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Tamias striatus. By Dana P. Snyder

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Tamias Illiger, 1811

Tamias Illiger, 1811:83. Type species Sciurus striatus Linnaeus,

CONTEXT AND CONTENT. Order Rodentia, Family Sciuridae, Subfamily Sciurinae. There is disagreement over whether all chipmunks (Tamias, Eutamias) should be included in Tamias, or only the eastern chipmunk on North America. See Remarks.

Tamias striatus (Linnaeus, 1758)

Eastern Chipmunk

[Sciurus] striatus Linnaeus, 1758:64. Type locality upper Savannah River, South Carolina; fixed by Howell, 1929:14.

Tamias americana Kuhl, 1820:69. Based on material in Bullock's museum; locality given only as "In America septentrionali. Sciurus (Tamias) lysteri Richardson, 1829:181. Type locality Penetanguishene, Ontario.

Tamias striatus, Baird, 1857:55. First use of name combination.

CONTEXT AND CONTENT. Context in generic account above. In his 1929 revision Howell recognized five subspecies and six more have been described since (Hall, 1981). Ellis (1979), basing his conclusions on cranial and external morphology and to some extent on coloration, accepted only five subspecies. Because Ellis' revision is not yet widely available, the eleven previously described forms are listed below (see Distribution).

- T. s. doorsiensis Long, 1971:201. Type locality Peninsula State Park, Door Co., Wisconsin.
 T. s. fisheri Howell, 1925:51. Type locality Merritt's Corners, 4
- mi E Ossining, Westchester Co., New York (see Paradiso,
- T. s. griseus Mearns, 1891:231. Type locality Fort Snelling, Min-
- T. s. lysteri (Richardson, 1829:181), see above. Regarding authorship see Merriam (1886).
- T. s. ohionensis Bole and Moulthrop, 1942:135. Type locality Cincinnati, Hamilton Co., Ohio.

 T. s. peninsulae Hooper, 1942:1. Type locality Barnhart Lake, 3
- mi SE Millersburg, Presque Isle Co., Michigan.
- T. s. pipilans Lowery, 1943:235. Type locality 5 mi S Tunica, West Feliciana Parish, Louisiana.
- T. s. quebecensis Cameron, 1950:347. Type locality St. Félicien, Lake Saint John Co., Quebec.
- T. s. rufescens Bole and Moulthrop, 1942:130. Type locality Chesterland Caves, Chester Township, Geauga Co., Ohio
- T. s. striatus (Linnaeus, 1758:64), see above (americana Kuhl a
- T. s. venustus Bangs, 1896:137. Type locality "Stilwell, I. T.," now Stilwell, Adair Co., Oklahoma.

DIAGNOSIS. Tamias striatus differs from other chipmunks (subgenus Eutamias, subgenus Neotamias) in the absence of P3, lack of fusion of hypohyal and ceratohyal bones, and presence of keel on ventral tip of baculum. It differs from these subgenera also in having a relatively shorter tail (less than 38% of total length versus more than 40% of total length in others). The innermost paired dorsal stripes are about twice the width of other stripes in T. striatus rather than being about equal in width to the remaining stripes as in the other chipmunks. The eastern chipmunk differs from small terrestrial squirrels in the form of the infraorbital foramen which consists of a short oval passageway perforating the zygomatic plate rather than a canal opening forward of the plate (White, 1953). Additional diagnostic characters are given by Bryant (1945), Howell (1938), and White (1953).

GENERAL CHARACTERS. The eastern chipmunk is a small, moderately heavy-set, sciurid with prominent longitudinal stripes (Fig. 1). Mid-dorsally a dark brown, quite narrow stripe extends from back of head to rump; this stripe is bordered on either side by a strip, about twice as wide, of agouti hairs varying from a grayish to reddish-orange or brownish in appearance. Lateral to these are two narrow, dark-brown stripes enclosing a slightly wider, yellowish-white stripe. These stripes fade into the vellowish- or reddish-brown rump. Yellow-orange sides grade into the whitish underside. The prominent eyes are bordered above and below by light facial stripes which are in turn bordered by darker stripes. The tail is dorsoventrally flattened, well haired but not bushy, and dark above with light gray border. The underside of the tail has a central reddish-orange strip enclosed by narrower blackish strips and is edged with light gray. Overall appearance is of a grayish- to reddish-brown small mammal. Intensity and shade of coloration varies geographically; the palest forms occur in southern Ontario, dark red forms in parts of the southern Appalachians, and the most brightly colored individuals in southwestern portions of the range. Along the northern parts of the range, reddish effects are reduced, giving a darker gray, less colorful, appearance. Ears are fairly prominent, less than 20 mm to tip from notch, and more or less rounded at apex. There are four functional toes on the forefeet (pollex vestigial with a flat nail) and five on the hindfeet. Internal cheek pouches are large. There are four pairs of mammae-1 pectoral, 2 abdominal, and 1 inguinal. Smallest forms occur in the southeastern portion of the range and largest in the northwest and southwest. Average measurements (mm) for seven populations from widely scattered points over the geographic range of the species are: total length, 225 to 268; length of tail, 72 to 101; greatest length of skull, 39.4 to 43.8. Adult weights range from less than 80 g to 125 g or more.

