Mammalian Species  No. 390, pp. 1–8, 4 figs.

Tamias amoena.  By Dallas A. Sutton

Published 5 June 1992 by The American Society of Mammalogists

Tamias Bachman, 1839

Tamias illigeri, 1811:83. Type species Scirius striatus Linnaeus.
Eutamias Trouessart, 1880:86. Type species Scirius striatus asiaticus (Gmelin).
Neotamias Howell, 1929:26. Type species Tamias asiaticus merriami Allen.

CONTEXT AND CONTENT. Chipmunks are small squirrels classified in the family Sciuridae, tribe Tamini, and either subfamily Sciurinae (Black, 1963) or Marmotinae (Gromov et al., 1965). There is no agreement over whether all chipmunks in North America should be included in the genus Tamias or whether the eastern chipmunk should be Tamias and the western forms Eutamias. The following key is adapted from distribution, measurements (mm), color, and call characteristics (Fig. 1) taken from Hall (1981), Honacki et al. (1982), Howell (1929), Patterson (1984), Patterson and Henney (1987), Sutton (1987), and White (1953a):

Key to Species of Tamias

1 Occurring in northern Europe, Russia, Siberia, China, Korea, Sakhalin, S Kurile Islands, and Japan (Fig. 1-R) T. sibiricus
   2 Occurring in North America T. striatus
   2 Occurring in North America E. of meridian 95 (Fig. 1-V) T. sibiricus
   3 Dorsal dark stripes (except median one) indistinct T. sibiricus
   3 Dorsal dark stripes all distinct T. striatus
   4 Occurring E. of California and Baja California; length of baculum 3.8 (T. dorsalis), shaft slender 0.4, depth of keel 0.5; color gray, average tail length 11.5; no notch between anterior nasals; greatest length of skull 36–40 (Fig. 1-F) T. dorsalis
   5 Occurring in California and/or Baja California T. sibiricus
   5 Length of baculum 4.3 mm (for T. o. obscurus), dorsoventral shaft thickness, depth of keel 2.1; average tail length 98; dark stripes reddish; greatest length of skull 33–40 (Fig. 1-I) T. obscurus
   6 Length of baculum 5.2 (T. m. merriami), shaft slender, depth of keel 0.5; average tail length 112 (84–140); color grayish to ochraceous, dark stripes gray or brown; small notch between anterior nasals; greatest length of skull 36–40 (Fig. 1-G) T. merriami
   7 Average greatest length of skull >36.5 T. merriami
   7 Average greatest length of skull <36.5 T. obscurus
   7 Occurring only in Mexico (T. m. merriami), length of baculum 4.1, depth of keel 0.8; ventral tail reddish; greatest length of skull 36–40 (Fig. 1-C) T. balleri
   8 Occurring in western United States or Canada T. obscurus
   8 Occurring in Arizona, New Mexico, or Texas T. sibiricus
   9 Occurring in other areas of United States and Canada T. obscurus
   10 Length of baculum <4; angle of tip/shaft about 120°; hind foot grayish; average head-body length 143 (136–149); greatest length of skull 36–39 (Fig. 1-D) T. canipes
   11 Back of ears not distinctly bicolored in summer pelage; tips of nasal bones separated by a small median notch; length of baculum 3.7 (T. s. somonae), shaft slender; greatest length of skull 37–40 (Fig. 1-T) T. somonae
   12 Ears relatively long, notch average 18.8, pointed; submalar dark stripe expands to conspicuous black area below ear; baculum 5.0, shaft somewhat thick, depth of keel 0.4; greatest length of skull 36–39 (Fig. 1-M) T. quadrimaculatus
   13 Ears shorter, notch average 16.8, rounded; no conspicuous black area below ear T. sibiricus
   14 Baculum tip 1.7, longer than shaft, 1.4, shaft dorsoventrally thick, 0.7; greatest length of skull 39–41 (Fig. 1-S) T. sibiricus
   15 Baculum tip longer than shaft T. sibiricus
   16 Baculum keel depth <25% of tip length, length of shaft 2.8, moderately thick; upper body dark tawny olive; greatest length of skull 39–41 (Fig. 1-J) T. ochrogenys
   17 Baculum keel depth >25% of tip length T. ochrogenys
   18 Baculum area 3.9, shaft dorsoventrally thick, keel depth 0.4; color ochraceous, washed with gray on shoulders and rump; hind feet gray; greatest length of skull 37–40 (Fig. 1-Q) T. senex
   19 Baculum area 2.7 (T. e. cooperi), shaft slender, keel depth 0.2; color cinnamon buff to tawny, not gray; hind foot buff to brown; greatest length of skull 37–40 (Fig. 1-W) T. townsendii
   20 Baculum keel thickness <25% of tip<br>length (Fig. 1-Q) T. townsendii<br>21 Baculum keel thickness >25% of tip<br>length (Fig. 1-Q) T. townsendii
   22 Baculum keel thickness >25% of tip<br>length (Fig. 1-Q) T. townsendii
   23 Baculum keel thickness <25% of tip<br>length (Fig. 1-Q) T. townsendii
   24 Baculum keel thickness >25% of tip<br>length (Fig. 1-Q) T. townsendii
T. a. amoenus Allen, 1890:90. Type locality "Fort Klamath, Oregon."

