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Author(s): Bradley J. Bergstrom and Robert S. Hoffmann

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## DISTRIBUTION AND DIAGNOSIS OF THREE SPECIES OF CHIPMUNKS (*TAMIAS*) IN THE FRONT RANGE OF COLORADO

BRADLEY J. BERGSTROM AND ROBERT S. HOFFMANN

*Department of Systematics and Ecology and Museum of Natural History,  
University of Kansas, Lawrence, KS 66045*

*Present address of BJB: Department of Biology, Valdosta State College,  
Valdosta, GA 31698*

*Present address of RSH: Assistant Secretary for Research, Smithsonian Institution,  
1000 Jefferson Drive, Washington, DC 20560*

**ABSTRACT**—Three species of chipmunks, *Tamias minimus*, *Tamias quadrivittatus* and *Tamias umbrinus*, were studied on the eastern slope of the Front Range in Boulder and Larimer counties, Colorado. *Tamias quadrivittatus* and *T. umbrinus* are similar in size and appearance and are parapatric in distribution. The line of parapatry was found to occur at an elevation of 2,130 m in the study area, which is a revision of the 2,440 m previously reported in the literature. *Tamias minimus* differs in appearance and ecology from its two congeners and occurs sympatrically with them over a broad range of elevations and habitats. Overwinter survival rates for the populations are less than one third, and local population extinction or near-extinction is a common occurrence. Univariate and multivariate morphometric analyses are presented, as are electrophoretic comparisons of the three species. The three may be clearly diagnosed by a number of characters; no evidence of hybridization exists, although Front Range populations of *T. umbrinus* converge toward *T. quadrivittatus* in electrophoretic profile, as compared to other populations of the two species that are not in geographic contact. Analysis of sonograms of the common vocalizations of the three species also shows that each has unique features. Possible mechanisms for the maintenance of parapatry are discussed.

Throughout much of the mountainous region of western North America, one or more species of chipmunks (*Tamias*) can be found inhabiting most coniferous forest, woodland, shrub, and alpine tundra habitats. As many as 23 species and 69 subspecies of western chipmunks (subgenus *Neotamias*) are currently proposed. Levenson et al. (1985) reviewed the systematics of the genus, which also includes *Tamias sibiricus* (subgenus *Eutamias*), found across much of northern Asia, and *Tamias striatus* (subgenus *Tamias*), which is limited to deciduous forests of eastern North America. Considerable external phenotypic and ecological variability is displayed between related species and conspecific populations of *Neotamias* inhabiting different areas and in contact with different assemblages of congeners (see Patterson, 1981; Sullivan, 1985).

The divergence of *Neotamias* and *Tamias* (see Levenson et al., 1985) about 10 to 13 million years ago in the late Miocene (Ellis and Maxson, 1979) resulted from the drying trend caused by

mountain-building and the consequent rain-shadow effect that occurred at various times across western North America between the early Eocene and late Pliocene (Axlerod, 1979). By the end of this period, the Great Plains was firmly established as an effective barrier between the two lineages. Phyletic divergence within *Neotamias* may have begun in the Pliocene with the isolation of two lineages on either side of the Great Basin (see Levenson et al., 1985). Again, during various glacial periods in the Pleistocene, the Great Basin was continuously forested or wooded (see Wells, 1983); speciation may have taken place during interglacials when mountain ranges became "forest islands." Present distributional patterns of mammalian species in the Great Basin suggest differential extinction in the relatively warm, dry post-glacial period (Brown, 1971; Grayson, 1987). Permanent barriers to dispersal between forest islands have existed in the West since the late Pleistocene (10,000 YBP; see Patterson, 1982), which may have contributed to the most recent

pulse of speciation and intraspecific differentiation of isolated populations of *Tamias*.

On the eastern slope of the Front Range of north-central Colorado, three species of *Tamias* occur. The smallest, *Tamias minimus operarius* (average weight of 44 g), is widespread, occurring in most habitats from lower montane open woodland-scrub to alpine tundra. *Tamias umbrinus montanus* (average weight of 59 g) occurs in all habitats except alpine tundra and the lowest band of montane woodland, about 500 m in elevational width. *Tamias quadrivittatus* (average weight of 62 g) is parapatric with *T. umbrinus*, generally occurring only in low-elevation habitats; however, each species occupies a much greater elevational range in regions where the other is absent (Armstrong, 1972).

*Tamias minimus* is the most widely distributed of all North American *Neotamias* species (Hall, 1981) and is a member of the "boreo-cordilleran faunal element" of Armstrong (1972). *Tamias m. operarius* is the most widespread and most euryecious chipmunk in Colorado (Hall, 1981). *Tamias quadrivittatus* is a Coloradan autochthon with "Chihuahuan-like" distribution that probably evolved on the Colorado Plateau; it reaches its northernmost distribution in a narrow peninsular projection along the eastern slope of the Front Range in Larimer Co., Colorado (Armstrong, 1972). Other Chihuahuan species, including *Peromyscus difficilis*, *Neotoma mexicana*, and *Spermophilus variegatus*, share nearly identical distributions in this area, inhabiting only rocky, open woodland at foothills elevations. *Tamias umbrinus* is a Great Basin species with several major disjunct populations (Hall, 1981), the easternmost of which is *Tamias u. montanus*. The latter is parapatric with *T. q. quadrivittatus*, abutting its congener from the west and north in Colorado.

*Tamias u. montanus* was first recognized as distinct from *T. q. quadrivittatus* by White (1953a, 1953b), based mainly on the morphology of the baculum. Parapatric distributions are the rule among western chipmunks (Findley, 1969; Hoffmann, 1974), with sympatry often occurring only in narrow overlap zones (e.g., Brown, 1971; Heller, 1971; Sheppard, 1972). When two or more species' ranges approach each other, there is some evidence of ecological, as well as morphological, shifts. Often morphological shifts involve convergence (Long and Cronkite, 1970; Armstrong, 1972; Patterson, 1981) and represent evolution-

ary responses to the particular assemblage of congeners present (Patterson, 1981). Morphological, biochemical, and ecological variability can be equally pronounced among populations of widespread species such as *T. minimus* (Sullivan, 1985). *Tamias m. operarius* in the Front Range is widely sympatric with both of its larger congeners, and it is not elevationally restricted as are other populations of *T. minimus* in proximity to different assemblages of *Tamias* (Heller, 1971; Sheppard, 1972; Patterson, 1981).

This study documents the precise distributions of these three species of *Tamias* along a portion of the eastern slope of the Front Range. It also compares morphological, biochemical, and ecological attributes, including habitat distribution, relative abundance, and overwinter survival, of the populations in these areas.