The skull (Fig. 2) is lightly built and somewhat elongate with relatively small and weak postorbital processes. The zygomatic plate slants upward at approximately 45° from the occlusal plane of the cheekteeth. Small masseteric tubercles lie ventral and partially mesial to the infraorbital foramen. The frontoparietal suture is not ankylosed and temporal ridges do not meet to form a sagittal crest. There is no temporal foramen in the squamosoparietal suture. The superior outline of skull is shallowly convex. The braincase is shallow and the lambdoidal crest is well developed. Head of the malleus is more elongate than in other chipmunks and the auditory bulla has two transbullar septa. Dental formula is i 1/1, c 0/0, p 1/1, m 3/3, total 20. A succinct characterization of all the chipmunks as a group (including the subgenera Eutamias and Neotamias) was given by Moore (1959).

DISTRIBUTION. The eastern chipmunk ranges from the vicinity of Lake Manitoba eastward to the Quebec coastline just north of Anticosti Island and southward to the Gulf states (Fig. 3). It is present on Cape Breton Island but absent from Anticosti Island and (originally) from Newfoundland where, in the 1960's, chipmunks from Nova Scotia were introduced at three sites (Northcott et al., 1974). On the west, discontinous outposts occur in wooded habitats quite far from typical deciduous forest regions, particularly in river valleys (Black et al., 1977; Howell, 1929). În Louisiana it occurs only in a few parishes near the Mississippi River (Lowery, 1974), and in Florida only in the northwest part of the state near the Alabama line (Stevenson, 1962). It is absent from much of the coastal plain and some adjacent areas of piedmont in the Carolinas and Georgia. T. striatus occurs near human habitations as well as in uninhabited areas and is an 'urban" as well as a wilderness species.

FOSSIL RECORD. Chipmunks (sensu lato) appear to have been a distinct stock since at least the late Oligocene (Black, 1963) and are represented by later Tertiary fossil material from several widely scattered sites in North America (Black, 1963; Klingener, 1968; Lindsay, 1972; Sutton, 1972). Place of origin of



FIGURE 1. Photograph of *Tamias striatus* from Allegheny National Forest, Pennsylvania, taken by Kenneth E. Fisher.

this group and its later Tertiary migration history is not known, but several scenarios have been suggested (Black, 1972; Ellis and Maxson, 1979; Moore, 1961; Nadler et al., 1977). Ellis and Maxson (1979) postulated the time of divergence of chipmunks from the tree squirrel lineage as 38 million years BP (Oligocene) and that Tamias (sensu stricto) diverged from the other American chipmunks during late Miocene (10 million years BP).

Several Pleistocene species closely related to the eastern chipmunk have been described, but only one, T. aristus (Ray, 1965), appears to be distinct from T. striatus. Specimens definitely referable to T. striatus are common in late Pleistocene and early Recent deposits, particularly in caves, sinks, and fissures, and around prehistoric Indian sites within the current range of the species (Guilday, 1963; Ray, 1965). The stratigraphic range extends from late Sangamonian to Recent (Kurtén and Anderson, 1980). In late Pleistocene to early Recent time (approximately 8,000 to 11,000 years BP) the geographic range of T. striatus was at least several hundred km west of its present known limits (Dalquest et al., 1969; Roth, 1972). Ray (1965) summarized the Pleistocene to Recent material.

FORM. Pelage pattern and, more strikingly, color vary geographically (Allen, 1938). Neither melanic nor albino variants are common, but there are records of both from central and northeastern parts of the range (Goodpaster and Hoffmeister, 1968; D. Smith and L. Smith, 1972). There are two molting peaks each year, but there is difference of opinion over whether the same chipmunk molts twice in 1 year (Bole and Moulthrop, 1942; Ellis, 1979; Howell, 1929; Yerger, 1955). Yahner et al. (1979) found numerous sebaceous glands associated "... with hair follicles around the anal orifice and in the entire perineal region" Aggregations of glandular tissue, which they speculated might be a source of reproductive pheromones, were also noted in the walls of the anal canal extending into the perineum. Quay (1965) found sebaceous and mucous glands but not sudoriferous glands in the oral lips and angle of T. striatus.