T. a. caurinus Merriam, 1898:352. Type locality "Olympic Mountains, Washington, timberline near head of Soleduck River."

T. a. canicactus Merriam, 1903:77. Type locality "Spokane, Washington."

T. a. ludibundus Hollister, 1911:1. Type locality "Yellowhead Lake, British Columbia."

**CONTEXT AND CONTENT.** Order Rodentia, Suborder Sciuromorpha, Family Sciuridae, Subfamily Sciurinae (or Marmotinae), Tribe Tamini, Genus Tamias, and Subgenus Neotamias. Fourteen subspecies of Tamias amoenus are recognized as follows (Hall, 1981; Howell, 1929):

T. a. affinis J. A. Allen, 1890:103. Type from "Ashcroft, British Columbia."

T. a. albiventris (Booth, 1947:7). Type from "Wickiup Spring, 23 mi. W Anatone, Asotin-Garfield County boundary, Washington."

**DIAGNOSIS.** Like all chipmunks in western North America the skull of the yellow pine chipmunk is narrow and lightly built, the postorbital process is slender and fragile, the infraorbital foramen is relatively larger than in most sciurids and lacks a canal, the head of the malleus is not elongated, the plane of the manubrium of the malleus is 90° to the plane of the lamina, the adult hyoid apparatus has fused hypohyal and ceratohyal bones, the tip of the basiulium is upturned and has a dorsal keel, and the tail is >40% of total length. The color pattern includes five longitudinal dark stripes that are evenly spaced and subequal in width. The three dorsal stripes extend to rump and shoulder and the two lateral ones extend only along mid-body, whereas in the eastern chipmunk (T. striatus), all the lateral, dark stripes are short (White, 1953a).

The dental formula is 1/1, 0/0, 2/1, 3/3, total 22. The peglike upper premolar (P3) is present and distinguishes the western and Asiatic chipmunks from T. striatus of eastern North America. This tooth is considered by Hall (1981) and White (1953a) to be of generic significance; however, Bryant (1945) and Ellerman (1940) considered it to be vestigial and of little taxonomic value.

Average length of head and body of T. amoenus is about 15% more than that of the two smallest western chipmunks, T. alpinus and T. minimus. Average length of skull is about 8% more than that of the other two, and the average length of tail is about 14% greater than that of T. alpinus and equal to that of T. minimus (Hall, 1981). T. amoenus is more reddish than T. minimus; length of tail is about 74% of length of head and body compared with 88% for T. minimus; ratio of length of basiulium to length of shaft is 30–35% in T. amoenus and 18–28% for T. minimus (White, 1953b). The baubella (female genital bones) of the two species are so similar that a clear distinction cannot be drawn (Sutton, 1982). Certain subspecies of these two species so closely resemble each other that no specific diagnosis has been framed that will distinguish them in all parts of their geographic range. At any one place, however, the two are distinguishable, with T. minimus smaller, paler, underside of tail yellowish instead of reddish, the braincase less flattened, rygomatic arches less flattened, the rostrum shorter, and upper incisors less recurved (Hall, 1981).