**MATERIALS AND METHODS**—Sixty-eight sites located along several elevational transects ranging from 1,700 m to 2,900 m were chosen for live trapping and habitat analysis (Fig. 1). Most of these sites were located within the Roosevelt National Forest in Larimer and Boulder counties, Colorado. They represented ecosystems ranging from grassland-lower montane ecotone to upper montane-subalpine ecotone (Marr, 1961). Chipmunks were observed but not trapped at 11 additional sites, representing mostly subalpine-alpine ecotones up to 3,200 m. Live trapping was conducted at each site for at least 2 weeks, with traps checked twice daily during the summers of 1981 and 1982. Additional trapping and observational records were obtained in the fall of 1980 and the summers of 1983 and 1984. Sherman live traps (3.5 by 3.5 by 23.0 cm) were baited with a mixture of rolled oats, scratch grain, and sunflower seeds and provided with cotton nesting material. Trapping grids varied from 24 to 36 stations with a trap spacing of 25 to 35 m and 1 trap/station. Two grids used as part of a longer study consisted of 64 and 120 stations, respectively. A minimum, therefore, of about 300 trap-days/site was maintained. Since the effective area trapped by each grid was hard to determine and likely varied in different habitats (Van Horne, 1982), actual densities were not calculated, but rather a relative index of captures per unit trapping effort was used to represent abundance of the three chipmunk species on a scale of 0 to 4. In two cases, sight records of a species not captured were considered in the presence-absence data and caused a species' abundance rank to change from 0 to 1 for that site.

Information recorded for each chipmunk captured included standard body measurements, weight, sex, age (juvenile or adult), molt condition, reproductive condition, vocalizations and behavior during handling, and period of day when captured. One hundred-eighty

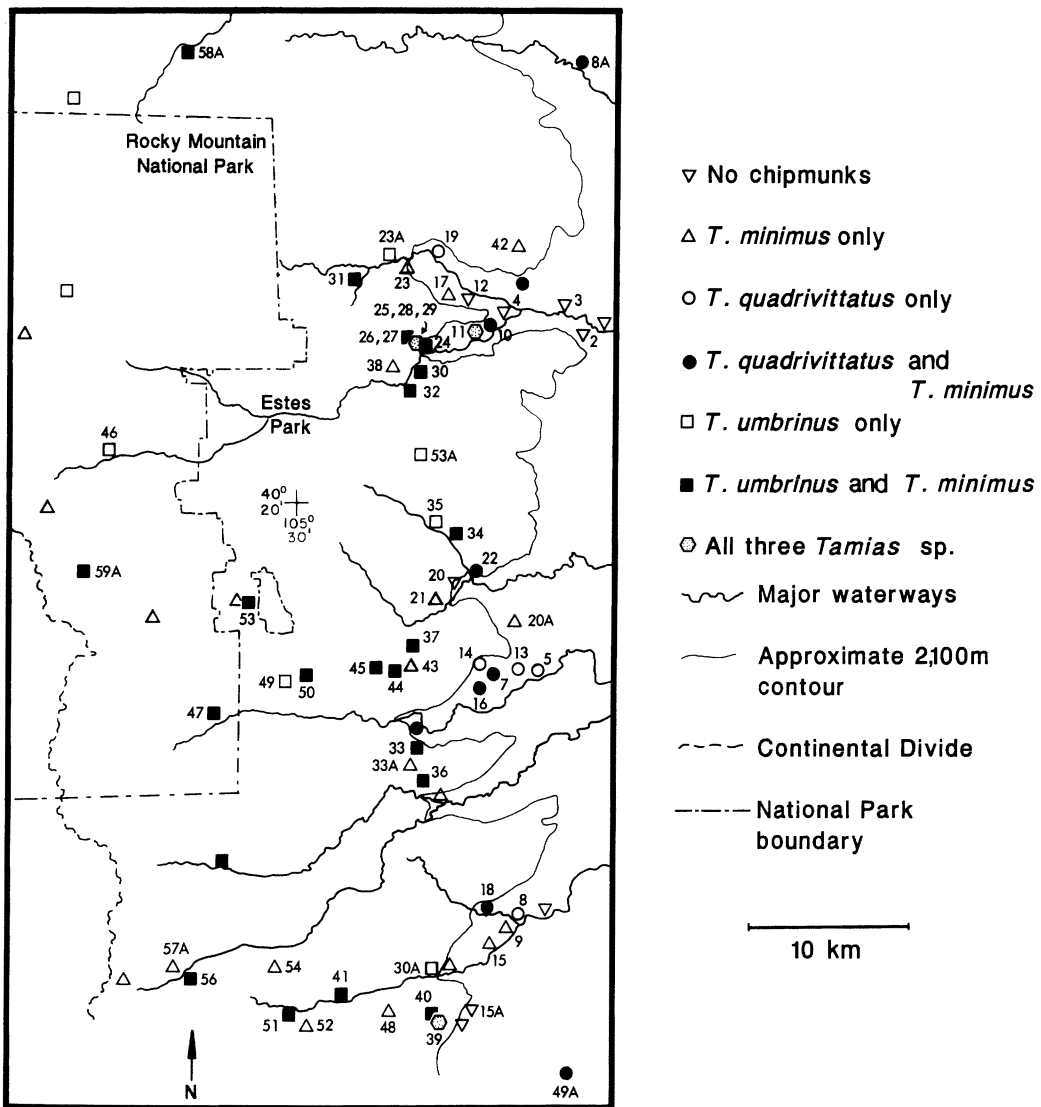


FIG. 1—Map of study areas along the Eastern Slope of the Front Range showing the 68 trapping sites (see Table 1) plus additional observation sites, indicating which of the three species of *Tamias* were present. Most of this area lies within the Roosevelt National Forest in Larimer and Boulder counties, Colorado. The 2,100-m contour line shows the approximate elevation of parapatry between *Tamias quadrivittatus* and *Tamias umbrinus*.

specimens were taken for morphometric and electrophoretic analysis. Skulls and postcranial skeletons were cleaned, and study skins were prepared. Bacula and baubella were prepared by a clear-and-stain procedure: tissues were cleared in a solution of 2% potassium hydroxide and stained with alizarin red, then destained in the potassium hydroxide solution, after which the bones were dissected out. Blood from live-trapped animals was obtained through cardiac puncture and separated by centrifugation. Red blood cells were lysed with distilled water, and both serum and hemolysate

were frozen immediately. Livers and kidneys of sacrificed animals were also frozen for electrophoresis.

Morphometric variables measured were as follows: length of body (BOD), length of ear (EAR), length of hind foot (HF), length of tail (TL), greatest length of skull (GLS), jugal diameter (JD), zygomatic breadth (ZB), cranial height (CH), condylozygomatic length (CZL), length of nasals (LN), length of diastema (LD), length of bacular shaft (BSL), width of bacular base (WBB), depth of bacular keel (DBK), maximum dorso-ventral depth of baculum (BDV), length of bacular

tip (BTL), angle of baculum tip to shaft (ABT), length of baubellar shaft (BAS), width of baubellar base (BAB), length of baubellar tip (BAT), maximum dorso-ventral depth of baubellum (BADV). Cranial measurements were made to the nearest 0.1 mm using dial calipers. Bacular and baubellar measurements were made to the nearest 0.05 mm with an ocular micrometer. Cranial and body measurements were also obtained from specimens examined in the research collections of The University of Colorado Museum, Colorado State University, United States Fish and Wildlife Service Denver Wildlife Research Center, and The University of Kansas Museum of Natural History (KUMNH). All newly collected specimens were deposited at KUMNH. Morphometric data analysis employed stepwise discriminant function analysis (BMDP7M) and principal components analysis (BMDP4M).

