biogeographic relationships of the Baja California chickarees (*Tamiasciurus*). Journal of Mammalogy, 63:446–452.

———. 1982. Systematic relationship of parapatric tree squirrel species (*Tamiasciurus*) in the Pacific Northwest. Canadian Journal of Zoology, 60:2149–2156.

Linzey, A. V., and D. W. Linzey. 1971. Mammals of Great Smoky Mountains National Park. The University of Tennessee Press, Knoxville, 114 pp.

Luttich, S., D. Rusch, E. Meslow, and L. Keith. 1970. Ecology of red-tailed hawk predation in Alberta. Ecology, 51:190–203.

Mahan, C. G., and R. H. Yahner. 1992. Microhabitat use by red squirrels in central Pennsylvania. Northeast Wildlife, 49: 49–56.

Mahrt, J. L., and S. J. Chai. 1972. Parasites of red squirrels in Alberta, Canada. Journal of Parasitology, 58:639–640.

Mayfield, H. 1948. Red squirrel nesting on the ground. Journal of Mammalogy, 29:186.

Mearns, E. A. 1890*a*. Observations on the avifauna of portions of Arizona. The Auk, 7:45–55.

———. 1890*b*. Description of supposed new species and subspecies of mammals from Arizona. Bulletin of the American Museum of Natural History, 2:277–307.

Meier, P. T. 1983. Relative brain size within the North American Sciuridae. Journal of Mammalogy, 64:642–647.

Meng, H. 1959. Food habits of nesting Cooper's hawks and goshawks in New York and Pennsylvania. The Wilson Bulletin, 71:169–174.

Mengel, R. M., and M. A. Jenkinson. 1971. A melanistic specimen of the red squirrel. American Midland Naturalist, 86: 230–231.

Millar, J. S. 1970. The breeding season and reproductive cycle of the western red squirrel. Canadian Journal of Zoology, 48: 471–473.

Mossman, H. W. 1940. What is the red squirrel? Transactions of the Wisconsin Academy of Science, Arts, and Letters, 32:123–134.

Nadler, C. F., and R. S. Hoffmann. 1970. Chromosomes of some Asian and South American Squirrels (Rodentia: Sciuridae). Experientia, 26:1383–1386.

Nellis, C. H., and L. B. Keith. 1968. Hunting activities and success of lynxes in Alberta. The Journal of Wildlife Management, 32:718–722.

Nelson, B. A. 1945. The spring molt of the northern red squirrel in Minnesota. Journal of Mammalogy, 26:397–400.

Nice, M. M., C. Nice, and D. Ewers. 1954. Comparison of behavioral development in snowshoe hares and red squirrels. Journal of Mammalogy, 37:64–74.

Obbard, M. E. 1987. Red squirrel. Pp 265–281, *in* Wild furbearer management and conservation in North America (M. Novack, M. E. Obbard, and B. Malloch, eds.). Ontario Ministry of Natural Resources, Toronto, Canada, 1150 pp.

Osgood, W. H. 1900. Results of a biological reconnaissance of the Yukon River region. General account of the region. Annotated list of mammals. Annotated list of birds. North American Fauna, 19:1–100.

Pauls, R. W. 1978. Behavioural strategies relevant to the energy economy of the red squirrel (*Tamiasciurus hudsonicus*). Canadian Journal of Zoology, 56:1519–1525.

———. 1979. Body temperature dynamics of the red squirrel (*Tamiasciurus hudsonicus*): adaptations for energy conservation. Canadian Journal of Zoology, 57:1349–1354.

Pike, G. W. 1934. Girdling of ponderosa pine by squirrels. Journal of Forestry, 32:98–99.

Pocock, R. I. 1923. The classification of the Sciuridae. Proceedings of the Zoological Society of London for 1923:209–246.

Price, K. 1992. Territorial bequeathal by red squirrel mothers: a dynamic model. Bulletin of Mathematical Biology, 54:335–354.