Comparative descriptions of the baculum have been published by Burt (1960) and Wade and Gilbert (1940). Average length of 31 bacula, mostly from Michigan, was 4.15 mm (Burt, 1960). The length of the os clitoridis is approximately 60% that of the baculum (Layne, 1954). The cutaneous maximus muscle is poorly developed with only a dorsal and a pudendal portion (Woods and Howland, 1977). Many detailed structural characteristics of the skeleton and musculature are given in the comparative descriptions by Bryant (1945).

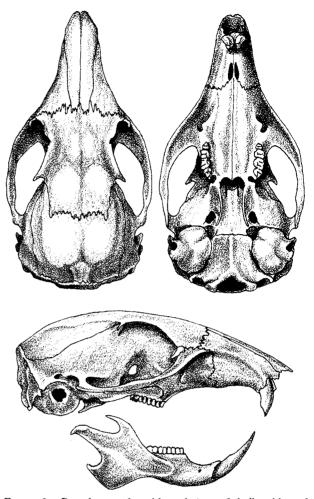


FIGURE 2. Dorsal, ventral, and lateral views of skull and lateral view of mandible of male *Tamias striatus* from West Feliciana Parish, Louisiana (Louisiana State University Museum of Zoology No. 16177). Drawing by H. D. Pratt from Lowery (1974), The mammals of Louisiana and its adjacent waters, by permission of Louisiana State University Press. Cranium measures approximately 44 mm.

Neuroanatomy has been little studied, but Simpson (1914) found a complete decussation of the pyramidal tracts which, after crossover, travel in the dorsal columns of the spinal cord as far as the lower sacral vertebrae, with a considerable number of fibers disappearing in the cervical region. Sealander (1964) gave values for several blood parameters. Anthony et al. (1963) described the histology of the digestive organs; they found no difference between active and hibernating chipmunks or between sexually active and sexually quiescent individuals. Mossman et al. (1932) found that Tamias striatus had large seminal vesicles, large prostate and Cowper's glands, and a small bulbar gland with no intermediate portion. The testes of an old adult in breeding condition measured $10 \times 10 \times 17$ mm. Dudkiewicz (1968) described the histology of the female reproductive tract. The ovary is approximately 2.5 mm long by 1.5 wide. The mature graafian follicle attains a diameter of about $560~\mu$, and the corpora lutea of pregnancy are approximately 800 μ in diameter.

FUNCTION. Mean minimum heart rate of normothermic animals at ambient temperatures of 30° to 31° C was found to be 165 beats/min. Rates increased at higher and at lower temperatures, reaching 530 at -5° C (Wang and Hudson, 1971). Spontaneous cardiac activity can be maintained in isolated atria at temperatures as low as 0° to 4° C; activity of isolated ventricles ceases at a slightly higher temperature (Angelakos et al., 1969; Lyman and Blinks, 1959). At about 20° C captive animals showed annual cycles in erythrocyte count (higher in summer than winter) and blood sugar (increased from January to July, then decreased) (Woodward and Condrin, 1945). Wang and Hudson (1971) found that mean oxygen consumption at ambient temperatures from

 28.5° to $32^{\circ}C$ was $1,030~mm^3~g^{-1}~h^{-1}$. Body temperatures were between 36° and $40.3^{\circ}C$ at ambient temperatures between -7° and $+32^{\circ}C$. Above $32^{\circ}C$ body temperature climbed and above $36^{\circ}C$ chipmunks had difficulty dissipating the heat load. Thermoneutrality was between 28.5° and $32^{\circ}C$. However, Neumann (1967) found the thermoneutral zone to extend from 28° to $36^{\circ}C$, and within this range mean body temperature was $39.2^{\circ}C$ and mean oxygen consumption $1,250~mm^3~g^{-1}~h^{-1}$.

Neff (1968) measured gross metabolic response in active chipmunks exposed to 3° ± 2°C for 30 days; body temperatures averaged 37° ± 1°C, the same as controls kept at 24° ± 1°C. He concluded that chipmunks have a well-developed capacity for acclimation to reduced temperatures by gross metabolic changes similar to those observed in homeotherms such as laboratory rats. Neal and Lustick (1975) found that artificial infra-red radiation at energy levels which might be expected in nature caused a downward shift of 3.5° to 8.2°C in the thermoneutral zone. This reduced O2 consumption, indicating that basking might be important to chipmunks. Importance of the nasal passage in heat exchange was demonstrated by Schmid (1976) who found a gradient of 10.7°C between back of passage (cribriform plate) and exhalent air. Chipmunks respond to hypoxia (8% O2) by an elevation in heart and respiratory rate and decrease in body temperature (Faleschini and Whitten, 1975). Blake (1977) found that minimum water requirements of captive chipmunks varied from about 24% of their weight per day in the reproductive season to 4% to 5% of weight during the hibernating season. Captive chipmunks studied by Forbes (1967) with a mean weight of 115 g utilized an average of 16.4 ml of H₂O per day.

