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Ecology, Vol. 59, No. 3. (Late Spring, 1978), pp. 565-579.

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BEHAVIORAL FACTORS IN THE ALTITUDINAL ZONATION OF CHIPMUNKS (*EUTAMIAS*)¹

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Abstract. Behavioral factors important in the determination of the lines of contact between 3 altitudinally zoned chipmunks, *Eutamias minimus*, *Eutamias amoenus*, and *Eutamias speciosus*, were investigated at a field site in the Sierra Nevada, California. These species are contiguously allopatric and restricted to particular vegetational communities.

Extensive mark-release-recapture studies and a removal experiment suggested that the *E. minimus*-*E. amoenus* border results from a physiological limitation of *E. amoenus* and competitive exclusion of *E. minimus* from *E. amoenus* habitat. In areas where *E. amoenus* were removed, *E. minimus* captures increased; the converse did not occur.

Behavioral observations coupled to vegetation surveys showed that *E. amoenus* had a much stronger preference for the vicinity of trees than the other species. *Eutamias minimus*, because it is physiologically more capable of handling dry heat loads than *E. amoenus*, showed a weaker orientation to trees. *Eutamias speciosus* shows even less orientation to trees, even though it is the most vulnerable of the 3 to heat stress.

Field observations of interactions revealed that all 3 species are highly aggressive intraspecifically, and that a clear-cut interspecific dominance hierarchy exists: *E. speciosus* dominates both *E. amoenus* and *E. minimus*, and *E. amoenus* in turn dominates *E. minimus*. The evolution of aggressiveness is explained in terms of the hibernation strategy of the animals and the concomitant need to store large quantities of food for the winter. Interspecific aggression is not selected against because of large overlaps in food utilization among the species.

It is concluded that physiological and behavioral factors interact to produce the contiguously allopatric distribution of these chipmunks: *E. speciosus* aggressively excludes other species from its forest habitat, to which it is restricted by physiological considerations and habitat selection; *E. amoenus* tolerates the more severe conditions in arid woodlands, from which it excludes *E. minimus*; *E. minimus* has extensive thermoregulatory adaptations enabling it to inhabit the extremely hot, dry sagebrush, which is intolerable for the more aggressively dominant species.

Key words: Aggression; California; competition; contiguous allopatry; *Eutamias*; habitat selection; niche partitioning; Rodentia

INTRODUCTION

This paper describes part of a study which analyzed a group of contiguously allopatric species in terms of Hutchinson's (1957) model of fundamental and realized niches. I wished to (1) examine and test a line of contact between 2 species to determine if it represented the edge of a fundamental or realized niche for each species; (2) describe the behavioral, morphological, or physiological characteristics of the species which result in their contiguously allopatric distribution; and (3) attempt to elucidate the selective pressures which led to the evolution of these characteristics. I worked with 3 closely related, morphologically similar chipmunk species, *Eutamias amoenus*, *Eutamias speciosus*, and *Eutamias minimus*, which are altitudinally zoned on the eastern slope of the Sierra Nevada near Yosemite National Park, California. Each species is restricted to a particular vegetational community: *E. speciosus* inhabits lodgepole pine forests; *E. amoenus* is found in piñon pine-mountain

mahogany woodlands; *E. minimus* occupies open sagebrush at the base of the Sierran scarp.

Extensive laboratory work with this species complex (Heller 1971, Heller and Gates 1971, Heller and Poulson 1972) had revealed pronounced differences in interspecific aggression and hinted at subtle physiological variation among the species. Further laboratory studies of their thermoregulatory physiology have demonstrated striking differences in heat-storage adaptations among these animals (Chappell et. al. 1978). When examined together, these behavioral and physiological differences could explain the observed distributions in the field. I felt that a field investigation involving extensive behavioral observations, population studies, and experimental population manipulations could yield extremely interesting information when coupled to the existing wealth of laboratory data. Accordingly, I concentrated my efforts on the border between *E. minimus* and *E. amoenus*, and made a more modest investigation of the *E. amoenus*-*E. speciosus* interaction when a small population of the latter was discovered in the study area. The work described in this paper concerns the examination and testing of the line of contact, and the roles of inter-

