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MICROHABITAT PARTITIONING BY TWO CHIPMUNK SPECIES (*TAMIAS*) IN WESTERN COLORADO

J. Jeffrey Root¹, Charles H. Calisher¹, and Barry J. Beaty¹

ABSTRACT.—We examined microhabitat use of sympatrically occurring *Tamias minimus* (least chipmunk) and *T. rufus* (Hopi chipmunk) in a piñon-juniper/sagebrush vegetative community near Molina, western Colorado, from October 1994 to June 1999. This community is dominated by 2 major microhabitat types: shrub (sage; *Artemisia* spp.) and tree (pine and juniper; *Pinus edulis* and *Juniperus scopulorum*). Small mammals were live-trapped, marked, and released throughout this study. When it was the most abundant *Tamias* species on the study plots (1994–1997), *Tamias minimus* captures were associated with trees. *Tamias rufus* also exhibited this association but was captured at very low abundances during this period. *Tamias rufus* abundance was much greater, on average, than that of *T. minimus* between 1998 and 1999. During this time *T. minimus* captures were not associated with trees, but *T. rufus* captures remained associated with trees. As has been previously reported for other *Tamias* species, the greater abundance of 1 of 2 coexisting congeners in select areas may play a role in the microhabitat use of these 2 chipmunk species.

Key words: microhabitat, sympatric species, *Tamias minimus*, *Tamias rufus*, Mesa County, Colorado.

Microhabitat partitioning has long been thought to contribute to the capacity of sympatric species of rodents to coexist, particularly in desert ecosystems (Price 1978). However, microhabitat associations have not been universally detected. For example, Thompson (1982), Bowers (1988), and Jorgensen et al. (1995) failed to detect microhabitat associations (open specialists [i.e., primarily using microhabitat with low-growing or no vegetation] vs. shrub specialists) by certain species in select vegetation types.

Competition may cause interspecific differences in selection of microhabitat in some rodent assemblages (Price 1978, Brown and Munger 1985) and may affect the home range size of some *Tamias* species (Trombulak 1985). Additionally, predation risk may affect foraging behavior of rodents (Pierce et al. 1992, Otter 1994) and may influence species composition of communities of prey when risk differs among habitats (Kotler 1984). For example, Otter (1994) found *Tamias striatus* to have shorter approach times to feed trays in the open than to trays among forest cover. Further, an interspecific dominance hierarchy may exist in *Tamias* communities (Chappell 1978, Bergstrom 1992), and this can cause a dominant, aggressive species to waste time and

energy chasing interspecifics out of its primary habitat (Brown 1971).

Most microhabitat studies of rodents have concentrated on open specialists vs. shrub specialists (e.g., Price 1978), which appear to be the 2 most dominant microhabitat associations for structurally simple desert ecosystems. However, in more complex vegetative communities, variations of the latter may exist. For example, if one considers a community dominated by both shrubs and trees and arboreal and/or semiarboreal/semiterrestrial mammal species, microhabitat partitioning may be strikingly different.

We investigated the influence of growth forms of microhabitats on habitat patch use of coexisting *T. minimus* (least chipmunk) and *T. rufus* (Hopi chipmunk) in a sagebrush/piñon-juniper community in western Colorado. The objectives of this study were to quantify capture rates of both species throughout the study plots, to quantify microhabitat types in which these captures occurred, and to relate this information to the longitudinal coexistence of the 2 species.

STUDY SITE AND METHODS

A study site was established near Molina in

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west central Colorado (Mesa County, 39°09' 45.8"N, 108°03'18.4"W). Calisher et al. (1999) provides a detailed summary of the natural history of this area. In general, sagebrush (*Artemisia* spp.), piñon pine (*Pinus edulis*), and Rocky Mountain juniper (*Juniperus scopulorum*) dominate the vegetative community.

Two trapping webs (Anderson et al. 1983) were established more than 500 m apart and were separated by an irrigation ditch. Each trapping web consisted of 12 trap lines and 12 trap stations per trap line. Trapping webs of this design are centered on a single trap station. Twelve 100-m trap lines radiated from the central trap station at 30° angles from one another. The first 4 trap stations were spaced 5 m apart, the remaining 8 trap stations 10 m apart. We placed a single Sherman nonfolding, aluminum live-trap (23 × 8 × 9 cm) at each trap station. Traps were baited with a mixture of rolled oats, cracked corn, and peanut butter and were sampled for 3, rarely 2, consecutive days and nights.

Every 6 weeks from October 1994 to June 1999, rodents were trapped, sampled, and released. However, trapping efforts generally ceased from December to March. Small mammal processing was conducted according to published protocols (Mills et al. 1995). The minimum number known alive (MNA) was tabulated for both chipmunk species on each sampling occasion to estimate relative abundances. These data were summarized with SAS (SAS Institute 1988).