The only other species with which T. amoenus is likely to be confused is T. speciosus. T. amoenus is smaller, has shorter and broader-appearing ears, less sharply contrasting pale and dark stripes, with the inner pair of pale dorsal stripes broader and the outer pair usually narrower and less conspicuous. The dark facial stripes are less blackish, light facial stripes more washed with ochraceous, the skull less massive, rostrum more pointed, and the incisive foramina are smaller. These characters are quantitative and not specifically distinctive (Hall, 1981). The genital bones of both sexes, however, provide a clear and unique differentiation, with long, slender bones in both sexes of T. amoenus and short, thick bones in both sexes of T. speciosus. In a similar way, characteristics of the genital bone distinguish T. amoenus from T. panamintinus and T. umbrinus,
with which it is sympatric in some areas of the Sierra Nevada of California (Sutton, 1982; White, 1953b).

Characteristics of the baculum provide powerful diagnostic criteria among sciurids in general and among chipmunks in particular. Forms with markedly different bacula represent distinct species and, by critical examination of the genital bones, parapatric forms may be distinguished with confidence (Patterson, 1984; Patterson and Heaney, 1987; White, 1951).

**GENERAL CHARACTERS.** *Tamias amoenus* (Fig. 2) is a small chipmunk. Average and range for measurements (in mm) for 48 males and 49 females, respectively, from a series including all 14 subspecies are: length of head and body, 116.7 (108-125), 121.3 (115-129); length of tail, 91.9 (78-108), 91.5 (72-109); length of hind foot, 31.9 (29-35), 32.3 (30.0-35.0), and length of ear from notch, 20.8 (18-24), 20.52 (18.0-22.0). Average and range of cranial measurements are: greatest length of cranium, 32.6 (29.9-34.5), 33.4 (31.5-36.3); cranial breadth, 29.0 (27.5-32.5), 29.9 (28.1-32.9); zygomatic width, 17.9 (17.2-18.9), 18.6 (17.3-21.5); cranial width, 15.5 (14.7-16.4), 15.8 (14.9-17.1); interorbital width, 7.4 (6.6-8.5), 7.8 (6.7-9.7); length of nasal bone, 9.9 (9.0-11.0), 10.5 (8.6-12); and length of lower tooth row, 5.2 (4.6-5.7), 5.2 (4.5-5.8). Females are slightly larger than males in all measurements except length of tail, length of lower tooth row, and length of ear from notch, which are essentially equal. Factors implicated in larger female size in chipmunks include hibernation and the timing of resource accumulation (Levenson, 1990).

The narrow braincase (Fig. 3) is evenly rounded and rather deep (not flattened). The zygomatic arches have little flare and often are nearly parallel with the axis of the skull. The rostrum is short and abruptly constricted near the base, the temporal region is flattened, the lambdoidal crest is barely discernable, and the supraorbital notches are even with, or posterior to, the posterior notch of the zygomatic plate (White, 1953a).

Color of the body is dark reddish, with the crown of the head black to smoke gray, mixed with cinnamon. Color differences among the subspecies are: sides of the body range from pinkish cinnamon (*T. a. affinis*) or cinnamon buff (*T. a. monodon*) through sayal brown to tawny and ochraceous tawny (T. a. luteiventris, T. a. ludibundus, and T. a. felix). Rump and thighs are cinnamon, pinkish cinnamon, cinnamon buff, or ochraceous tawny, mixed in each case with smoke gray; hind feet vary from pale-pinkish cinnamon through cinnamon buff to sayal brown. The upper surface of the tail is pinkish cinnamon, clay color, cinnamon, sayal brown, tawny, or ochraceous tawny. The ears are fuscous black, broadly margined posteriorly with buffy (Howell, 1929).