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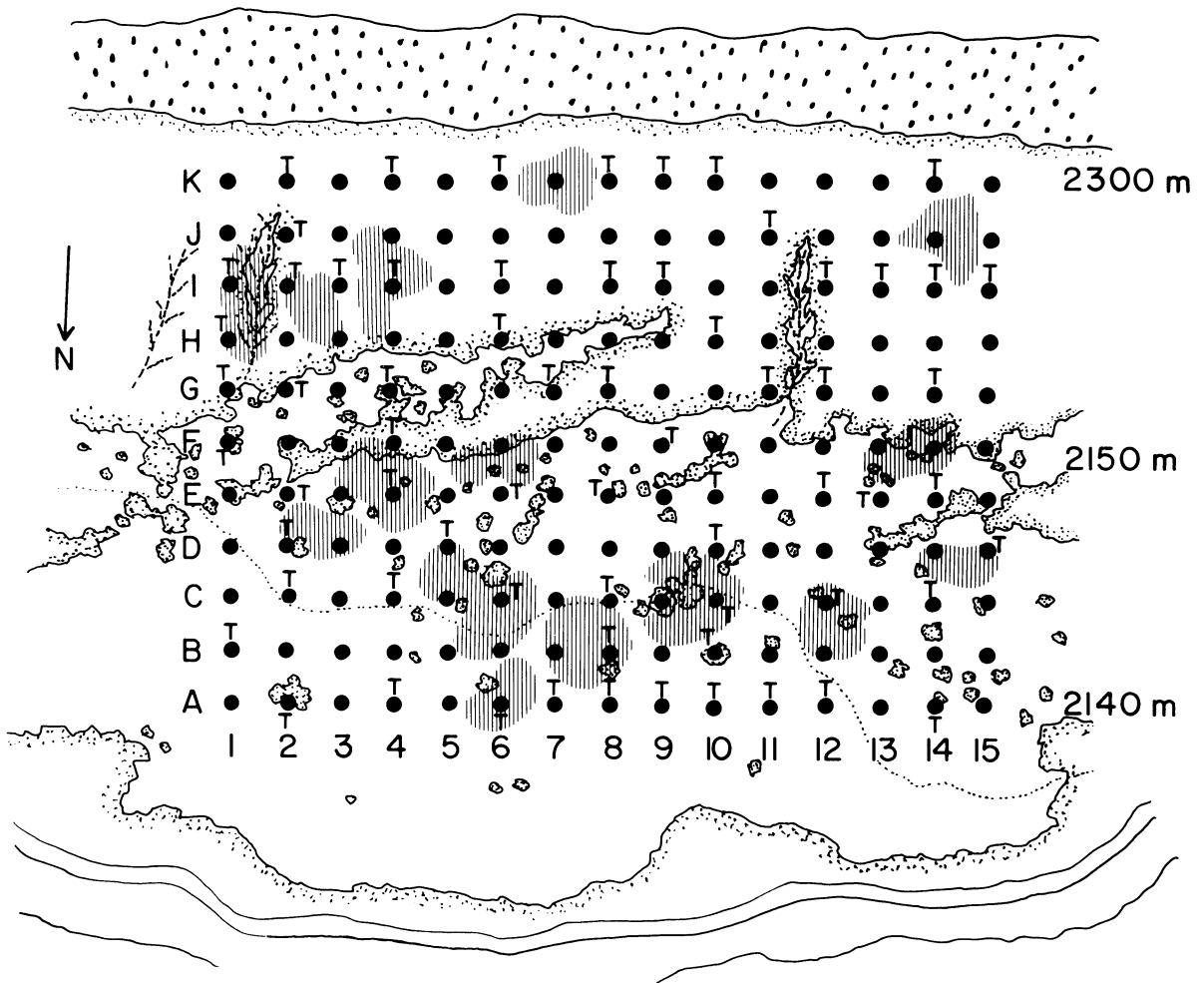


FIG. 1. Map of the trapping grid showing rows (A–K), lines (1–15), trap stations (black dots), and fields of view from observation stations (vertically shaded areas). Transected traps are marked with a "T." Outlined areas with stippled edges represent woodlands or individual trees, the area marked with heavy stippling at the top of the figure represents open Jeffrey pine forest, and the riparian forest along Lee Vining Creek is shown at the bottom of the figure.

specific aggression and habitat selection in delimiting this line.

MATERIALS AND METHODS

The study site was a 26.4 hectare rectangular trapping grid located on the south slope of Lee Vining Canyon, Mono County, California (elevation 2200 metres). This area was chosen for the study because it is a steep fault scarp with well-defined life zones separated by abrupt transitions (Grinnell and Storer 1924). The grid straddles the border between piñon pine–mountain mahogany woodlands and open sagebrush scrublands. Fieldwork in this area occupied the summers of 1975 and 1976, and short visits to the site were made in the winter of 1975, the early spring of 1976, and late spring 1977. Snow cover lasted from late October or early November through April. Because chipmunks spend most of their time hibernating during periods of snow cover (Heller and Poulson

1970), the study covered most of the active seasons of the animals during 1975 and 1976.

Live-trapping studies

A large livetrapping grid was set up in early June 1975, consisting of 165 trap stations placed at 40-metre intervals in a 440×600 metre array (Fig. 1). A single Sherman trap was placed at each station, shielded from direct sun with bark or dead branches, and baited with a combination of sunflower seeds and commercial birdseed mix. Traps were checked twice per day, and were closed on cold rainy days and extremely hot afternoons to prevent deaths from exposure. Several undergraduate students assisted in this work.

Trapped chipmunks were marked for permanent identification by toe amputation. We used only the hind feet for this process and removed no more than 1 toe from each foot, but by varying the number of joints taken from each digit and marking the species

and sexes independently we could toe-clip ≈ 690 animals without duplication. Metal ear tags were placed on many of the animals. These provided quick and unambiguous identification and enabled us to distinguish between some animals which had confusing toe numbers. All captured animals had a ring of fur removed from the tail, and males were clipped on the flank as well. These markings enabled us to ascertain the sex of animals being observed.