We characterized microhabitat into tree or nontree (generally shrub) categories. A trap station was considered to fall within the tree category if its radius was within 5 m of the trunk or canopy of a tree that was a minimum of 2.5 m in height. Trap stations in the nontree category had no trees associated with them. These data were analyzed with chi-square tests, which were conducted with EPI 6.02 Software (Centers for Disease Control and Prevention 1997). Trap stations were densely positioned within the center of the trapping web design we utilized (i.e., the first 4 trap stations in each trap line). Thus, in this small area multiple trap stations could be classified potentially as tree sites from the occurrence of a single tree. To minimize this and to promote independence of observations, the 1st and 3rd trap stations in odd-numbered trap lines (i.e., 1, 3, 5, 7, 9, and 11) and the first 3 trap stations in

even-numbered trap lines (i.e., 2, 4, 6, 8, 10, and 12) were not utilized for microhabitat analyses. Therefore, only 230 of the total 290 trap stations were used for microhabitat analyses.

RESULTS

In 17,400 trap-nights from October 1994 to June 1999, we recorded 320 *Tamias* captures (*T. minimus*, $n = 231$; *T. rufus*, $n = 89$). Results are presented for interspecific capture associations, microhabitat associations, and relative abundances.

We observed a difference in captures of the 2 *Tamias* species by trap station. Of 230 total trap stations (i.e., trap stations used for microhabitat analyses), 118 captured chipmunks (all years). Eighty-six (73%) of the 118 trap stations captured only a single chipmunk species. Sixty-four trap stations captured only *T. minimus*, and 22 stations captured only *T. rufus*. The remaining 32 trap stations captured both species. *Tamias minimus*, the smaller species, tended to be captured at trap stations where *T. rufus* was absent more than expected ($\chi^2 = 7.9$, $P < 0.01$, $df = 1$).

Captures of *T. minimus* tended to be associated with trees more than expected ($P < 0.01$, Table 1) from 1994 to 1997; captures of *T. rufus* showed a similar pattern during that period ($P < 0.02$, Table 1). However, when respective abundances of the 2 species shifted to a *T. rufus*-dominated community (1998–1999, Fig. 1), *T. minimus* captures were no longer associated with trees ($P > 0.50$, Table 1). *Tamias rufus* captures remained associated with trees during this time ($P < 0.01$, Table 1).

Of 230 (2 webs with 115 utilized trap stations each) trap stations, 114 had tree-covered microhabitat (Table 1). Most of the 116 nontree trap stations had shrub-covered microhabitats. However, a few (<10) trap stations had open or grass-covered microhabitats.

The mean MNA of *T. minimus* was greater than that of *T. rufus* from 1994 through 1997 (Table 2). During 1998–1999 the MNA of *T. rufus* was greater, on average, than that of *T. minimus* (Table 2). Wide fluctuations of abundances of both species were observed during the study (Fig. 1).

DISCUSSION

Use and avoidance of microhabitats by rodents are thought to be associated with many

TABLE 1. Association of captures of *Tamias minimus* and *T. rufus* (+ = species present, - = species absent) and trap-site microhabitat (+ = tree present, - = tree absent) in western Colorado.

Comparison/ time period	Species vs. microhabitat		χ^2	P	
	Tree+	Tree-			
<i>T. minimus</i> vs. microhabitat ^a					
1994–1997	<i>T. minimus</i> +	59	26	20.0	<0.01
	<i>T. minimus</i> -	55	90		
1998–1999	<i>T. minimus</i> +	9	6	0.3	>0.50
	<i>T. minimus</i> -	105	110		
<i>T. rufus</i> vs. microhabitat ^a					
1994–1997	<i>T. rufus</i> +	7	0	5.4	<0.02
	<i>T. rufus</i> -	107	116		
1998–1999	<i>T. rufus</i> +	33	14	9.0	<0.01
	<i>T. rufus</i> -	81	102		

^aTest figures tabulated from number of trap stations with trees, number of trap stations without trees, number of *T. minimus* / *T. rufus* captures at trap sites with trees, and number of *T. minimus* / *T. rufus* captures at trap sites without trees. Multiple captures at the same trap site were not included in analyses.
^bFisher's exact test P-value is furnished because a small expected cell size was observed in this comparison.

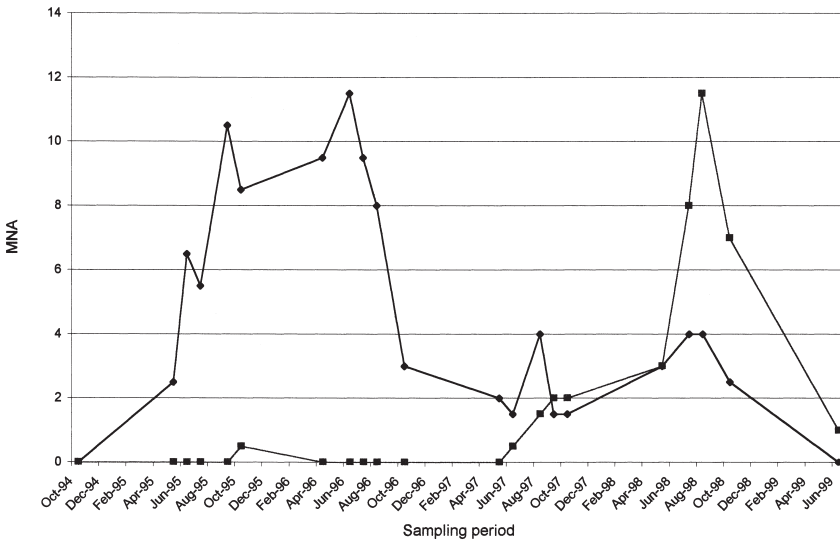


Fig. 1. Minimum number known alive (MNA; average of both sites) of *Tamias minimus* and *T. rufus* sampled within a sagebrush/piñon-juniper vegetation association in western Colorado, 1994–1999.