From late fall to early spring chipmunks are mostly underground in various degrees of torpor, but sometimes appear above ground in favorable weather. Some remain dormant throughout the winter. Juveniles tend to remain active until later in the fall than do adults. In captivity a variable proportion of chipmunks become torpid at ambient temperatures ranging from 0° to 22°C, but only during the winter and spring months (Pivorun, 1976b; Wang and Hudson, 1971). The annual torpidity cycle appears to be endogenous and is probably independent of temperature (Scott and Fisher, 1972). However, Woodward and Condrin (1945) reported that if blood sugar of captive chipmunks were lowered by insulin, torpidity could be easily induced by a temperature of 5° to 10°C. Differences in photoperiod do not seem to affect entry into torpor but do affect length of torpor (Brenner and Lyle, 1975). Body temperature usually remains several degrees (often more than 10) above ambient, but two individuals observed by Wang and Hudson (1971) maintained only a 1° gradient during torpor at 4°C ambient. Torpidity allows chipmunks to reduce their metabolic needs by 85% or more (Neumann, 1967; Pivorun, 1976a; Wang and Hudson, 1971). Length of torpid bouts varies from less than 24 hours to several days and is a function, according to Pivorun (1977), of body temperature attained during torpor. Winter inactivity occurs even in northern Florida (Stevenson, 1962) and continues as long in some southern areas as in the north (Engels, 1951). Arousal occurs fairly rapidly, taking from less than 0.5 h to 2 h depending on depth of torpor. Temperatures in abdominal areas tend to lag behind those of the thorax and other anterior regions of body during warming (Schaffer and Bullard, 1970; Wang and Hudson, 1971). Schaffer (1971) discussed the importance of brown fat in arousal from torpidity. Anthony et al. (1967) and Munro and Anthony (1965) discussed other physiological aspects of hibernation. Captives exhibit an annual cycle in body weight (Allen, 1938; Brenner and Lyle, 1975; Panuska, 1959; Schaffer, 1973), but Forbes (1966a) found no evidence of fall accumulation of fat in free-ranging chipmunks.

Thyroid activity appears to be greatest in the fall and lowest in summer, and females show higher activity than males (Fisher, 1972; Kodrich and Tryon, 1971). Adrenal weights of captive chipmunks at room temperature increased nearly 3-fold from a January low to a plateau from April to September and then regressed (Woodward and Condrin, 1945). Clulow et al. (1969) found that adrenocortical activity was positively correlated with density in populations of wild caught animals introduced onto islands.

ONTOGENY AND REPRODUCTION. Most matings occur between late February and early April and again from late June to early July. Males come into breeding condition in mid-February or earlier and testes begin to regress in July or August. Females are in breeding condition by the time of emergence, usually in March. Females may breed in either the spring or summer period or both (L. Smith and D. Smith, 1972; Yerger, 1955). D. Smith and L. Smith (1975) found that estrus, as defined by morphological characteristics of the external genitalia, lasted

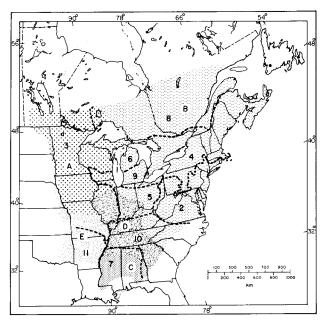


FIGURE 3. Geographic range of Tamias striatus showing the 11 described forms and the subspecies considered valid by Ellis (1979). Named forms, bounded by dashed lines are: 1, T. s. doorsiensis; 2, T. s. fisheri; 3, T. s. griseus; 4, T. s. lysteri; 5, T. s. ohionensis; 6, T. s. peninsulae; 7, T. s. pipilans; 8, T. s. quebecensis; 9, T. s. rufescens; 10, T. s. striatus; 11, T. s. venustus. Subspecies according to Ellis, denoted by shading are: A, T. s. griseus; B, T. s. lysteri; C, T. s. pipilans; D, T. s. striatus; E, T. s. venustus. Populations introduced into Newfoundland are indicated by solid circles. Adapted from Hall (1981) and Ellis (1979). Drawn by K. A. Sargent.