Five longitudinal stripes on the body are separated by four subequal light stripes. Three dark stripes, separated by two light stripes, are on each side of the head. The dark, dorsal stripes are black or fuscous black, often shaded or mixed with tawny, ochraceous tawny or cinnamon. The median pair of pale dorsal stripes is smoke gray or pale smoke gray, usually mixed with cinnamon or tawny. The outer pair of pale stripes is clear, creamy white, narrower, and less conspicuous than the inner, and in *T. a. felix* is mixed with ochraceous tawny. In locomotion away from an observer, the stripe pattern has an effacing effect in the eyes of a pursuer above the level of the chipmunk. Cheek pouches are internal. Body mass varies considerably with the average (and range) of 10 largest males, from a series collected in September when young of the year appear to be grown, 49.7 g (30.0-57.5) and the average of 10 largest females 53.5 g (29.0-58.3; Grinnell et al., 1930).

**DISTRIBUTION.** The yellow-pine chipmunk is found in mountain areas of California northward from Mammoth Pass and the Yolla Bolly Range; northward from northern Nevada and northwestern Utah, and from western Wyoming and western Montana westward through Oregon and Washington (Fig. 4). In Canada it is found from the mountains of southwestern Alberta through most of southern British Columbia (Hall, 1981). It usually is found in the Transition Zone, extending its range into the Canadian Zone in some areas where conditions are favorable. The altitudinal range in California extends from about 975 m to timberline at about 2,900 m (Johnson, 1943).

**FOSSIL RECORD.** North American chipmunks first appear in Miocene deposits, having diverged from tree squirrels about 3.8 x 10^6 years ago during the Oligocene (Ellis and Maxson, 1979). Some time shortly after first appearing on this continent, a tree squirrel or chipmunk-like animal appears to have migrated into Eurasia and spread rather rapidly during the Pliocene into western Europe (Black, 1972). The Pleistocene history of *Tamias* is unclear, with records from North America as well as from Poland and China. Evidence from karyotypes (Nadler et al., 1977) suggests that Neartic species evolved from Palearctic immigrants of *T. sibericus*. The species *T. amoenus* has not been identified specifically in any fossil fauna.
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FORM AND FUNCTION. The baculum (os penis or male genital bone) of *T. amoenus* has a thin shaft, a low keel with a height 20% of the length of the tip, and a tip 30–35% of the length of the shaft. The angle formed by the tip and shaft is about 130°; the distal 20% of the shaft is slightly compressed laterally and the length of the shaft is 2.37–2.96 mm (White, 1936b).

The baubellum (os clitoris or female genital bone) has a rounded proximal end (base) and bends gradually into the shaft without a definite base-shaft angle apex. The bone is tapered toward the proximal end and the rounded base-shaft angle averages about 90°. The tip is slightly longer than the shaft, with which it makes an abrupt angle, and it is bent from the shaft to the right about 7°. The keel is thin and stands out clearly from the tip. The flat flanges on each side of the tip are about 0.2 mm wide, making the tip in some specimens as wide as it is deep. The baubella of five subspecies of *T. amoenus* are all similar in form and size, but that of *T. a. craticus* is thicker and much larger (Sutton, 1982).

An autumn molt begins in September or October, with the winter pelage similar to that of the summer, except for a duller tone, with the median pair of pale stripes darker and the sides slightly paler, about saiyal brown. A spring molt begins near 1 June, with irregular patches of new pelage appearing in the mid-back and progressive replacement proceeds forward from mid-back and anterior areas, then posteriorly and ventrally. Both melanistic and albino variants are believed to occur although none are known (Broadbunds, 1968b; Howell, 1929).

The estimated basal metabolic rate of *T. amoenus luteiventris* is 628 ml O₂ kg⁻¹ h⁻¹, somewhat lower than that of three subspecies of *T. minimus*. Between ambient temperatures of 3–32°C the body temperature ranged from 36–38°C. The estimated basal heart rate is 264 beats/min. Cardiovascular modifications provide extra reserves when demand for aerobic metabolism rises during bursts of activity (Jones and Wang, 1976).