Price, K., and S. Boutin. 1993. Territorial bequeathal by red squirrel mothers. Behavioral Ecology, 4:144–150.

Price, K., K. Broughton, S. Boutin, and A. R. E. Sinclair. 1986. Territory size and ownership in red squirrels: response to removals. Canadian Journal of Zoology, 64:1144–1147.

Pruitt, W. O., and C. V. Lucier. 1958. Winter activity of red squirrels in interior Alaska. Journal of Mammalogy, 39:443–444.

Quay, W. B. 1965. Comparative survey of the sebaceous and sudoriferous glands of the oral lips and angle in rodents. Journal of Mammalogy, 46:23–37.

Rathcke, B. J., and R. W. Poole. 1974. Red squirrel attacks a pileated woodpecker. The Wilson Bulletin, 84:465–466.

Rausch, R., and J. D. Tiner. 1948. Studies on the parasitic helminths of the north central states. Part I. Helminths of Sciuridae. American Midland Naturalist, 39:728–747.

Reitsma, L. R., R. T. Holmes, and T. W. Sherry. 1990. Effects of removal of red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunks, *Tamias striatus*, on nest predation in northern hardwood forests: an artificial nest experiment. Oikos, 57:375–380.

Reynolds, J. C. 1985. Autumn/winter energetics of Holarctic tree squirrels: a review. Mammal Review, 15:137–150.

Riege, D. A. 1991. Habitat specialization and social factors in distribution of red and gray squirrels. Journal of Mammalogy, 72:152–162.

ROTHWELL, R. H. 1977. The effects of forest type and mast crop on winter territories and population of red squirrels (*Tamiasciurus hudsonicus baileyi*) in the Laramie Range of southeastern Wyoming. M.S. thesis, University of Wyoming, Laramie, 142 pp.

———. 1979. Nest sites of squirrels (*Tamiasciurus hudsonicus*) in the Laramie range of southeastern Wyoming. Journal of Mammalogy, 60:404–405.

RUSCH, D. A., AND W. G. REEDER. 1978. Population ecology of Alberta red squirrels. Ecology, 59:400–420.

SALT, J. R., AND C. A. ROTH. 1980. Bark of pine galls eaten by red squirrels. The Canadian Field-Naturalist, 94:196.

SHERBURNE, S. S., AND J. A. BISSONETTE. 1993. Squirrel middens influence marten (*Martes americana*) use of subnivean access points. American Midland Naturalist, 129:204–207.

SMITH, A. A., AND R. W. MANNAN. 1994. Distinguishing characteristics of Mount Graham red squirrel midden sites. The Journal of Wildlife Management, 58:437–445.

SMITH, C. C. 1965. Interspecific competition in the genus of tree squirrels, *Tamiasciurus*. Ph.D. dissertation, University of Washington, Seattle, 269 pp.

———. 1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. Ecological Monographs, 38:31–63.

———. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs, 40:349–371.

———. 1978. Structure and function of the vocalizations of tree squirrels (*Tamiasciurus*). Journal of Mammalogy, 59:793–808.

———. 1981. The indivisible niche of *Tamiasciurus:* an example of nonpartitioning of resources. Ecological Monographs, 51:343–363.

SMITH, C. C., AND O. J. REICHMAN. 1984. The evolution of food caching by birds and mammals. Annual Review of Ecology and Systematics, 15:329–351.

SMITH, H. C. 1984. Malocclusion of incisor teeth in a red squirrel, *Tamiasciurus hudsonicus*. Canadian Field-Naturalist, 98: 506–507.

SMITH, M. C. 1968. Red squirrel responses to spruce cone failure. The Journal of Wildlife Management, 32:305–316.

STILLIGER, C. R. 1944. Damage to conifers in northern Idaho by the Richardson red squirrel. Journal of Forestry, 42:143–145.

STONE, W., AND J. A. G. REHN. 1903. On the terrestrial vertebrates of portions of southern New Mexico and Western Texas. Proceedings of the Academy of Natural Sciences of Philadelphia, January:15–34.