Removal experiment

In 1976, a removal experiment was performed to clarify the nature of the border for *E. minimus* and *E. amoenus*. I divided the grid into 3 equal-area sections across the ecotone between sagebrush and woodlands. Section 1 comprised lines 1–5 (Fig. 1), section 2 comprised lines 6–10, and section 3 comprised lines 1–15. I chose 3 July for the start of the experiment for 2 reasons: (1) because the young animals had started to disperse and were no longer dependent on their mothers, and (2) because I had accumulated fairly complete information on the home ranges of most individuals in the area during 3 wk of previous trapping. Beginning on this date and continuing for the remainder of the summer, all *E. amoenus* in section 3 and all *E. minimus* in section 1 were removed from the grid as soon as they were trapped (the few *E. speciosus* in section 3 were also taken). Section 2 was left undisturbed as a control area. Chipmunks whose home ranges overlapped 2 sections were removed if more than half of their capture sites lay in the removal area for their species, and immigrants to removal areas for their species were taken out as soon as they appeared. Movements of the remaining animals were monitored through normal trapping procedures.

Field observations

Behavioral studies of free-ranging animals were made from 15 observation stations in the grid area (Fig. 1). Observers remained at a station for 2 or 3 h, arriving 10 min before beginning observations. Preliminary observer bias testing indicated that interobserver differences were minimal; however, personnel were rotated randomly among different stations in order to minimize the effects of any possible biases.

All observations were recorded directly onto computer-compatible checksheets. For observations of single animals, a form of state sampling (Altmann 1974) was utilized, with the observer recording behavior at 10-s intervals. When 2 chipmunks encountered each other, recording shifted to event sampling. Each event in the interaction sequence was transcribed as it occurred. Details of these procedures can be found in Chappell (1977).

Feeding-station observations

To obtain a large sample size of all possible combinations of interactions among the 3 chipmunk spe-

cies in the study area, 3 feeding stations baited with sunflower seeds were set up ≈ 300 metres outside of the grid. The feeders attracted large numbers of individuals into a small area, so that interactions were common. Regular visitors were trapped and marked with ear tags and individual fur-clipping patterns on flanks and tail. The observation techniques were identical to those used for interactions in the grid area, except that no single-animal recording was done.

Scoring of encounters

Encounters were scored, primarily from their outcome, as friendly (grooming, playful chasing, mounting), aggressive (fighting, displacement, etc.), and neutral (aggressive but outcome uncertain). Winning animals in aggressive encounters were those who actively displaced, aggressively chased, or successfully resisted displacement attempts by other animals; losers, in turn, were displaced, chased away, or failed in attempts to displace others. Two other scoring methods for aggressive encounters were used as tests of the primary technique. One method summed the aggressive and submissive acts by each animal in the interaction sequence; winning animals were those with the highest proportion of aggressive and the lowest proportion of submissive behaviors. The second method utilized the observer's opinion of the outcome, recorded on the checksheet immediately after the encounter terminated. These 3 techniques yielded very similar results, with $>90\%$ agreement in independent tests.

Vegetation transects

Sixty-five of the 165 trap stations were transected for vegetation and cover analysis (Fig. 1). Each transect was based on two 40 m perpendicular lines, crossing in the middle and intersecting at the trap station. We measured vegetation and other ground-cover types at 3 heights above the ground along the entire 80 metres of transect lines: herb layer (0 to 1 m high); shrub layer (1 to 3 m high); and tree layer (> 3 m high). Visibility through the habitat at 3 levels above the trap station (0, 1, and 2 m) was measured by estimating the proportion of a 0.5-m² card visible from the trap station when placed at various distances along the transect lines. The distance to the tree nearest the trap in each of the 4 quadrats delineated by the transect lines was measured at all 165 stations (details of these procedures can be found in Chappell 1977).

Within the fields of visibility at each of the 15 behavioral observation stations (Fig. 1), additional measurements were made to allow analysis of microhabitat selection. The proportion of the visible area within 3 metres of the trunks or low branches of trees was estimated from photographs and measurements. We similarly calculated the proportions of the field of view within 1.5 m of large rocks (>50 centimetres diameter) or fallen logs, and within 1.5 m of shrubs (these 3

TABLE 1. Trapping data summary, 1975–1976

Species Year Category*	<i>Eutamias minimus</i>				<i>Eutamias amoenus</i>				<i>Eutamias speciosus</i>			
	1975		1976		1975		1976		1975		1976	
	A	C	A	C	A	C	A	C	A	C	A	C
Breeding ♀♀	18	28	23	204	10	101	18	147	0	0	4	12
Nonbreeding adult ♀♀	7	33	49	76	4	27	14	63	0	0	1	11
Young ♀♀	14	26	53	193	22	95	41	337	2	20	5	19
Adult ♂♂	32	74	59	152	19	152	38	229	1	1	9	46
Young ♂♂	26	32	85	189	38	109	76	252	0	0	9	14
Total young	40	58	138	382	60	204	117	589	2	20	14	33
Young/♀	2.22		6.0		6.0		6.5		...		3.5	
Total ♂♂	58	106	144	393	57	261	114	481	1	1	18	60
Total ♀♀	39	88	125	421	36	224	74	548	2	20	10	42
Sex ratio (♂:♀)	1.49		1.15		1.58		1.54**		...		1.80	
Total animals	97	194	269	814	93	485	188	1029	3	21	28	102
Estimate of grid population	150		340		100		205		...		33***	