factors, including risk of predation, inter- and intraspecific interactions, and differential resource availability (Brown 1988, Kotler and Brown 1988, Bowers 1995). Thus, it is conceivable that the habitat used by a species may not be the preferred habitat, especially if a superior competitor occupies the preferred habitat type (Meredith 1976).

Some habitat attributes (e.g., grassy areas and farmland away from wooded areas) have been thought to be inhospitable habitat for certain chipmunk species (Bennett et al. 1994).

In our study during 1998–1999, *T. minimus* showed no significant association with trees. Competition may have affected habitat use by *T. minimus* once *T. rufus* became the more abundant species. Sheppard (1971) concluded that aggressive behavior of *T. amoenus* enabled it to exclude *T. minimus* from forested habitat. Similarly, *T. umbrinus* may force *T. minimus*, at least partially, into open-overstory habitats in north central Colorado (Bergstrom 1992). Thus, when *T. rufus* was relatively rare within the sagebrush/piñon-juniper community we

TABLE 2. Minimum number known alive of *Tamias minimus* and *T. rufus* sampled within a sagebrush/piñon-juniper vegetation association in western Colorado, 1994–1999.

Time period	Species					
	<i>T. minimus</i>			<i>T. rufus</i>		
	\bar{x}	$s_{\bar{x}}$	range	\bar{x}	$s_{\bar{x}}$	range
1994–1997	5.5	0.98	0–15	0.4	0.16	0–3
1998–1999	2.3	0.64	0–5	6.1	2.02	0–18

sampled, *T. minimus* may have been able to exploit tree-covered portions of our study site more exclusively. However, the small, presumably less aggressive *T. minimus* may have been forced out of at least a portion of the trees during and after the increase in abundance of *T. rufus*. Notably, Trombulak (1985) found that when *T. townsendii* was experimentally removed from his study area, the home range size of *T. amoenus* increased considerably, but the 2 species did not partition the environment based on any measured habitat attributes.

Tamias minimus is known to occur sympatrically with other species that occur only parapatrically with one another (e.g., *T. quadrivittatus* and *T. umbrinus*; Bergstrom and Hoffman 1991). Additionally, *T. umbrinus* and *T. dorsalis* have been shown to occur together only in a very narrow strip of intermediate habitat (e.g., Brown 1971). Similarly, Sheppard (1971) determined that *T. minimus* was largely confined to alpine habitat but also ranged into subalpine forest, where its distribution narrowly overlapped that of *T. amoenus*. Heller and Poulson (1972) found that *T. minimus* could be active in areas of hot, arid sagebrush by minimizing water loss and tolerating increased body heat content through hyperthermia and use of its burrows (Heller and Gates 1971). The aggressively dominant *T. amoenus* could exploit these areas only when patches of shade were available from trees. Thus, the line of contact between *T. amoenus* and *T. minimus* coincided with the lower limits of distribution of piñon pine (Heller and Poulson 1972). Aggression has not been selected for in *T. minimus* because it is not metabolically feasible to engage in aggressive interactions in the hot sagebrush desert (Heller 1971). Thus, when both *T. minimus* and *T. rufus* are well represented within a given community, their sympatry may be limited to edges.

Interspecific territoriality appears to be common among many chipmunk species

(Brown 1971, Bergstrom 1992). For example, foraging collection times of eastern chipmunks, *T. striatus*, increased in the presence of competitors, due primarily to time spent alert or engaged in interactions with other individuals (Giraldeau et al. 1994). Brown (1971) noted that when *T. umbrinus* was found in higher abundance than *T. dorsalis*, the situation actually became disadvantageous for *T. dorsalis* (the more dominant species) because it wasted a great deal of time and energy on fruitless chases of interspecifics. The low abundance of *T. rufus* we observed from 1994 to 1997 may have allowed *T. minimus* to exploit tree-covered microhabitats, but the increase in abundance of *T. rufus* in 1998–1999 may have forced at least some *T. minimus* out of tree-covered microhabitats. *Tamias minimus*, which range over more habitat types than any chipmunk in Colorado, typically occupy areas on the edge of escape cover (Fitzgerald et al. 1994). Thus, the seemingly better escape cover on the wooded portions of our study plots, compared with open sagebrush areas, leads us to believe that wooded portions of our study plots may be the most suitable habitat for both *Tamias* species. However, the habitat used by a species may not be its preferred habitat, especially if a superior competitor occupies the preferred habitat type (Meredith 1976). This may be directly related to the relative abundance of a congener.

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