*T. amoenus* and *T. spectiosus* have high thermosensitivity. When the hypothalamus was cooled to 35.2°C, metabolic rate increased immediately. For three *T. amoenus* species, response by *T. amoenus* was intermediate and it always assumed a prone, sprawling posture as the critical upper temperature was reached. *T. amoenus* has well-developed passive heat-loss mechanisms. Predictions are made that *T. amoenus* can remain exposed to severe heat loads about half as long as the other *Tamias* species. These findings have implications for the distributions of *T. amoenus*, which is typically found in open forest areas with patches of shade and elevated perches out of the hot boundary layer (Chappell et al., 1978). *T. amoenus*, living in open forest with low ground cover, has a brain size that is intermediate for the genus. Males and females have similar brain size (Bideau and Verts, 1986).

ECOLOGY. The yellow-pine chipmunk occupies a much broader range of habitat types than *T. senex*, *T. spectiosus*, or *T. quadrimaculatus*, with which it is sympatric; populations in breeding condition exist within the grazing range of individuals of each of the other species (Sharples, 1983). *T. amoenus* usually is found in brush-covered areas where snowberry (Symphoricarpos), chinquapin (Castanopsis), mountain mahogany (Cercocarpus), service berry (Amelanchier), antelope brush (Rhibes), and buckbrush (Ceanothus) are found, providing abundant fruits seasonally. Such shrub areas are interspersed with a variety of grasses and herbs as well as open conifer stands, all producing favored food seeds.

The yellow-pine chipmunk is mainly omnivorous, consuming a wide variety of food items, including seeds, fruits, bulbs or tubers, insects, bird eggs, berries, flowers, green foliage, roots, small animals, and buds of woody plants (Bailey, 1936; Gordon, 1943). Seeds of most conifers are frequently found in the cheek pouches (Tevis, 1952, 1953). Merriman (1891) found 332 seeds of the lodgepole pine (*Pinus Murrayana*) in the pouches of one *T. amoenus* in Idaho. The fungus Rhizopogon was present in 90% of the stomachs of *T. amoenus* in Oregon. Winter food stores contained 14,000–68,000 corns and seeds weighing 70–190 g in a subterranean nest chamber. At least 59 species of plants, fruits, seeds, corns, fungi, and several kinds of insects were eaten during the year by yellow-pine chipmunks in central Washington (Maser and Maser, 1987).

Over a three-year study there was little fluctuation in population density (1.25/ha). The home ranges were stable with few transients. About 90% of the animals captured in May and early June had been marked by toe clipping the previous year. Young-of-the-year accounted for about 50% of the animals caught from June through late October. Thus, the safest time of the year is the winter hibernation period, with almost 97% of the animals trapped in October recaptured 6 months later. Summer survival from July to October ranged from 33–88% (Broadbunds, 1958, 1970a).

Dens are maintained within or beneath stumps or logs, especially where these are overgrown with bushes. In Alberta, rocky
areas provided the best concealment cover and nest sites, especially when food plants and scattered trees were near (Meredith, 1972, 1977). Their dens have a complex, lobed room 80–90 cm long, 16 cm in diameter, and 0.7–1.5 m underground, reached by a tunnel 2–3 m long. One was filled with dry grasses and thigh-deep sediment. These dens were similar to those of T. sibericus, except that food was kept in a separate chamber (Anthony, 1924). In Montana, a nest of T. amoenus was nearly 3 m above the ground in a willow thicket. It was made of dry grasses, was 30–35 cm wide and 15 cm deep, and had an entrance 4 cm wide on the flattened top. A male and four young used a ground nest nearby. There also were tree nests made of dry grass as much as 18 m high in Engelmann spruce-timber (Engelmannia). These nests were from about 36 cm in diameter and over twice as large as chambers of ground nests examined. Nests may be placed in trees for several reasons; the ground nest is crowded with young; young explore and feed above ground; parasites and debris are reduced in a new nest; trees are a better refuge from predators (but not from hawks and owls); play and socializing is safer; a more favorable microclimate is provided in summer; there is a better view of surroundings; and conifer twigs and seeds are available for food. Tree nests resemble bird nests and there is the possibility that a bird nest has, at least at times, been taken over and modified for use by the yellow pine chipmunk (Broadbooks, 1974).