* A = no. animals; C = no. captures; ** = significantly different from 1.0; *** very approximate because of limited data.

categories covered essentially all of the habitat). Combinations (e.g., shrubs <3 m of trees) were assigned according to the following priorities: (1) <3 m or tree; (2) <1.5 m or rock or log; (3) <1.5 m or shrub. Microhabitat selection by the animals could be estimated by comparing the percentage of observations falling within each part of the habitat with the actual availability of these habitat parts within the field of view (as in States 1976).

RESULTS

General distributional data

Populations.—Livetrapping ($\approx 43,000$ total trap checks) yielded extensive background information on the populations of the 3 *Eutamias* species inhabiting the grid. These data, necessary for interpretation of the removal experiment and behavioral observations, are summarized below and in Table 1 (see Chappell 1977 for more details):

1) Large populations of *E. minimus* and *E. amoenus* occurred in the grid; the former being $\approx 1.5\times$ commoner than the latter. *Eutamias speciosus* accounted for $\approx 10\%$ of the total captures. Most *E. speciosus* were transients from a larger population in a riparian lodgepole pine forest ≈ 140 metres outside of the grid (Fig. 1), although a small number established home ranges within the grid itself.

2) Populations of all 3 species increased sharply in 1976. Populations of *E. minimus* increased $2.5\times$, *E. amoenus* populations doubled, and *E. speciosus* populations increased 9-fold over the previous year. These expanded populations were probably due to the wet summer of 1975 and the mild winter of 1975–1976, conditions leading to high reproductive success and low overwinter mortality.

3) Trapping success (individual capture rates) differed among the species and sexes. Females were trapped more readily than males, and *E. amoenus*

were more readily trapped than *E. minimus*. Also, a higher percentage of the resident *E. amoenus* were eventually caught ($\approx 90\%$) than of resident *E. minimus* ($\approx 70\%$), based on Lincoln Index (mark–release–recapture) estimations. Populations of *E. speciosus* were too small to provide meaningful capture rate data.

4) Sex ratios of all 3 chipmunks are skewed in favor of males, although the ratio differs significantly ($P < .05$) from 1:1 only for *E. amoenus* in 1976. Young animals as well as adults show a skewed sex ratio, so differential mortality (if it is the cause of skewness) must take place prior to the emergence of young from their natal burrows.

5) Young animals of all 3 species first appeared in large numbers beginning in early July of 1975 and mid-June 1976. Because the young first emerge when 4 to 6 wk old and the gestation period is ≈ 5 wk (Broadbrooks 1958), mating presumably took place in March and April. Litter size could be roughly estimated by dividing the number of young by the number of breeding females, although actual parentage usually could not be ascertained. Estimated litter size for *E. minimus* was 2.2 in 1975 and 6.0 in 1976. The rather low value for 1975 is probably an underestimate resulting from the low trapping success of *E. minimus* that year; the 1976 figure is probably more accurate. Litter size for *E. amoenus* was 6.0 in 1975 and 6.5 in 1976. The very rough estimates were supported by observations of a female *E. amoenus* escorting her litter of 6, an *E. minimus* brood of 6 in the laboratory, and reports in the literature (e.g., Broadbrooks 1958).

Home range and movements.—The home ranges of the 3 *Eutamias* species in this study were quite similar to each other and to those described elsewhere (Martinsen 1968, Broadbrooks 1970, Meredith 1972, Shepard 1972). Table 2 shows the average home range size of various sex and age classes for animals captured 6 or more times during a summer. This table is based

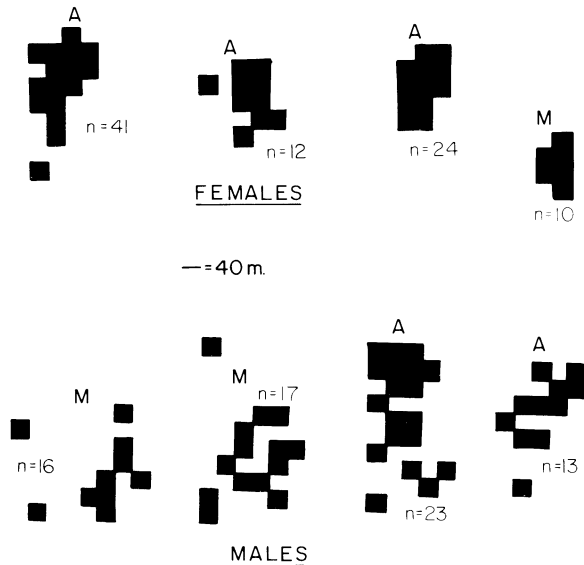


FIG. 2. Representative trapping-revealed home ranges of ♂♂ (bottom) and ♀♀ (top). Each small square represents 1 capture site; N is the total number of captures of each animal. *Eutamias amoenus* = A; *Eutamias minimus* = M.

simply on the number of traps utilized by each individual, a method adequate for females and young animals but misleading for adult males. The capture sites for males were often scattered, especially during the reproductive season (Fig. 2), and therefore the adult male home ranges in Table 2 are probably underestimates.