Blood and tissue samples were scored for 16 presumptive gene loci using standard starch-gel allozyme electrophoresis (Nadler et al., 1982). Vocalizations of chipmunks in the field were recorded using a Uher 4000 Report-L tape recorder; sonagrams were made on a Kay Sona-Graph 7029A 5-16000 Hz spectrum analyzer.

**RESULTS—Distributional Patterns**—Distribution of the three species of *Tamias* indicates that the 2,130-m contour line is a good predictor of parapatry between *T. umbrinus* and *T. quadrivittatus* along each of the elevational transects (Fig. 1). Table 1 gives the exact elevation and relative densities of the three species at each site, along with the designation of those of the 14 major plant community types (see Fig. 2) that occurred at each site. *Tamias minimus* was common at all elevations above 1,980 m. Chipmunks of all species were uncommon below 1,890 m (although B. J. Bergstrom has seen *T. minimus* as low as 1,750 m elsewhere in Larimer Co.). *Tamias umbrinus* was found at numerous localities near and slightly above 2,100 m, whereas *T. quadrivittatus* was common up to 2,130 m, and was occasionally found in low densities up to 2,200 m; its lower limit in the study area was 1,890 m. A single *T. quadrivittatus* was found as high as 2,375 m. However, at only three trapping sites were *T. quadrivittatus* and *T. umbrinus* captured in close proximity (<100 m horizontal distance). Only at one of these areas (Long Gulch: sites 25, 28, 29) did the two species have overlapping home ranges (at site 11, only one *T. umbrinus* was caught at the upper end of a tributary gulch at 2,130 m, about 30 m elevation above where the highest *T. quadrivittatus* was captured). Long Gulch was a gently falling tributary, where actual horizontal

overlap between the two species of 500 m occurred over a mere 15-m gradient in elevation.

These transects generally followed the most monotonic gradients in elevation up the eastern slope, i.e., the major drainages. However, there are several areas east of the parapatric boundary that exceed 2,130 m in elevation. These are the easternmost pre-Cambrian fault blocks of the Front Range. At one of these areas (Green Mountain, 5 miles W Boulder, 2,590 m elev.) *Tamias minimus* and *T. quadrivittatus* were common, but *T. umbrinus* was absent. At another such area in Larimer Co. (Lory State Park), B. J. Bergstrom has seen *T. quadrivittatus* up to 2,350 m.

**Patterns of Relative Abundance**—In 30 of the 68 study sites, *T. minimus* was sympatric with one or both congeners. There was a trend toward higher average abundance of *T. minimus* in allopatry ( $\bar{X} = 2.2$ ,  $n = 9$ ) than in sympatry ( $\bar{X} = 1.97$ ,  $n = 30$ ), although not statistically significant (Mann-Whitney  $U$ ,  $P = 0.1$ ). Also, in the 30 sympatric sites, *T. minimus* was the most abundant species in eight and tied for most abundant in seven. The expected decline of abundance of a species toward the periphery of its range (Brown, 1984) was displayed by *T. minimus*, as its abundance correlated negatively with elevation across the study area ( $P < 0.006$ ). This effect could not be explained by the presence of *T. umbrinus*, as already discussed. The study area also included peripheral populations of both *T. quadrivittatus* and *T. umbrinus*. No relationship with elevation was detected for *T. umbrinus*, and *T. quadrivittatus* is "peripheral" everywhere it occurs in north-central Colorado, so the comparison is not possible in this study.

By dividing the 68 study sites (Table 1) into potential *T. quadrivittatus* sites (<2,170 m) and *T. umbrinus* sites (>2,100 m), we tested for patterns of reciprocal abundance between each of these species and *T. minimus* (generally considered a necessary but not sufficient pattern for demonstrating competition). Overall, there was no significant correlation in either case ( $r = 0.092$  and 0.009, respectively), although *T. minimus* was most abundant in a site (38) with no other congeners and a habitat type not generally occupied by the other two species (i.e., low-gradient ponderosa pine "parkland"). In general, therefore, *T. minimus* was broadly sympatric with both *T. quadrivittatus* and *T. umbrinus* in this area, contrary to the findings of Long and Cronkite (1970) in central Colorado.

TABLE 1—List of localities, habitat designations (see Fig 2), and rank abundance classes of the three species of chipmunks (M = *Tamias minimus*; Q = *Tamias quadrivittatus*; U = *Tamias umbrinus*). See text for further explanation.

Locality	Elevation (m)	Habitat designation	M	Q	U	Total
1	1,705	1	0	0	0	0
2	1,770	5	0	0	0	0
3	1,830	2	0	0	0	0
4	1,950	1	0	0	0	0
5	1,890	2, 3	0	4	0	4
6	1,980	4, 2	2	4	0	6
7	1,980	5	2	2	0	4
8	1,980	4, 2	0	3	0	3
8A	1,980	5	2	2	0	4
9	1,990	4, 3	1	0	0	1
10	2,010	5	2	3	0	5
11	2,030	5	2	3	1	6
12	2,050	5, 3	0	0	0	0
13	2,040	4	0	1	0	1
14	2,040	4	1	1	0	2
15	2,040	4, 3	1	0	0	1
15A	2,050	2	0	0	0	0
16	2,070	5	1	4	0	5
17	2,070	5, 1	2	0	0	2
18	2,080	4	2	1	0	3
18A	2,100	5	0	0	3	3
19	2,105	5	0	3	0	3
20	2,100	5	0	0	0	0
20A	2,100	3	4	0	0	4
21	2,140	4, 5	3	0	0	3
22	2,140	5	1	2	0	3
23	2,130	1, 5	1	0	0	1
23A	2,160	5	0	0	2	2
24	2,110	5, 4	3	1	2	6
25	2,115	4, (9, 10)	2	1	4	7
26	2,160	10, 4	1	0	4	5
27	2,225	5	2	0	3	5
28	2,195	5	2	1	2	5
29	2,160	5, 4	3	1	3	7
30	2,165	5	0	0	4	6
30A	2,170	5	0	0	2	2
31	2,180	5	2	0	3	5
32	2,190	4	1	0	2	3
33	2,190	4, 5	3	0	1	4
33A	2,250	5, 3	2	0	0	2
34	2,255	5	2	0	2	4
35	2,285	4	0	0	3	3
36	2,315	5	2	0	1	3
37	2,345	4, 3	2	0	2	4
38	2,260	3	4	0	0	4
39	2,375	4	1	1	1	3
40	2,440	4	1	0	2	3
41	2,440	4	3	0	2	5
42	2,320	3, 5	2	0	0	2
43	2,470	4	1	0	0	1
44	2,500	5	1	0	3	4
45	2,560	4	3	0	0	5

TABLE 1—Continued.