Routes of travel between retreats are maintained along fallen logs or branches rather than over open spaces. Where chapparal grows on the edges of talus slopes or over rock outcrops, the crevices among the rocks are used for refuge and dens. T. amoenus occupies new territory as it searches for sources of food (Grinnell et al., 1930).

The summer home range of most yellow-pine chipmunks remains the same from one summer to the next, indicating strong attachment to a discrete area which varies from 2 to 2.4 acres. A female singleton chipmunk used in sequence fouled room 3 areas which comprised her home range for two summers. The smallest area was occupied from June 14 to 18 while she was nursing young in a burrow. The home range then increased by 24% to include a portion of a cutover plot that was used intensively until about August 15, 1976. The home range became 32% larger than the smallest area, encompassing the second area as well as some surrounding land. From August 18 until 11 September she confined her movements to the woods near the nest site. Males and non-pregnant females are observed with greater frequency and have larger home ranges during the reproductive season than lactating females. After young emerge, lactating females increase their home range as much as 240%. Reproductive activity and availability of selected food plants appear to be most influential in altering the movement patterns (Martin, 1968). T. amoenus are curious, bold, and fearless after emerging from the den. They are especially wary of the long-tailed weasel (Mustela frenata), goshawk (Accipiter gentilis), bobcat (Lynx rufus), coyote (Canis latrans), badger (Taxidea taxus), sparrow hawk (Falco sparverius), rattle-snake (Crotalus viridis), and Buteo sp. (Broadbooks, 1970a).

In a study of Colorado tick fever and Rocky Mountain spotted fever richness, the least important host animals were T. amoenus and T. rufescens, with about 37% infected with larvae, 41% infected with nymphs, and an average of 7.3 ticks/host. Larval activity was restricted to a 9–11 week period between mid-June and early September, peaking in late July and early August. Activity of nymphs remained constant until it declined after mid-August. Utilization of hosts largely depended upon availability, with Neotoma cinerea, Spermophilus lateralis, and Peromyscus maniculatus more abundant and having more ticks than yellow-pine chipmunks (Sonenshine et al., 1985).

Yellow-pine chipmunks given inoculations of the virulent spotted fever agent, Rickettsia rickettsii, responded with rickettsemia detectable as early as 3 days and as late as 18 days after intrauterine inoculation. Antibody titers ranged from 1:16 to 1:64 after 23 days in 14% infected in nymphal ticks that had fed as larvae on T. amoenus. Thus, T. amoenus is a significant source of the virulent R. rickettsii to ticks and, subsequently, of spotted fever to humans. Yellow-pine chipmunks were immune to non-virulent R. montana and R. typhosa following intrauterine inoculation and examination as nymphs (Norment and Burgdorfer, 1985).

In late summer, T. amoenus is heavily infested with hot fly warbles. In Craters of the Moon National Monument, Idaho, 6 of 8 T. amoenus had 13 unidentified warbles (probably Catteretra emasculator) in August; three were under the skin in the neck area, four on the thorax, and one was scrotal. C. approximata, common in Missouri, was introduced as larvae into T. amoenus; over 14% became established and the host died 13 days later (Smith, 1977).

At Crater Lake National Park, Oregon, 51 of 110 T. amoenus were infested with flies, 73 flies were Monopospha leucomela, 32 were M. ciliatus, 4 were Oropsylla idahoensis and Calligrapha sculleni, and 1 each were Thrassus sp. and M. wagneri. The significance is unknown, but about 67% of male T. amoenus were infested, compared to 27% of the females (Greshirt and Hopkins, 1982). In central Oregon, M. eumolpae makes up about 85% of the total fleas collected (T. amoenus) (Hopkins, 1985). Small numbers of Oropsylla idahoensis, M. ciliatus, and Malaratus euphorbi were also found. Thirty-six female T. amoenus were collected, with 64% infested as compared to 71% of 35 males. Males had an average of 2.7 flies/infested host, whereas females had 2.3. Nineteen males with descended testes had higher infestation rates (79%) and mean numbers of flies (3/animal). Seventeen males with abdominal testes had only 65% infestation and an average of 2 flies/animal. Among reproductively inactive females, 61% were infested with a mean of three flies each, compared to 65% and two flies per animal in breeding condition (Greshirt and Hopkins, 1982). The mite, Acarus monoposphaelus, was discovered in phoretic association as a parasite on the flea, Monopospha leucomela, on T. amoenus in California (Fain and Schwan, 1954).