Within each species, there was considerable home range overlap between individuals in each sex and age class. Breeding females had the most exclusive home ranges, with each individual sharing $\approx 50\%$ of her capture sites with other breeding females. Males and young animals of both sexes showed considerably more overlap than breeding females. Male and female home ranges seemed to overlap at random. In view of this amount of superimposition, it is unlikely that chipmunks defend large, exclusive territories.

Most home ranges of adults remained essentially constant during a summer and were similar from 1 summer to the next in individuals who overwintered. Adult males wandered widely early in summer when they were in reproductive condition, decreasing their movements as the summer progressed. Young animals initially remained in a relatively small area, presumably within the home range of their mothers. About 2 wk after their first appearance (early August 1975 and mid-July 1976), $\approx 50\%$ of the young dispersed, moving to new areas within the grid or leaving the area completely. Simultaneously, other young began to appear, probably entering the area from birth sites outside of the grid. The remaining 50% of the young continued to occupy their original home ranges. There was no

TABLE 2. Home-range size of 3 species of Chipmunks, *Eutamias* spp. Means for all animals captured 6 or more times; 1975–1976

Species	N	Mean no. traps	Home range size (hectares)
Breeding ♀♀			
<i>E. minimus</i>	8	6.50	1.04
<i>E. amoenus</i>	14	8.14	1.30
<i>El. speciosus</i>	1	8	1.28
Adult ♂♂			
<i>E. minimus</i>	13	6.62	1.06
<i>E. amoenus</i>	18	8.27	1.32
<i>E. speciosus</i>	3	9.3	1.49
Young ♀♀			
<i>E. minimus</i>	18	4.94	.79
<i>E. amoenus</i>	26	7–19	1.15
<i>E. speciosus</i>	1	10	1.6
Young ♂♂			
<i>E. minimus</i>	7	5.86	.94
<i>E. amoenus</i>	28	5.64	.90
<i>E. speciosus</i>	0

difference between the movements of male and female young.

Habitat utilization.—Within the grid area, *E. minimus* were found primarily in sagebrush and *E. amoenus* were primarily in piñon pine–mountain mahogany woodlands. Less than 20% of the captures of each species, neglecting those affected by the removal experiment (see below), occurred in “abnormal” habitat (e.g., *E. minimus* trapped in *E. amoenus* woodland habitat, or *vice versa*). Capture frequencies in abnormal habitat decreased as the distance from the species’ typical habitat increased. Those *E. amoenus* captured in sagebrush were often found in traps close to the scattered trees in this habitat.

Almost 100% of the *E. speciosus* trapped were captured in the wooded areas of the grid. Only 5 captures (out of 130) were in sagebrush. These animals were caught in the northwest and northeast corners of the grid, close to riparian lodgepole pine forest (typical *E. speciosus* habitat). Of the total of 31 individuals of this species found during the study, only 7 (3 females and 4 males) had stable home ranges. The rest of the animals were almost certainly transient visitors from the nearby riparian forest, since many of them were recaptured during occasional trapping in this area.

Removal experiment

About 120 animals were taken out of the grid area during the removal experiment. Of these, 75–80 were old residents, and the rest were immigrants. The majority of the residents were captured in the first 2 wk of the experiment, after which the rate of removals fell sharply to ≈ 10 animals per week and remained at this level for the rest of the summer. After 4 wk, the remaining populations of *E. minimus* in section 1 and

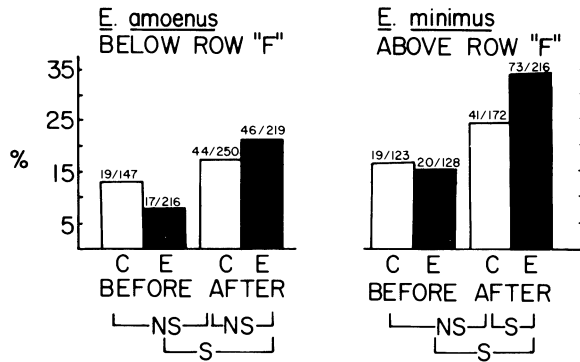


FIG. 3. Removal experiment results for *Eutamias amoenus* and *Eutamias minimus*. Percentages (%) of captures in abnormal habitat (above or below row "F") in experimental (E) and control (C) sections before and after the start of removal procedures. Comparisons labeled S are statistically significant ($P < .05$ that the 2 percentages are equal); those labeled NS are not significant. The actual number of captures is given at the top of each bar.

E. amoenus in section 3 (Fig. 1) were estimated (from trapping results) to be between 10 and 20% of pre-manipulation levels. Sightings of *E. minimus* and *E. amoenus* in their respective removal areas also declined rapidly as the experiment progressed, supporting the conclusion that the bulk of the residents had been removed.