Locality	Elevation (m)	Habitat designation	M	Q	U	Total
46	2,560	5, 10	0	0	3	3
47	2,570	7	3	0	2	5
48	2,590	3	3	0	0	3
49	2,590	6	0	0	1	1
49A	2,590	5	3	3	0	6
50	2,620	4, 6	1	0	1	2
51	2,665	5	1	0	2	3
52	2,750	5, 6	3	0	0	3
53	2,740	5, (9, 10)	3	0	4	7
53A	2,750	6	0	0	1	1
54	2,925	8	3	0	0	3
55	2,070	5	3	3	0	6
56	3,230	7	3	0	2	5
57A	3,240	7	3	0	0	3
58A	3,430	7, 8	2	0	2	4
59A	3,440	11, 8	3	0	1	4

**Habitat Distribution**—Fourteen major types of plant community were defined in the study area (Fig. 2). *Tamias minimus* clearly was more euryecious than its congeners in its use or tolerance of “marginal” chipmunk habitats. It is the only species that is frequently found outside of forest or woodland habitat (such as habitats 9 through 13). In other areas of Colorado, it is found in greasewood and sagebrush flats (Armstrong, 1972; J. H. Honacki, pers. comm.), as well as pinyon pine (*Pinus edulis*)-juniper (*Juniperus scopulorum* or *Juniperus monosperma*), oak (*Quercus gambellii*), and aspen (*Populus tremuloides*) woodlands (Sullivan, 1985). In this study, it was the only *Tamias* species found above treeline, in meadows (see Telleen, 1978), in level, non-rocky shrubby habitats, or in wooded areas with dense, herbaceous understory. *Tamias minimus* was common also in unbroken montane forests of ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga mensiezi*), contrary to Armstrong (1972), and subalpine forests of spruce and fir, where it occurred sympatrically with one or the other congener. The only type of closed forest in which Telleen (1978) and we did not find *T. minimus* was lodgepole pine (*Pinus contorta*) stands, where only low densities of *T. umbrinus* were found. In the other type of single-species tree community, limber pine (*Pinus flexilis*) woodland, Telleen (1978) reported predominantly *T. umbrinus*. The present study included only one such stand (locality 54, Fig. 1), and it contained only *T. minimus*. This limber pine site

was an edaphic climax growing on mine spoils, whereas Telleen's (1978) sites were at higher elevations and were climatic climaxes. All three species of chipmunks may be found and are potentially abundant in habitats 2 through 5 (i.e., lower montane coniferous woodland). *Tamias quadrivittatus* appears the most ecologically restricted of the three, but only five habitat types (see Fig. 2) occurred within its 400-m elevational range, and it inhabited four of them (2, 3, 4, 5; though it was uncommon in 3). In contrast, there was a greater diversity of habitats (13 types) available to *T. umbrinus*, and it was not found in six of them (found in 2, 3, 4, 5, 6, 7, 11; though uncommon in 3 and 11). Four of the 14 habitats potentially occupied by *T. minimus* probably only supported low-density populations or transient individuals (1, 9, 10, 14); *T. minimus* was commonly found in all others but was absent from 6.

**Survival and Population Patterns**—Survivorship over winter could be determined accurately only between 1983 and 1984, when 14 of 51 chipmunks (three species combined) or 27.5% were recaptured in areas trapped both years. There were three cases of survival over 2 years; one female survived 3 years and was judged to be at least a year old upon first capture. Local population extinction was documented twice in the course of fieldwork. The small population of *T. quadrivittatus* at adjacent sites 25, 28, and 29 in the parapatry zone numbered six in 1982 and five in 1983 (a previously unmarked lactating female and four young-of-the-year, all trapped

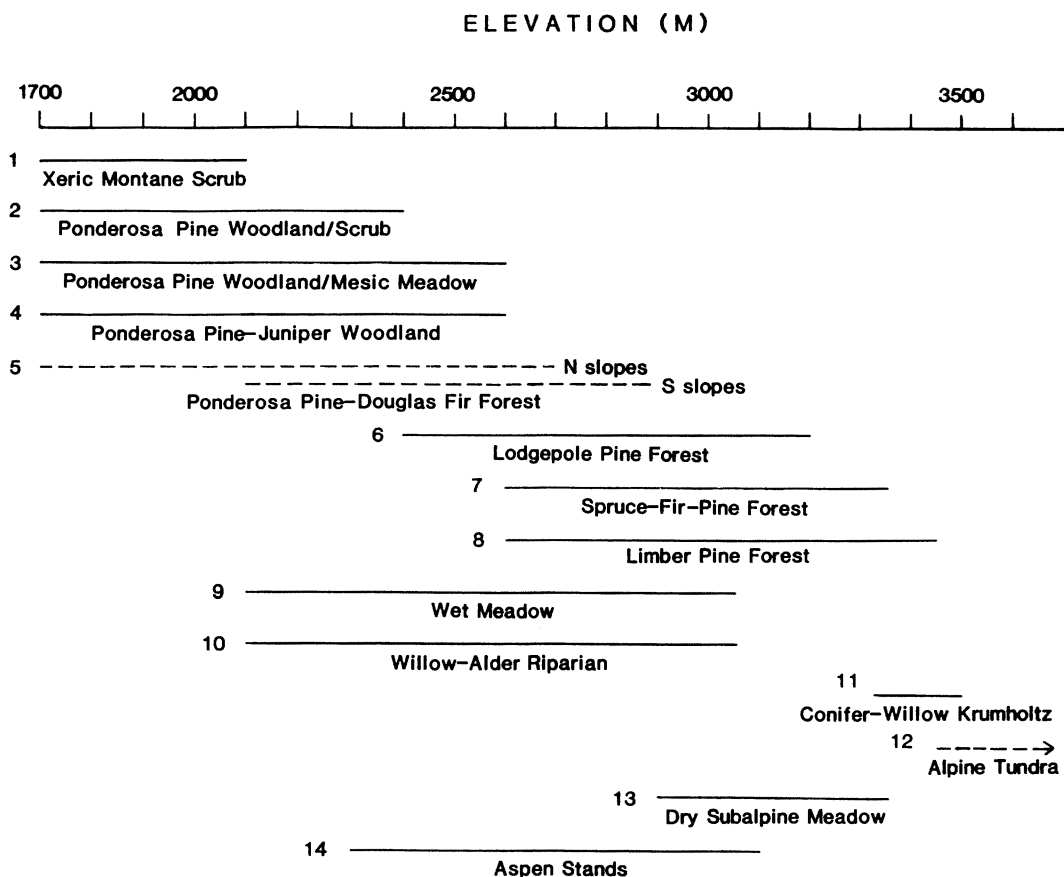


FIG. 2—Elevational distribution of 14 major plant community types found in the study area. Chipmunks were most common in habitats 2 through 5, 7, and 11. Chipmunks were rarely found in habitat 1. Other habitats were not extensively sampled in this study, but generally only *Tamias minimus* was observed in habitats 9 through 14 (see Table 1). Some terminology is after Marr (1961).

within 200 m of one another) and was extinct from late 1983 through 1985. Populations of *T. umbrinus* and *T. minimus* in the same area were initially much larger (minimum number alive, MNA = 40, 30, respectively) and also declined (MNA = 20, 15) from 1982 to 1984. At locality 53 (a 7.5-ha grid at 2,700 m), 25 *T. umbrinus* were known to be alive in late summer 1983. Only one (pregnant) female *T. umbrinus* was left by May 1984, and she disappeared before parturition. No other *T. umbrinus* were found on this grid in May or June; on 7 July a single adult male, presumably a migrant, was trapped on the edge of the grid and was occasionally trapped again in August and September. The population of *T. minimus* on this grid also declined, from 27 to five (MNA), over this period.