**BEHAVIOR.** Access to food and space is controlled in T. amoenus and T. townsendii by aggressive interactions, with T. townsendii dominant (Trombulak, 1985). Removal of T. townsendii led to an increase in the home range size of T. amoenus and also led to an increase in survival during winter, suggesting an advantage for the intruder. In western Alberta, the area occupied by T. amoenus was larger than the area occupied by T. townsendii, a result of the higher ridges above tree line. This distribution appears to be at least partly because of interspecies competition, with T. amoenus dominant. T. amoenus was clearly dominant in 33 of 68 matches in laboratory experiments and 74 of 108 in the wild. There was no significant interaction. Variability in aggressiveness was shown by T. amoenus. One female never attacked a T. minimus yet lost in only three encounters and, even against a submissive T. amoenus, T. minimus did not display much aggressiveness. T. amoenus was more active than T. minimus in the experimental conditions, first to emerge from the next box in 60 contests compared with 11 for T. minimus. Also, T. amoenus was active >2,000 of the 3,000 min of observation, compared to only about 1,000 min for T. minimus (Sheppard, 1971).

T. amoenus was dominant to T. minimus when the two were introduced into a large, structurally complex area in the mountains of southern Alberta, however, if T. minimus was introduced one day before T. amoenus, the dominance was balanced, with each winning the same number of agonistic matches. Observation continued for three seasons in areas where the ranges of T. amoenus and T. minimus overlapped, and only four events of interaction between the two species were noted. No aggression was observed and the animals tended to avoid each other, possibly an indication of a previous aggressive experience, or an indication that, once dominance has been established, individuals may avoid their opponents in areas where aggression would not be beneficial. Structure of the habitat may facilitate encounters as interactions as well as prior residence (Meredith, 1975, 1977). Interspecific aggression and possibly habitat selection are of far more importance than physiological adaptations in determining the lines of contact between traditionally zoned, contiguous allopatric populations of T. amoenus, T. alpinus, T. spectabilis, and T. minimus. Interspecific aggression is an extension of intraspecific territoriality, selected for because of properties of the cover in their habitats and the seasonality and defendability of a limited food supply (Heller, 1971).

In central Oregon, activities of T. amoenus are placed in five behavior categories as follows: foraging, in which the animal is in jerky, hesitant rushes, random searching, casual movement, digging without depositing anything or covering the hole; food gathering, handling, storing, or caching; protection, in which flight, conflict, alertness, retreat and alarm vocalizations are involved; positive social interaction such as chasing another animal, fighting, sexual behavior, tail twirling, nose another animal, and threat posturing; and maintenance, in which grooming, dust bathing, gathering nest materials, and resting were involved. With high population density intraspecific
competition increases for both *T. amoenus* and *T. townsendii*, although there was no observable change in the home ranges. Distributional variation may result more from differences in habitat selection than from aggressive interactions. Most active foraging by *T. amoenus* did not occur until sunrise or until higher temperatures were reached on cloudy days. In areas of high daily temperatures, foraging was mostly in early morning and late afternoon in areas of shrub cover and shade. In cooler areas, the major foraging activity was during warmer parts of the day, especially where shade was available. There appeared to be a tendency to confine activity to dense cover in high wind. A high, positive orientation to trees occurred when ponderosa pine (*Pinus ponderosa*) comes opened to recharge their stores, mainly with abundant food for winter storage. Alarm vocalizations had the effect of each chipmunk serve, to some extent, as a lookout for others, especially noticeable in open sites. There was greater exposure to predators in open areas as was evident from more vocalizations and higher levels of watchfulness (States, 1976). Foraging away from cover was possible when the animals were more watchful (Broadbents, 1970a). Territoriality suggested by Broadbents appears to have resulted from observing females chasing other chipmunks away from their den sites (States, 1976).