Important quantitative and qualitative differences between the movements of *E. minimus* into vacant *E. amoenus* habitat (woodlands) and *E. amoenus* into vacant *E. minimus* habitat (sagebrush) were revealed in this experiment. Quantitative differences between the species occurred in their capture rates in abnormal habitat, which was defined as above row F (rows G–K) for *E. minimus* and below row F (rows A–E) for *E. amoenus* (Fig. 1). The number of captures in abnormal habitat in each of the 3 sections of the grid was expressed as a percentage of the total captures in all of that section. Percentages were used to eliminate any bias caused by unequal population sizes of the 2 species. I made statistical comparisons of these percentages (a) within the experimental areas before and after the removal, (b) within the control area before and after the removal, and (c) between experimental and control areas after the removal.

As can be seen in Fig. 3, the percentages of both species' captures in abnormal habitat were higher after the removal than before. For both species, the change was significantly greater in experimental than in control sections ($P < .05$), although both areas showed some increase. Similar changes in these sections were noted the previous summer, when no manipulations took place. These increases are temporary and probably represent the dispersal of young. A definite difference between the species can be seen when comparing postremoval captures in experimental and control areas. The percentage of *E. minimus* captures

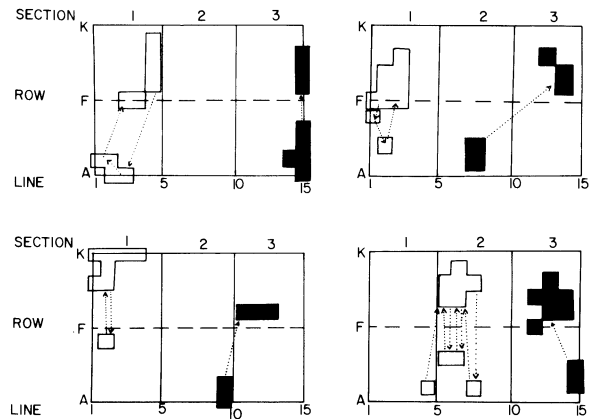


FIG. 4. Representative movements of *Eutamias amoenus* (open areas) and *Eutamias minimus* (shaded areas) during the removal experiment. Each simplified grid map displays the home range of 1 member of each species. Note that *E. minimus* often completely shift their home ranges to the woodland (F–K) area of the *E. amoenus* removal area (section 3), but that *E. amoenus* visits to the sagebrush (A–F) tend to be temporary.

in *E. amoenus* habitat after the removal was significantly higher in the *E. amoenus* removal area (section 3) than in the control section ($P < .05$). However, the percentage of *E. amoenus* captures in sagebrush did not differ significantly between the *E. minimus* removal area (section 1) and the control area. No significant difference between the 2 species' movements into abnormal habitat was noted during the previous summer.

Qualitative differences between *E. minimus* and *E. amoenus* movements into abnormal habitat are also important. None of the *E. amoenus* that entered the sagebrush in section 1 established permanent home ranges, even after *E. minimus* were removed. Essentially all of these *E. amoenus* were either new immigrants passing through the area or old residents of the woodland making transient excursions out of their normal home ranges. In contrast, several resident *E. minimus* shifted their home ranges completely, moving permanently from the sagebrush into the vacant woodland of section 3. These animals included 3 adult males, several juveniles, and at least 2 adult females who had bred in the sagebrush earlier in the season. Some of these home-range shifts are shown in Fig. 4. Additionally, several new *E. minimus* entered section 3 from outside the grid. Some of these new residents of the woodland were able to maintain their home ranges through the winter (despite the relaxation of trapping pressure against *E. amoenus* in September 1976). In 2 days of trapping in June 1977, 1 of these animals was captured and another sighted in section 3.

Observational data

Behavioral observations were used to obtain information on the chipmunks' daily activity cycles, food

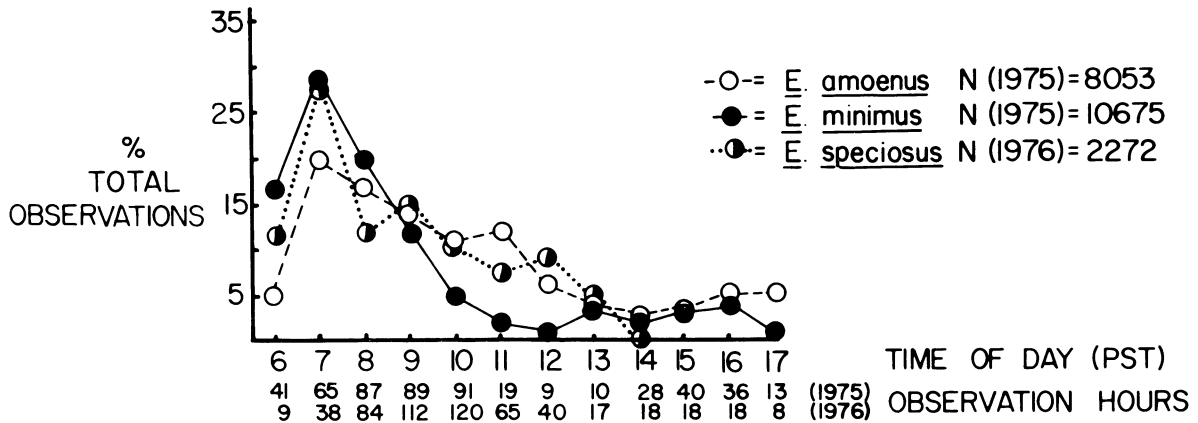


FIG. 5. Daily activity patterns of the 3 *Eutamias* species (data from all habitat types combined). Vertical axis represents the percentage of daily activity occurring within each hourly period. Total observations for each hourly period are shown at the bottom of the figure.