SULLIVAN, T. P. 1990. Responses of red squirrel (*Tamiasciurus hudsonicus*) populations to supplemental food. Journal of Mammalogy, 71:579–590.

SULLIVAN, T. P., AND W. KLENNER. 1992. Response to Koford: red squirrels and supplemental feeding. Journal of Mammalogy, 73:933–936.

———. 1993. Influence of diversionary food on red squirrel populations and damage to crop trees in young lodgepole pine forest. Ecological Application, 3:708–718.

SULLIVAN, T. P., AND D. S. SULLIVAN. 1982. Barking damage by snowshoe hares and red squirrels in lodgepole pine stands in central British Columbia. Canadian Journal of Forest Research, 12:443–448.

SULLIVAN, T. P., AND A. VYSE. 1987. Impact of red squirrel feeding damage on spaced stands of lodgepole pine in the Caribou Region of British Columbia. Canadian Journal of Forest Research, 17:666–674.

SULLIVAN, T. P., J. A. KREBS, AND P. K. DIGGLE. 1994. Prediction of stand susceptibility to feeding damage by red squirrels in young lodgepole pine. Canadian Journal of Forest Research, 24:14–20.

SULLIVAN, T. P., H. COATES, L. A. JOZSA, AND P. K. DIGGLE. 1993. Influence of feeding damage by small mammals on tree growth and wood quality in young lodgepole pine. Canadian Journal of Forest Research, 23:799–809.

SVIHLA, R. D. 1930. Development of young red squirrels. Journal of Mammalogy, 11:79–80.

SWARTH, H. S. 1921. The red squirrel of the Sitkan District, Alaska. Journal of Mammalogy, 2:92–94.

VAHLE, J. R., AND D. R. PATTON. 1983. Red squirrel cover requirements in Arizona mixed conifer forests. Journal of Forestry, 81:115–127.

WALTON, M. A. 1903. A hermit's wild friends. D. Estes, Boston, Massachusetts, 304 pp. (not seen, cited in Layne, 1954).

WEBSTER, W. D., J. F. PARNELL, AND W. C. BIGGS, JR. 1985. Mammals of the Carolinas, Virginia, and Maryland. University of North Carolina Press, Chapel Hill, 255 pp.

WEIGL, P. D., AND E. V. HANSON. 1980. Observations on learning and the feeding behaviour of the red squirrel *Tamiasciurus hudsonicus*: the ontogeny of optimization. Ecology, 61:213–218.

WOOD, T. J. 1965. Albino red squirrel collected in Wood Buffalo Park. The Blue Jay, 23:90.

———. 1967. Ecology and population dynamics of the red squirrel (*Tamiasciurus hudsonicus*) in Wood Buffalo National Park. M.S. thesis, University of Saskatchewan, Saskatoon, 97 pp.

WRIGLEY, R. E. 1969. Ecological notes on the mammals of southern Quebec. Canadian Field-Naturalist, 83:201–211.

WUNDER, B. A., AND P. R. MORRISON. 1974. Red squirrel metabolism during incline running. Comparative Biochemistry and Physiology, 48A:153–161.

YAHNER, R. H. 1980. Burrow system use by red squirrels. American Midland Naturalist, 103:409–411.

———. 1986. Microhabitat use by small mammals in even-aged forest stands. American Midland Naturalist, 115:174–180.

———. 1987. Feeding site use by red squirrels, *Tamiasciurus hudsonicus*, in a marginal habitat in Pennsylvania. Canadian Field-Naturalist, 101:586–589.

YEAGER, L. E. 1937. Cone piling by the Michigan red squirrel. Journal of Mammalogy, 18:191–194.

ZIRUL, D. L., AND W. A. FULLER. 1970. Winter fluctuations in size of home range of the red squirrel (*Tamiasciurus hudsonicus*). Transactions of the 35th North American Wildlife and Natural Reservation Conference, 70:115–127.

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