Although the cause of this precipitous decline could not be determined, two plausible possibilities exist. Bubonic plague is known to affect chipmunk populations in this area. Although no outbreaks were reported at that time, plague epizootics can be highly localized and species-specific (G. O. Maupin, pers. comm.). A dead *T. minimus* found on the site in early May appeared emaciated and had an empty stomach, but no other injuries or signs of disease were noticed upon necropsy. A more likely explanation was the poor Douglas-fir cone crop in 1983, followed by a harsh and unusually prolonged winter, with snow depths well above average in May 1984. *Tamias umbrinus* is more reliant on the mast crop than is *T. minimus*, which can more easily meet its energy requirements by exploiting a variety



of herbaceous seeds of small size (see Bergstrom, 1986).

**Cranial and External Morphometrics**—Using the 11 cranial and body measurements in a stepwise discriminant function analysis, the sexes could not be distinguished within any species (multivariate analysis of variance, all  $P > 0.05$ ) and were pooled for further analyses. Principal components analysis of these 11 variables produced two components that accounted for 72% of the variation. The first was a general size component, with all variables showing strong positive loadings. This ordered the species as *T. quadrivittatus* (Q) > *T. umbrinus* (U) > *T. minimus* (M). The second component was a contrast between tail length and JD. This ordered the three species from M (which had the relatively longest tail and relatively and absolutely thinnest jugal) to Q (which had the thickest jugal). A univariate comparison of the three species showed that M was significantly distinct from both Q and U in all 11 measurements except TL ( $t$ -tests, all  $P < 0.05$ ). Of course, univariate statistics represent only size, not size-independent shape. Table 2 gives the means and standard deviations of body and skull measurements for the three species (body weights: M,  $43.56 \pm 6.43$ ,  $n = 176$ ; Q,  $61.5 \pm 7.27$ ,  $n = 102$ ; U,  $59.32 \pm 7.67$ ,  $n = 146$ ). Coefficients of variation for GLS are larger than those reported for *T. quadrivittatus* by Patterson (1984), who used mostly single localities for samples. The samples in our study may include some micro-geographic variation.

Discriminant function analysis produced a 97% correct jackknifed classification of all individuals in two canonical axes (Fig. 3) by a model incorporating seven variables. Axis 1 was mainly a contrast of JD and CH (loading positively) with LD; the second axis contrasted JD with LD and ZB. To determine which variables best distinguished *T. quadrivittatus* from *T. umbrinus*, we ran a separate analysis which produced one axis that was a contrast between JD (loading positively) and LD; CZL and EAR had relatively small positive loadings. Jackknifed classification was 98% accurate with this four-variable model, although the F-ratio for group separation was most significant with only JD in the model. Thus, JD was a nearly diagnostic feature, as Armstrong (1972) suggested. *Tamias quadrivittatus* also had a relatively higher cranium and shorter rostrum than *T. umbrinus*, as White (1953a) suggested.

To see whether there was any convergence (or

TABLE 2—Means, standard deviations, and coefficients of variation for 11 cranial and body measurements of *Tamias quadrivittatus* (Q), *Tamias umbrinus* (U), and *Tamias minimus* (M).

Variable	Q	U	M	All species
Means				
JD	1.800	1.423	1.247	1.476
GLS	35.232	35.564	32.036	34.539
ZB	19.455	19.043	17.702	18.797
CH	14.162	13.858	12.902	13.685
CZL	27.321	26.692	24.547	26.289
LN	11.147	11.142	9.655	10.747
LD	8.923	8.814	7.943	8.612
CB	16.770	16.439	15.753	16.345
TAIL	95.511	98.120	90.064	95.288
HF	34.447	34.084	31.340	33.452
EAR	19.660	18.410	16.170	18.147
BOD	130.191	126.507	110.128	123.136
<i>n</i>	47.000	83.000	47.000	177.000
Standard deviations				
JD	0.153	0.117	0.133	0.132
GLS	2.927	0.696	0.727	1.623
ZB	0.452	0.469	0.516	0.477
CH	0.273	0.254	0.292	0.270
CZL	0.604	0.708	0.580	0.649
LN	0.398	1.028	0.471	0.774
LD	0.338	0.359	0.337	0.348
CB	0.396	0.291	0.285	0.321
TAIL	14.911	10.020	12.423	12.120
HF	1.897	1.242	1.323	1.463
EAR	1.536	1.240	1.592	1.421
BOD	12.064	6.133	8.329	8.634
Coefficients of variation				
JD	0.085	0.082	0.107	0.089
GLS	0.083	0.020	0.023	0.047
ZB	0.023	0.025	0.029	0.025
CH	0.019	0.018	0.023	0.020
CZL	0.022	0.027	0.024	0.025
LN	0.036	0.092	0.049	0.072
LD	0.038	0.041	0.042	0.040
CB	0.023	0.018	0.018	0.020
TAIL	0.156	0.102	0.138	0.127
HF	0.056	0.036	0.042	0.044
EAR	0.078	0.067	0.098	0.078
BOD	0.093	0.048	0.076	0.070

divergence) in cranial morphology between *T. quadrivittatus* and *T. umbrinus* near their contact zone, we calculated the linear distance of the point of capture for each animal from the nearest location of parapatry (ranging from 0 to 170 km) and then calculated a Spearman's rank correla-

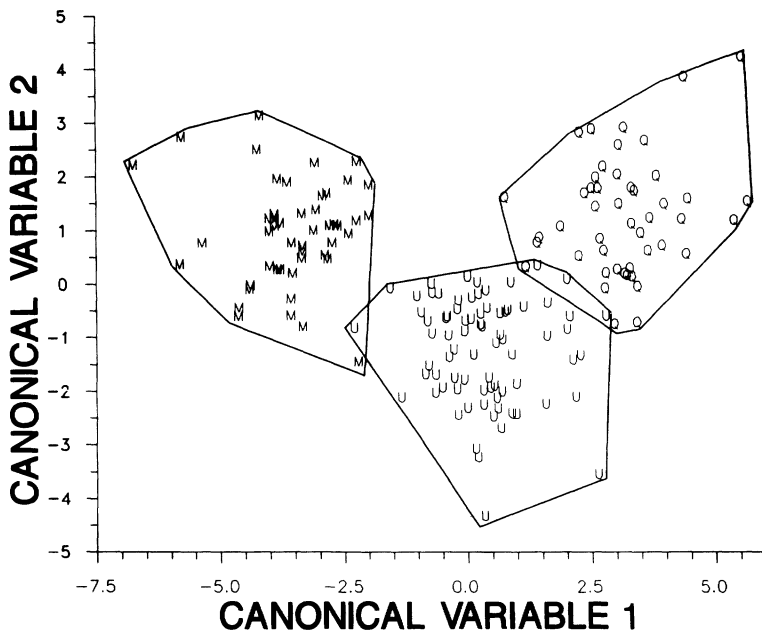


FIG. 3.—Discriminant function analysis of cranial and body measurements showing relative separation of *Tamias minimus* (M), *Tamias umbrinus* (U), and *Tamias quadrivittatus* (Q) in two canonical dimensions.

tion of this variable with the Mahalanobis distance of each animal from the centroid of the other species. There was no relationship (two-tailed test,  $P > 0.5$ ).