habits, microhabitat selection tendencies, and inter- and intraspecific aggression patterns. A total of 1075 h was spent observing chipmunk behavior within the grid area, during which 5498 sightings totalling 30,802 observations of 10-s intervals were recorded. In addition to the field observations, ≈ 300 h were spent watching animals interact at the feeding stations.

Daily activity patterns.—The daily activity cycles of the 3 chipmunk species were computed for each of the 3 different habitats in the grid (woodlands, sagebrush, and the ecotone), and also for all habitats combined. The 3 species had very similar activity patterns, as can be seen in Fig. 5. The figure represents activity in all habitats combined; no major interhabitat differ-

ences were found in any of the species. There was an activity peak in midmorning followed by a decline to low levels in the afternoon (*E. speciosus* seemed to show no activity at all after 1400 h, but this finding may have been an artifact of the relatively small sample size for this species).

Food utilization.—Analysis of food habitats was based primarily on observations of foraging chipmunks, in contrast to other studies which have sampled the stomach or cheek-pouch contents of sacrificed animals (e.g., Sheppard 1971). I did unearth several temporary pit-storage seed caches made by animals foraging on substances unidentifiable through binoculars; these caches invariably contained seeds from the common plants in the grid. Chipmunks fed on a wide variety of plant and animal materials. Figure 6 displays the most commonly utilized foods, in all habitats combined, for each of the 3 species in 1976 (1975 values for *E. amoenus* and *E. minimus* were quite similar, but too few *E. speciosus* were seen that year for meaningful conclusions). The figure is based only on the number of observations of chipmunks feeding on each category, and does not take into account possible differences in feeding efficiency or nutritional values of the various food types. There were only slight differences in food utilization between the 3 habitat types, and these changes were qualitatively similar in the 3 chipmunk species. The shifts were probably due to unequal distribution of the foodplants among habitats—e.g., *Purshia* is more abundant in sagebrush than in woodlands. Although there are differences in the food utilization curves of these animals (e.g., *E. minimus* eats significantly [$P < .05$] less *Purshia* than *E. speciosus*), it is clear that considerable overlap does exist.

Habitat selection and utilization.—Differential use of the microhabitat was marked among the chipmunks, and varied with behavior and major habitat type. Figure 7 shows microhabitat selection tendencies in the

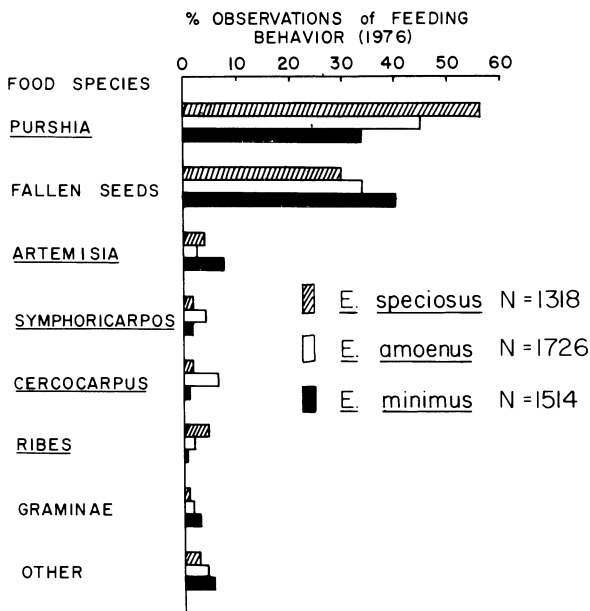


FIG. 6. Food utilization of the 3 *Eutamias* species (data from all habitats combined, except for removal areas—see text).