at least 3 days and up to 10 days. However, on behavioral criteria Elliott (1978) considered that estrus lasted only about 6.5 h. Gestation is 31 to 32 days (Allen, 1938; Burt, 1940). Behavior of a captive animal during parturition was described by Allen (1938). Litter size averages between 4 and 5. Newborn weigh 2.5 to 5.0 g; a female measured by Allen (1938) was 66 mm in total length, with a 12 mm tail, and a 7.5 mm hindfoot. By 1 month of age juveniles are 140 mm long and weigh 30 g; eyes are open, body is well furred, and they have an adult appearance. They emerge at 5 to 7 weeks of age (Pidduck and Falls, 1973; L. Smith and D. Smith, 1972; Yerger, 1955). Adult size and permanent dentition are achieved by 3 months. By 1 year the teeth are well worn. Additional growth-rate data were given by Pidduck and Falls (1973) and Yahner (1978a). Individuals are usually not sexually mature until after their first winter, but some spring-born females mate in the following summer. Males rarely, if ever, become sexually mature their first summer (L. Smith and D. Smith, 1972; Yerger, 1955). Seasonal changes in the male reproductive tract were studied by Neff and Anthony (1963). Characteristics of teeth, skull, and long bones have been used to determine age (Allen, 1938; Ellis, 1979; Yerger, 1955).

ECOLOGY. Tamias striatus inhabits primarily deciduous wooded areas; it occurs in open bushy habitats as well as mature forests, especially in habitats with abundant crevices for refuge along with elevated observation and vocalization posts. Ryan and Larson (1976) reported habitat characteristics of chipmunks in residential areas. Density is temporally and geographically variable, ranging from 0.3 to 37.6 per ha (Yerger, 1953). Annual variation is commonly 2- to 5-fold and tends to be greater in areas with the lower population densities. Sex ratios of trapped chipmunks are quite variable; differences likely result from chance variation in small samples and from differences between sexes in sizes of home ranges. Tryon and Snyder (1973a) published life tables for populations in Pennsylvania and Vermont. Male-female ratios of 1,507 juveniles from several different locations varied from 52:48 to 45:55, but the overall ratio was 50:50. Survival rates were fairly constant over much of the adult life but varied geographically and by season of birth; spring litters survived better than those born in late summer. Some chipmunks lived at least into year 8; average annual survival and mean life 4 MAMMALIAN SPECIES 168

expectancy from time of first capture (shortly after emergence) was 0.43 and 1.3, respectively. There is annual variation in age structure as a result of different numbers of juveniles entering the population in different years. Roberts (1976) made an extensive analysis of age, sex, and native/immigrant population structures.

Panuska and Wade (1956), Thomas (1974), and Elliott (1978) made detailed studies of burrow systems. Some are single tunnels, but more complex systems contain one or more large storage chambers and various smaller galleries and short pockets in which food or debris is stored. Length is up to 10 m, depth less than 1 m. The nest, of chewed or crushed leaves, occupies one of the larger chambers. A female in Michigan utilized a hollow tree as a nest site in which to bear and raise a litter (Getty, 1979). Entrances are 40 to 60 mm in diameter; usually only one is in active use, but plugged alternate passages frequently reach the surface.

Mean minimum area home range varies temporally and geographically from 0.03 to 0.40 ha with individual home ranges varying from under 100 m² to more than a hectare. Elliott (1978) found that ranges usually were more or less symmetrical with centrally located burrows and that use-intensity was highest near the burrow and gradually decreased toward the periphery. Detailed breakdowns of ranges according to age, sex, time of year, and other factors were made by Ickes (1974) and West (1975). Chipmunks make long excursions outside their usual range, in part to exploit concentrated food sources. Roberts (1976) found that some resident (non-dispersing) individuals have lifetime range lengths of at least 484 m; dispersal movements extended at least 857 m, with males making longer movements. Mares et al. (1976) were able to induce a contraction in size of ranges (from an average size of 0.02 to 0.11 ha) by providing a concentrated and unlimited food source within core areas. Most chipmunks are relatively sedentary and retain their burrow systems and range for long periods, often for life (Yahner, 1978b).