**Bacular and Baubellar Variation**—Bacular shape was conservative within species (Fig. 4A) and was used as a reliable diagnostic feature for identification of questionable specimens (see White, 1953a). In general the baculum of *T. quadrivittatus* is long and thin with a pronounced keel and obtuse angle ( $125 \pm 6.1^\circ$ ) between base and shaft (ABT). That of *T. umbrinus* is short, robust, with a pronounced keel, and more rectangular ( $100 \pm 8.8^\circ$  ABT). The baculum of *T. minimus* is of intermediate length, slender, and obtuse ( $136 \pm 7.4^\circ$  ABT). Stepwise discriminant function analysis of bacular metrics produced a three-variable model (BSL, WBB, BTL) with 100% jackknifed classification.  $F$ -tests for pairwise comparisons were all highly significant ( $P \ll 0.001$ ). Coefficients of variation for the six variables ranged from 0.06 to 0.11 ( $\bar{X} = 0.08$ ). The baubellum, in contrast, is much more variable within species, though still diagnostic (Fig. 4B). That of *T. umbrinus* is the most robust (greatest BADV) and has a pronounced lip surrounding the tip laterad and producing a bump dorsad, which makes an acute angle between the tip and the dorsal surface

of the shaft. In *T. quadrivittatus*, this angle is much smaller, but shaft length is about equal to *T. umbrinus*. The baubellum of *T. minimus* is the smallest and most variable in shape of the three species. In each species, the baubellar base varies from those having two pronounced prongs to those in which the prongs are progressively more coalesced. Stepwise discriminant function analysis of baubellar metrics chose only BADV, which distinguished *T. umbrinus* and *T. minimus* but could not discriminate *T. quadrivittatus*, which was variable and intermediate for BADV. The presence of the dorso-lateral lip on the tip distinguished *T. umbrinus*, and *T. quadrivittatus* and *T. minimus* were significantly different ( $F = 10.11$ ,  $P < 0.02$ ) in BADV. Coefficients of variation were higher for baubellar than for bacular measurements, ranging from 0.08 to 0.28 ( $\bar{X} = 0.17$ ).

**Allozymic Variation**—*Tamias m. operarius* from the Front Range was allozymically similar to other populations of *T. minimus* with the A-karyotype (Nadler et al., 1977) for the 16 loci scored (see Levenson et al., 1985). *Tamias quadrivittatus* from this area was electrophoretically identical to other populations examined; however, allozymes of *T. u. montanus* converged toward those of *T. quadrivittatus* in the Front Range in four loci, as compared to populations of the same and

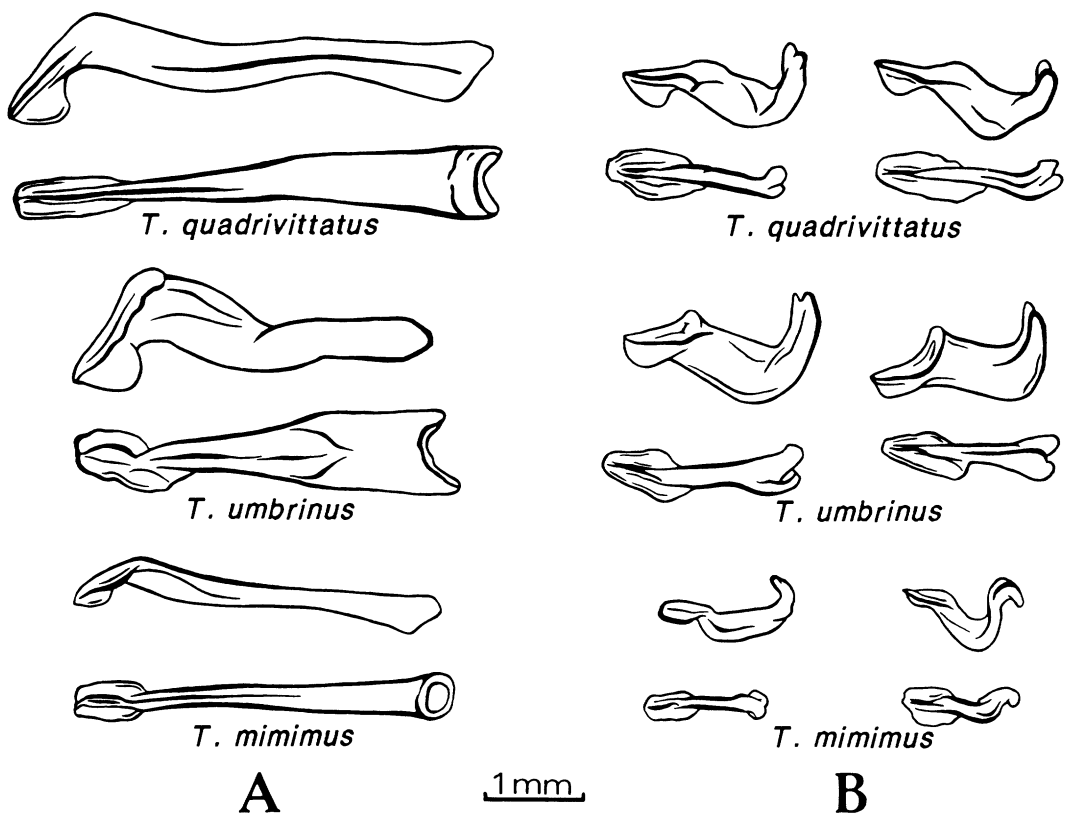


FIG. 4—Lateral (top) and dorsal (bottom) views of the genital bones of three species of *Tamias*. Base (proximal) is to the right and tip (distal) is to the left. A) bacula; B) baubella: two individuals from each species chosen to represent intraspecific variation in shape.

different subspecies elsewhere (data included in Levenson et al., 1985). Whereas these latter populations differed diagnostically from *T. quadrivittatus* at five loci, in this study *T. umbrinus* from the Front Range differed from *T. quadrivittatus* at only one locus (an esterase), for which the two species were fixed for different alleles. No heterozygotes were found in 138 individuals, indicating no evidence for hybridization.