In the Cascade Mountains of central Washington, Broadbents (1970a) found *T. amoenus* active above ground about 7 months of the year. Winter dormancy, interrupted by brief activity and feeding about every 2 weeks, lasts about 5 months, from November through March.

Seasonal adjustment in *T. amoenus* involves changes in food consumption, fat storage, food storage, metabolism, growth, and activity. In general, hibernators store energy as fat, but chipmunks hoard food and build up little body fat, so they have short periods of hibernation. *T. amoenus* is an intermittent or, in some areas, even a non-hibernator. It may even lose weight before entering the winter den so it survives mostly on stored food. Energy is conserved by entering various depths of torpor and decreased activity (Steblins and Orich, 1977).

Dietary adjustments influence the control of body temperature by the central nervous system, and thus influence hibernation. Animals fed a diet rich in polyunsaturated fatty acids showed shorter periods of torpor, higher minimum body temperature, and higher metabolic rates. Males tended to emerge from hibernation 1–2 weeks ahead of females (Geiser and Kenagy, 1987).

When exposed to constant photoperiod and temperature for as long as 20 months, yellow-pine chipmunks showed both reproductive and hibernatory cycles that resembled the natural rhythms that were endogenously circannual and spontaneously repeated in a period of <1 year. Torpor was not required for the progression of the seasonally reproductive rhythm. Cycles of approximately equal periodicity with an emphasis on grazing animals are isolated from environmental cues. Chipmunks live in strongly seasonal environments that demand a precise annual schedule, but during hibernation, exposure to environmental cues and also the sensitivity of the animals to cues is reduced. An endogenous annual temporal program should prepare them to meet their growing season, which is only 2–3 weeks breeding period directly following hibernation. Young born in early June coincide with strong summer productivity that follows the spring snow melt. Food supply and weather are natural conditions that influence the rather flexible host of hibernation in chipmunks. Both reproduction and hibernation are influenced by exposure to different photoperiods. Eight of 12 h of light per day permit normal seasonal cycles, but 16 h of light per day block both gonadal cycle and hibernation. A variety of factors, including temperature, seasonal biotic productivity, social interactions, and length of day, synchronize the internal program with the external environment (Kenagy, 1981).

**GENETICS.** Characteristics of chromosomes of the subspecies of *T. amoenus*, except for *T. a. septentrionalis*, were determined through examination of karyotypes. The modal diploid number was 38, with five pairs of metacentric, six pairs of sub-metacentric, four pairs of acrocentric, and three pairs of small metacentric or acrocentric chromosomes. The sex chromosomes in the female consist of a pair of sub-metacentric X and, in the male, of a sub-metacentric X and a small acrocentric Y. Chromosomes of subspecies of *T. amoenus* were typical of karyotype B, a characteristic of all western *Tamias* species, except *T. cinereoulis* and seven of the subspecies of *T. minimus* that were karyotype A (Sutton and Nadler, 1969). The suggestion of two groups of species among the western chipmunks based on karyotypes disagrees with the existence of five groups based on morphology and pelage characters (Hoffman, 1939; White, 1935), and three groups based on characteristics of the baculum (White, 1953b). There is no satisfactory explanation for the existence of the two karyotypes. A mechanism like stasis speciation is unlikely since chromosome rearrangement probably would not occur in widely scattered localities. Karyotype patterns are uniform among the *T. amoenus* subspecies, but chromosome characters have been of little value in determining taxonomic relationships among western chipmunks (Nadler, 1964; Sutton and Nadler, 1969).

Electrophoretic data for 20 proteins has been used to suggest that there are five subspecies within the Subjects *Tamias*, with *T. amoenus* along with *T. umbrinus* making up one of these subspecies. This *T. amoenus-T. umbrinus* species group is geographically cohesive, all taxa being in the Sierra Nevada, Pacific Northwest, and Rocky Mountains, so peripheral isolation or major allopatric speciation could have resulted (Levness, et al., 1985).

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Editors of this account were TROY L. BEST, GUY N. CAMERON, and KARL F. KOOPMAN. Managing editor was CRAIG S. HOOD.

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