Various aspects of the diet and feeding ecology have been studied by Elliott (1978), Forbes (1966b), Frost (1968), Graybill (1970), Wrazen and Svendsen (1978), and Yerger (1955). Graybill (1970) listed published references to food items. Staple, over-wintering food consists of seeds, nuts, and acorns larder-hoarded in burrow systems. Frost (1968) and Wrazen and Svendsen (1978) found that nuts and acorns, apparently from the winter food cache, were used during the spring and summer. Elliott (1978) estimated that some hoards which he excavated in May and June could have lasted their owners well into the next winter. Yahner (1975) and Elliott (1978) discussed the significance of scatterhoarding outside burrows. Invertebrates (especially insects) and fungi also are important foods during the growing season (Elliott, 1978; Frost, 1968; Wrazen and Svendsen, 1978). Chipmunks prey on frogs, snakes, birds, and small mammals (see Graybill, 1970). Graybill (1970) found that captive chipmunks kept under outdoor conditions in Pennsylvania utilized an average of 32.7 to 35.7 kcal per individual per day during a 1 year period. He estimated that free-ranging chipmunks in areas he studied consumed more than half of their potential food resource.

Tamias striatus is prey for snakes, hawks, weasels, foxes, and bobcats (Hamilton and Whitaker, 1979). Peifer (1979) saw a great blue heron, Ardea herodias, take chipmunks, and Symington (1907) observed a "large frog" capture and eat a chipmunk.

Antibodies to the La Crosse strain of California Encephalitis virus have been detected in chipmunks in Ohio and Wisconsin, and the virus has been isolated from Wisconsin chipmunks (Berry et al., 1975). Known protozoan parasites are Trypanosoma tamiasi, Eimeria ovata, and E. vilasi (Dorney, 1966; Duncan, 1968; Riedel, 1975). Helminths reported are: Cestoda-Hymenolepis diminuta, H. sp., Taenia mustelae (bladderworm), Cladotaenia globifera (plerocercoid), and Paruterina rauschi (plerocercoid) (Freeman, 1956, 1957, 1959; Rausch and Tiner, 1948); Trematoda—Scaphiostomum pancreaticum and Postharmostomum helicis (Elwell, 1967; Rausch and Tiner, 1948); Nematoda-Trichostrongylus sp., a metastrongyloid (paratenic), Rictularia halli, Spirura michiganensis, Trichuris madisonensis, and Capillaria tamias-striati (Lankester and Anderson, 1966; Rausch and Tiner, 1948; Read, 1949; Tiner, 1950); and Acanthocephala-Macracanthorhynchus hirudinaceus and Moniliformis clarki (Van Cleave, 1953). Infestations by larval Cuterebra emasculator are common from July to October, generally occurring near the urogenital openings or between them and base of tail. Infested animals may exhibit splenomegaly, thymic involution, anemia, elevated leucocyte counts, and purulent wounds after larval emergence. There is little direct evidence of death from this parasitism (Bennett, 1973; Dorney, 1965; McKinney and Christian,

1970). Aedes cinereus and A. triseriatus commonly feed on T. striatus (Wright and DeFoliart, 1970). Ticks and mites found on chipmunks include Dermacenter variabilis, Haemaphysalis leporispalustris, Ixodes marxi, I. muris, I. dammini, Haemolaelaps glasgowi, Eulaelaps stabularis, Euschongastia peromysci, Sciurocoptes tamias, and Trombicula harperi (Carey et al., 1980; Fain and Hyland, 1970; Jones and Thomas, 1980; Parsons, 1962). Hypopial nymphs recorded from T. striatus are Aplodontopus sciuricola and one attributed to Dermacarus hylandi (Fain et al. 1971). Seasonal infestation rates by A. sciuricola were discussed by Tadkowski and Hyland (1979) who found 95% of 77 specimens infested. Fleas recorded from T. striatus are Tamiophila grandis, Stenoponia americana, Megabothris acerbus, M. quirini, Ceratophyllus gallinae, Ctenophthalmus pseudagyrtes, Monopsyllus vison, Orchopeas howardii, O. caedens, O. leucopus, Nosopsyllus fasciatus, Epitedia wenmanni, and Peromyscopsylla catatina (Amin, 1976; Lovejoy and Gaughan, 1975; Parsons, 1962). Parsons (1962) listed lice found on eastern chipmunks as Hoplopleura erratica and Enderleinellus tamiasus.

Aerial spraying of forests in Ohio with 0.81 kg/ha of malathion resulted in a 55% reduction in the chipmunk population (Giles, 1970). Chronic exposure of free-ranging chipmunks to gamma radiation resulted in a temporary weight loss of several grams (Buech, 1977). Acute exposure of free-ranging individuals to gamma radiation (200 to 400 roentgens) resulted in an increase in survival rate (Tryon and Snyder, 1973b), and in a reduction of range size and/or mobility of a population normally exhibiting relatively large home ranges (Snyder et al., 1976).