**Vocalizations**—Four classes of calls were recognized and recorded: chip, trill, chipper, squeal (Brand, 1976). Chips commonly were emitted by all species, usually from a promontory in bouts ranging from a few seconds to 15 min. In most of these cases, especially the longer bouts, the regularly spaced chips were given in synchrony with a tail flick (see Bergstrom, 1986). Chipping displays seldom were given in response to any predator apparent to the observer and often were initiated long after he had sat down to observe

feeding-station activity. In fact, on three occasions when accipiters made low passes through an area where chipmunks were present, either no chips were given, or only single, scattered chips or short bouts of chips were given. However, on two other such occasions, chipmunks did conduct chipping bouts of 2 min and 5 min each. Trills were sometimes interjected into bouts of chips. Both chips and trills were emitted by animals in traps when observers approached. There were interspecific differences in tendency to vocalize in the trap: *T. umbrinus* vocalized 55% of the time ( $n = 370$ ); *T. quadrivittatus* 11% of the time ( $n = 120$ ); *T. mimimus* 19% of the time ( $n = 262$ ). Squeals were often emitted during handling of animals. These were similar to sounds made by juveniles when distressed but were made by animals of all ages. Again, there were species differences in rates of squealing during handling: 46% for *T. quadrivittatus*; 16% for *T. umbrinus*; 0.4% for *T. mini-*

*mus*. Curiously, *T. quadrivittatus* and *T. umbrinus* also frequently entered a "trance" lasting about a minute after being held by the nape during handling, during which they were completely immobile, whereas *T. minimus* never responded in this way to handling. Chippers were emitted typically during flight but were sometimes difficult to distinguish from trills.

Sonagrams were made of several calls in each category for each species (Fig. 5). All chips were sharp (peaked) tones in the form of chevrons, usually with several harmonics. In certain individuals of each species, a short, low-frequency pulse immediately followed the chevron. Dominant frequencies varied widely (4.5 to 15 kHz in *T. umbrinus*, generally lower for the other species, down to 2.5 kHz in *T. minimus*). The chips of *T. quadrivittatus* had distinctive tonal quality in that they were raspy, whereas the chips of the other two species were clearer. Chips of *T. quadrivittatus* also had the longest and greatest variation in syllable length ( $77.9 \pm 25.0$  ms), compared to *T. minimus* ( $45.8 \pm 4.15$  ms) and *T. umbrinus* ( $54.8 \pm 4.49$  ms). Trills (*sensu* Brand, 1976) were recorded only for *T. umbrinus*, and consisted of an initial chip followed by several lower-frequency pulses spaced at about 30 ms, which alternated in tonal quality between clear and raspy. Chippers were highly variable in number and spacing of pulses, frequency, and tonal quality; some consisted of steadily falling frequencies, others of rising and falling frequencies.

Squeals consisted of pulses ranging from 290 to 375 ms and had either one intense band with several harmonics or two or more equally intense bands at different frequencies. Lowest bands in *T. quadrivittatus* and *T. minimus* occurred at 6 kHz, whereas the squeal of *T. umbrinus* seemed more complex, having a lowest frequency band at 4 kHz and more harmonics than the squeals of its congeners.

Observations of 21 bouts of chipping (>1 min) indicated that pulse frequency varied from 80 to 315 chips/min, with *T. minimus* ( $257 \pm 35$ ) averaging higher than *T. umbrinus* ( $194 \pm 41$ ) and *T. quadrivittatus* ( $186 \pm 53$ ). Brand (1976) reported that pulse frequency of chipping correlated inversely with body size over broader comparisons of *Tamias*. Tail movements usually were associated with chipping bouts (see Bergstrom, 1986). Tail movements of *T. quadrivittatus* and *T. umbrinus* typically had a horizontal component

(a slow, side-to-side "sway"), whereas those of *T. minimus* were typically vertical (a rapid upward "flick").

**DISCUSSION**—The estimate of 2,440 m (8,000 feet) for the line of parapatry between *T. quadrivittatus* and *T. umbrinus* (Armstrong, 1972) should be revised downward to 2,130 m (7,000 feet) for the study area. The precise parapatry exhibited in the Front Range between *T. umbrinus* and *T. quadrivittatus* is similar to the distributions of other species assemblages of *Tamias* (e.g., Brown, 1971; Heller, 1971), consisting of elevational bands with little overlap. However, at least in this study, it is apparent that the species do not respond precisely or exclusively to any environmental factor controlled by elevation (the line of parapatry is better regarded as an east-west separation). If such were the case, we would expect a more fine-grained mosaic of distributions, corresponding faithfully to the topography. That this does not occur perhaps implies only a historical accident. Limited vagility alone probably does not account for the absence of *T. umbrinus* on Green Mountain, for example, which is no more than 8 km east of its range and an elevation of 2,590 m, since individual chipmunks can move up to 3.2 km in a few days to get to large, unnatural food concentrations (Telleen, 1978). The intervening lower-elevation habitats are not likely to act as dispersal barriers, as *T. u. montanus* is found in open pinyon-juniper habitats at 1,700 m along Douglas Creek, south of Rangely, Rio Blanco Co., Colorado (B. J. Bergstrom, pers. obser.). Localized population extinctions and near-extinctions were documented within large, continuous habitat patches during this 4-year study, and, of course, "island" populations such as Green Mountain would be even more susceptible to extinction.

Interspecific interactions are strongly implicated as the causal mechanism of parapatry, especially given that the ecologically divergent *T. minimus* is capable of sympatry with each of its larger congeners. However, in light of the fact that the more widely distributed species across all taxa tend to be more locally abundant (Brown, 1984), the finding of this study that *T. minimus* was not decidedly the most abundant chipmunk may suggest that the presence of a congener negated the expected trend for populations of *T. minimus* in the Front Range. Another factor potentially affecting the local abundance of *T. min-*