BEHAVIOR. Social organization was studied by Elliott (1978), Ickes (1974), and Yahner (1978c, 1978d). More restricted aspects of social behavior were reported by Aniskowicz and Vaillancourt (1979), Brenner et al. (1978), Dunford (1970), Herbig (1978), Wolfe (1966), Yerger (1953), and others. A solitary individual occupying a single burrow system is the basic social unit, except for the brief mother-offspring grouping (Yahner, 1978c). Individuals occupy broadly overlapping home ranges, but each spends most of its time within a core area defended by threat behavior, or by a chase which is usually short (3 to 4 m), but may extend up to 15 m (Ickes, 1974; Yahner, 1978c). Reversal of the dominant-subordinate relationship usually occurs if the chase extends into the core area of the intruder. Most chases do not result in physical contact, but biting by the dominant, and/or actual fights occur occasionally though no serious injury seems to result (Dunford, 1970; Elliott, 1978; Ickes, 1974). Space-independent factors affecting dominance relationships are weight, sex, age, and previous encounter experience (Brenner et al., 1978; Ickes, 1974; Wolfe, 1966). When they meet on "neutral" ground, chipmunks tolerate conspecifics at distances of 0.5 to 1.0 m, which are maintained by periodic short chases (Elliott, 1978; Yahner, 1978c). Yahner (1978d) found that behavior is more stereotyped in adults than young, in males than females, in breeding than nonbreeding seasons, away from rather than near home sites, and when a conspecific is nearby rather than when no conspecific is in the vicinity. Agonistic behavior accounted for less than 3% of a chipmunk's time budget.

During breeding periods, males are active early in the morning, inspecting burrow entrances, core areas of other chipmunks, and conspecifics encountered, and congregating on ranges of estrus females. According to Yahner (1978c), when only two or three males were involved in a mating bout, the dominant always copulated with the female and prevented access by others. If a large number of males (7 to 8) were present, however, the dominant male spent so much time chasing rivals that he never copulated with the female. One male may copulate several times with the same female and different males may also copulate with her during her estrus period.

Some mothers transport young to a neighboring burrow prior to emergence. Others may make a separate nest in their own burrow. Mothers become intolerant a few days after young emerge and the latter establish their own home within 2 weeks or less after emergence. Until then, they stay close to their burrows, remain friendly to each other, and frequently group together (Elliott, 1978; Yahner, 1978c). Roberts (1976) believed that most young make only short dispersal movements and that the average movement of a juvenile from its natal burrow to its later residence is less than the average radius of home range.

Captives studied by Wolfe (1969) explored extensively when first placed in an unfamiliar cage, but this tendency decreased as familiarity with surroundings increased. This behavior first appeared at 26 days of age, 4 days after young gained ability to walk and about a week before their eyes opened. Wolfe (1969)

found that both captive and free-ranging chipmunks generally exhibited neophilia in response to a new object although some transitory neophobia was noted in captives. Herbig (1978) found less neophilia in captives than did Wolfe; she also found that when chipmunks were allowed access to a large unfamiliar enclosure from an adjacent nest box, they more commonly explored visually by sitting at the entrance and peering than by actually entering the area.

Both sexes vocalize prominently; frequencies range from 1 to 11 kHz. Although the sounds form a graded series, at least four types can be distinguished: a single high-pitched "chip," a chiptrill, a series of chips close together referred to as chipping, and a low-pitched "cuk" given repeatedly. The chips are given as frequently as 130 times a minute and for as long as 11 minutes (Seton, 1929); sometimes several chipmunks form a chorus of chipping calls. See Dunford (1970) and Elliott (1978) for sonograms. All calls function as alarm signals, but most especially the chip-trill which is given frequently during an escape rush. Vocalizations also may have a territorial function (Dunford, 1970) or may alert individuals to presence of a predator (Elliott, 1978). There is some decrease in activity in late summer following the second breeding period and prior to juvenile emergence. Yahner (1977) also noted an activity lull after the late winter breeding.

The eastern chipmunk is strictly diurnal, and intensity of activity varies throughout the day; several authors have noted mid-morning and mid-afternoon peaks (Burt, 1940; Dunford, 1972; Wolfe, 1966). However, Yahner (1977) found that no individuals showed a bimodal pattern, but males were more active in morning and less active in afternoon than females. Thibault's (1969) results showed a primarily unimodal pattern with greatest activity between 0900 and 1300 and a peak from 1100 to 1200. This tended to decrease possible conflict with Tamiasciurus whose activity peak was between 1600 and 2000. Greatest activity occurs on bright, warm, quiet days (Forbes, 1966b). Graefe (1961) found that 35 to 45 Lux were sufficient to stimulate chipmunks to activity. Tamias has an endogenous free-running circadian rhythm of activity and can be entrained to a wide range of schedules (6L:18D to 21L:3D) (DeCoursey, 1972). In activity wheels, chipmunks show a strong directional tendency and apparently get their bearings from the light source or features of the environment (Kavanau, 1969). He raised the possibility that chipmunks may, therefore, use celestial objects and landmarks as navigational

Several investigators have studied homing behavior (Layne, 1957: Seidel, 1961). Individuals released at 100 or 200 m from point of capture were recaptured frequently at or near that point within a day or two, but some were recaptured in the opposite direction (Layne, 1957) or not seen again. Return frequency decreased when release distances were 300 m or more, but Seidel (1961) recovered two of four chipmunks from a distance of nearly 500 m. Return rate of juveniles is much poorer than that of adults. Although these return distances are greater than the span of the usual home range, Roberts' (1976) results demonstrating large lifetime home range size indicate that one cannot be sure the homing chipmunks were released into completely unfamiliar areas. Chipmunks can leap 380 to 610 mm on the level and more than 760 mm from a log or similar elevation (Jackson, 1961). Layne and Benton (1954) determined the average maximum running speed as 11.2 ft/s (12.2 km/h) with an extreme of 15.6 ft/s (17.1 km/h).

GENETICS. Karyotypes derived from bone marrow chromosomes have been discussed and figured (Nadler et al., 1977; Thompson, 1971). The diploid number is 38 and little or no intraspecific karyotypic variation is present. There are four pairs of large metacentric, six pairs of large submetacentric, and one pair of small metacentric autosomes. In addition, 3 pairs of autosomes are large acrocentrics and 4 pairs are small with terminal or subterminal centromeres. The X chromosome is a large submetacentric and the Y is minute and dot-like or submetacentric. Fundamental number is 58 (Nadler and Hoffmann, 1970). Based on size and G-bands, nine structural chromosomal differences between Tamias (Tamias) and Eutamias (Neotamias) have been demonstrated. Eutamias (Eutamias), for which G-banding data are not yet available, differs from Tamias (Tamias) in three autosomal arrangements and in having a larger Y chromosome with some structural differences.

Santiago and Rake (1973) estimated from reassociation kinetics that Tamias chromosomes have three different DNA fractions: a unique portion making up 75% of the total; a highly repeated portion (\sim 6,730 copies) constituting 12%; and a section with intermediate repetitiveness (\sim 99 copies) totaling 13%. They also estimated a genome size of 1.3×10^9 nucleotide pairs.

REMARKS. The genus Tamias was erected by Illiger (1811) for the chipmunks, those members of his "squirrel" family possessing cheek pouches. Trouessart (1880) created the subgenus Eutamias for the Siberian chipmunk and all American forms (including some ground squirrels) except the eastern chipmunk. Merriam (1897) raised Eutamias to generic rank, thus leaving the eastern chipmunk as the only species in the genus Tamias. Workers on the Siberian chipmunk tended to follow this separation and placed them in Eutamias also. Ellerman (1940) and Bryant (1945) argued for a single genus for all chipmunks, but White (1953) marshalled considerable evidence for the generic separation of the eastern chipmunk from all others as proposed by Merriam (1897), and until recently this arrangement was fairly widely followed. However, Nadler et al. (1977) suggested, primarily on the basis of karyotypic comparisons, that all chipmunks should be placed in the genus Tamias. Hight et al. (1974), using immunological evidence, seemed to lean toward this view also; but Ellis and Maxson (1979), utilizing a micro-complement fixation technique to quantify immunological characteristics of serum albumen, believed that two genera should continue to be recognized. Regardless of these questions the Recent species can be placed readily into three groups: subgenus Eutamias, the Siberian chipmunk, Eutamias sibiricus; subgenus Neotamias, the western (and northern) North American chipmunks; and subgenus Tamias, the eastern North American species. However, firm generic allocation of these groups is premature, and established usage (Hall, 1981) should be retained until additional cytological and biochemical data can be obtained from the Siberian chipmunk for comparison with those already available from the American forms.

Linnaeus' (1754) description of *T. striatus* was based on an American specimen (*fide* Baird, 1858) and the accounts of Catesby (1743) and Edwards (1751). In the 10th edition of *Systema Naturae*, Linnaeus (1758) referred to his 1754 description and cited Kalm (1756) in addition to Catesby and Edwards. The type locality restriction by Howell was based on the region Catesby was known to have traveled. There has never been any confusion concerning the distinctness of *T. striatus* from other North American chipmunks since their discovery, although it was regarded as conspecific with the Siberian chipmunk by some early workers (e.g. Gmelin, 1788; Linnaeus, 1766), who had no knowledge of other New World chipmunks.

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