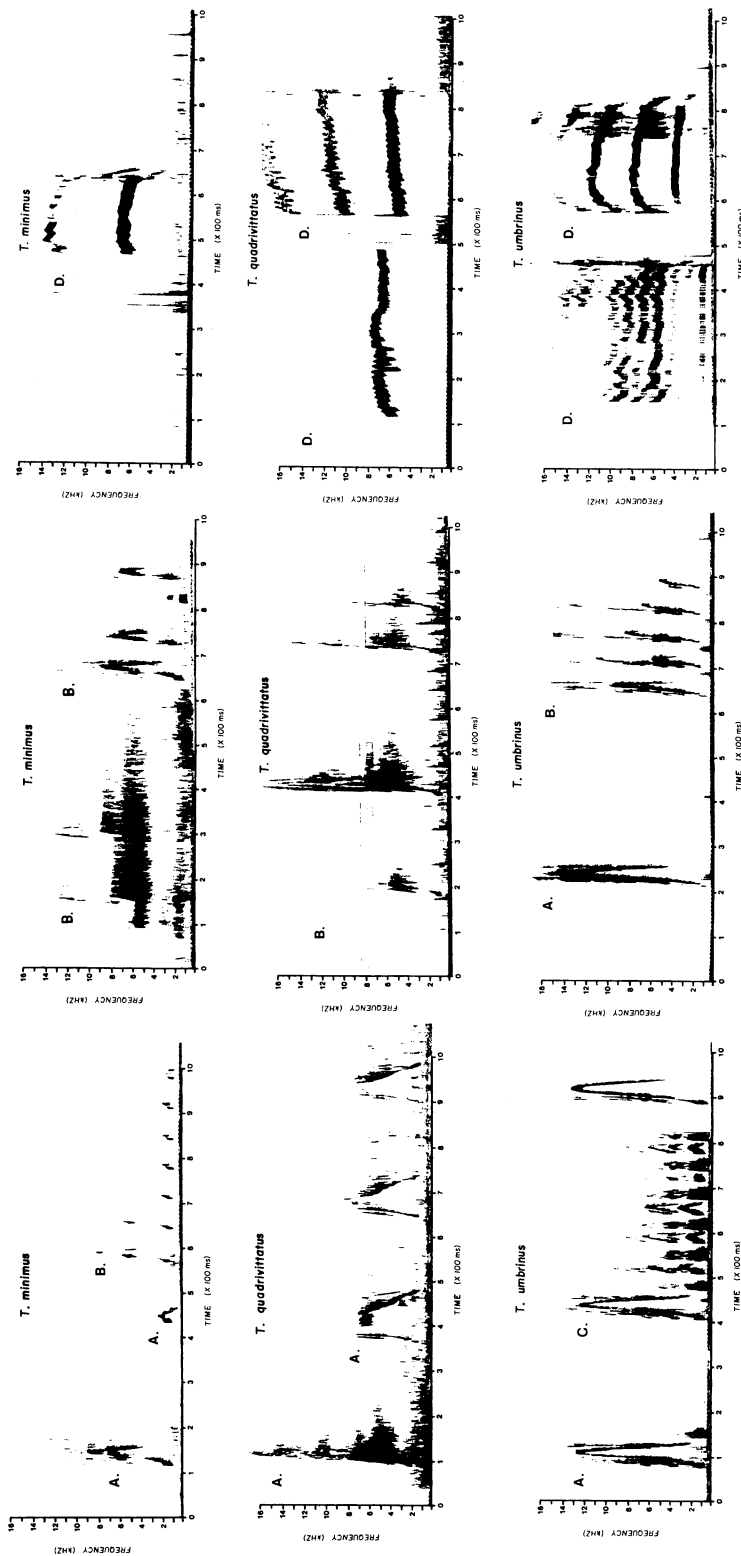


FIG. 5—Sonograms of vocalizations by the three species of *Tamias*. Different classes of calls are labeled as follows: A) chip, B) chipper, C) trill, and D) squeal. Terminology is after Brand (1976).

*imus* is the abundance of *Spermophilus lateralis* (Carey et al., 1980), which is more likely to compete for food with *T. minimus* than with the other two species of *Tamias*. Aggression or territorial defense (a spacing mechanism) between the two larger species may limit dispersal by preventing high enough densities of the dispersing species from penetrating the other's range (Bergstrom, 1986). Even if habitat preferences differed between the two species, there is no sudden change in habitat occurring at 2,130 m (Fig. 2 and Bergstrom, 1986), sufficient to account for their abrupt distributional limits. In fact, as much variation in habitat structure exists between north- and south-facing slopes at the same elevation as normally occurs over a 300-m range of elevation (Bergstrom, 1986).

It may be reasonable to assume that morphological similarity in many respects implies ecological similarity (Hespenheide, 1973; Karr and James, 1975; Holbrook, 1982); perhaps the most tractable arguments for this relationship involve body size (see Peters, 1983). It is plausible either that important ecological variables determining whether sympatry (or "ecological fitting"; Janzen, 1985) is possible between species of *Tamias* are allometric or that body size itself is an important and evolutionarily dynamic variable in the interactions among the three species of *Tamias*. It is usually assumed that body size is the underlying attribute that constrains ecological niche and thereby plays a causal role in community structure (e.g., Schoener, 1984). However, it has long been known from domestic breeding experiments that body size is responsive to selection. This fact also has been established for wild populations (Boag and Grant, 1978; Smith and Zach, 1979), as has the ecological explication of body-size selection (McNab, 1971; Brown, 1975; Davidson, 1977; Noordwijk et al., 1980; Murie and Boag, 1984). The most conspicuous of the relatively rare cases of broad sympatry between pairs of species of *Tamias* are those involving either *T. minimus* or *Tamias amoenus*, two of the smallest species in the genus and also the two most widely distributed (Hall, 1981), and a distinctly larger congener. Whether body size is a cause or an effect of species distributions, it does seem to be an important biogeographic variable.

That body size and perhaps pelage coloration are not overwhelmingly constrained by phylogeny within *Tamias* may be confirmed by noting that, for example, *T. minimus* is closely related to the

much larger *Tamias ruficaudus*, and *T. quadrivittatus*, one of the brightest chipmunks, is the sister species of *T. dorsalis*, the dullest species (Levenson et al., 1985). This suggests that morphological phenotype is strongly affected by either genetic drift (as Sullivan, 1985, suggested) or selection in response either to local environmental regimes (see Heller and Gates, 1972; Heller and Poulson, 1972; Patterson, 1981) or to direct evolutionary pressure from ecologically similar congeners (i.e., character displacement). Cranial and body morphology in this study did not show any convergent or divergent trends related to parapatry, but allozymic characters in *T. umbrinus* appeared convergent toward *T. quadrivittatus* as compared to other conspecific populations with disjunct ranges. Cranial shape showed greater differences between *T. quadrivittatus* and *T. umbrinus* (relative to *T. minimus*) than did body size. The hypothesis that pelage coloration in *T. umbrinus* converged toward *T. quadrivittatus* over a smaller geographic scale (as reported by Long and Cronkite, 1970, in central Colorado) could not be tested adequately, because of a lack of replication related to molt and time of collecting at different localities. Bacular morphology and, to a lesser extent, baubellar morphology were comparatively conservative within species, which is a general trend (White, 1953b) implying strong stabilizing selection for reproductive function (Long and Frank, 1968; Patterson and Thaler, 1982).

Two ecologically similar species whose ranges approach each other may avoid competition by exclusion based on either behavioral dominance (Heller, 1971) or partitioning of space by interspecific territoriality (Orians and Willson, 1964; Wolff et al., 1983). The two mechanisms are not mutually exclusive, however, and both were implicated at at least one Front Range chipmunk site where *T. quadrivittatus* and *T. umbrinus* co-occurred (Bergstrom, 1986). Convergence in behavior and external phenotype may facilitate "communication" in such a system of partitioning (Cody, 1969). Vocalizations in chipmunks are ubiquitous, diverse, and undoubtedly vital to the defense of territories in these solitary animals (see Brand, 1976). The prediction of convergence or close similarity in information content of calls is difficult to evaluate, as in this study a relatively great amount of variation existed within species. The chip call of all species is recognizable, as it elicits alert reactions from other sciurids, including tree squirrels and ground squirrels (pers. ob-

ser.; corroborated by Brand, 1976, and J. H. Honacki, pers. comm.). Behaviors associated with calling (e.g., tail movements, location when calling) clearly are similar between *T. quadrivittatus* and *T. umbrinus*, as compared to *T. minimus* (Bergstrom, 1986).

The consistency of the elevation of parapathy between the two species in this study calls for a further explanation. In a concurrent study, the possibility of a parasite mediating competition and delimiting the line of parapathy between *T. quadrivittatus* and *T. umbrinus* was suggested by data on larval infestations by an elevationally restricted bot fly (Bergstrom, 1986). Barbehenn (1969) and Cornell (1974) have implicated host-parasite interactions in other cases of parapathy and distributional gaps.

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