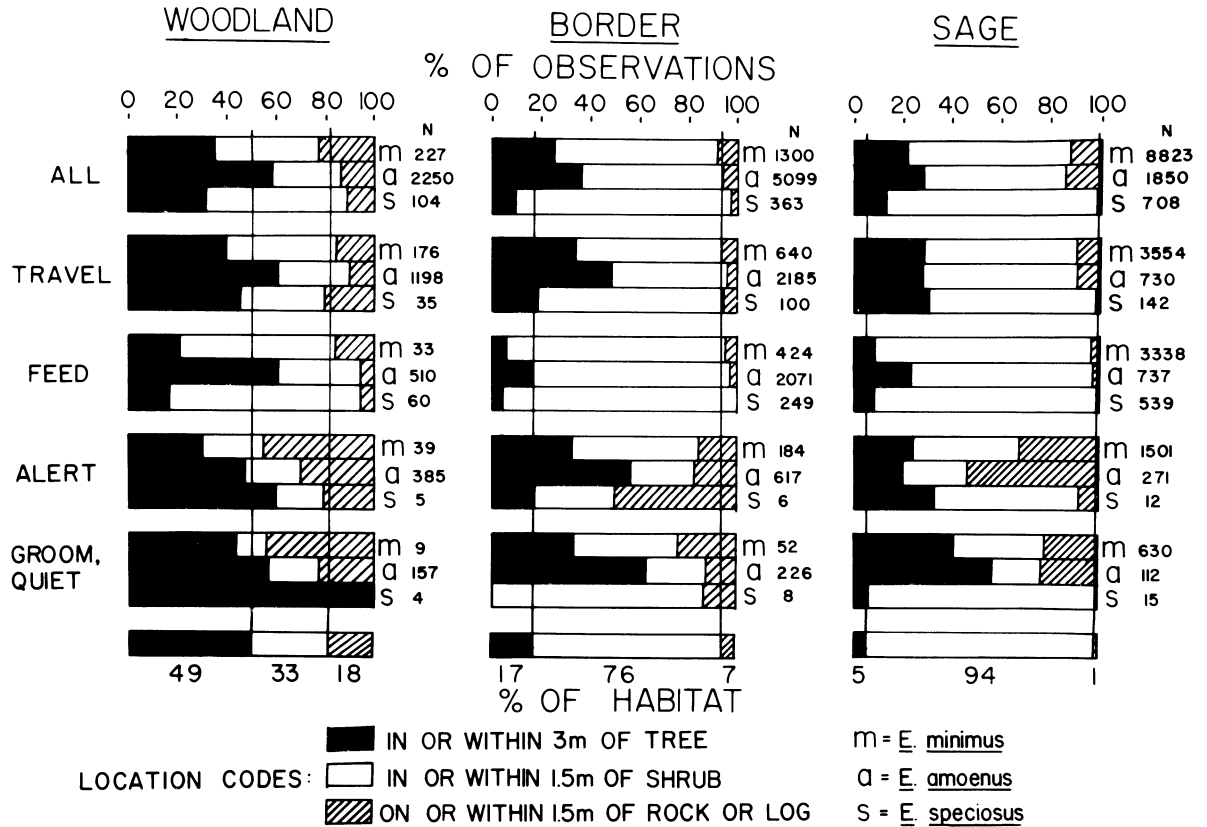


FIG. 7. Microhabitat selection by the 3 *Eutamias* species. Percentage of behaviors occurring in 3 microhabitat types (bottom) in each of the 3 major habitat types. The percent of each microhabitat in the fields of view of the observation stations is shown by the bottom bars; deviations from these percentages (shown by the vertical lines extending upward through the figure) are indications of selection by the animals.

3 habitat types (woodland, sagebrush, and the ecotone) for all observations combined, and for the 4 most common behaviors. The measured proportions of the 3 microhabitat categories (<3 m from trees, <1.5 m from rocks or logs, and <1.5 m from shrubs) within the fields of view of observers are shown at the bottom of the figure for each habitat. Where data from >1 observation station were combined, corrections were made to compensate for interstation differences in microhabitat availability. These differences were slight in most cases, and correction factors were therefore minimal. The figure includes all observations except those made in removal areas in 1976.

Microhabitat selection is indicated wherever the observed utilization of microhabitats deviates strongly from the availability of microhabitats (indicated by the vertical lines extending from the “% of habitat” bars). In all habitats, *E. amoenus* spent a significantly greater proportion of its time near trees than did *E. minimus*. This preference is reflected in most of the different types of behavior as well as overall. On the other hand, *E. speciosus* showed less preference for trees than the other species. All 3 chipmunks preferentially select areas near trees in sagebrush habitats (*E.*

amoenus to a greater extent than the others). Similarly, all species select some type of cover (trees, rocks, logs) when alarmed (“alert”) or relaxed (“groom,” “quiet”), spending more time in the open when feeding or traveling. Comparison of control-section observations to those made in experimental sections before and after the removal revealed few differences, indi-

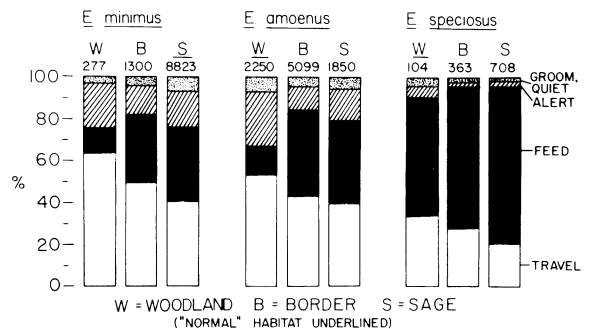


FIG. 8. Activity budgets of the 3 *Eutamias* species in each of the 3 major habitat types. The different portions of the bars represent the percentage of total observations consisting of various behaviors (shown at right).

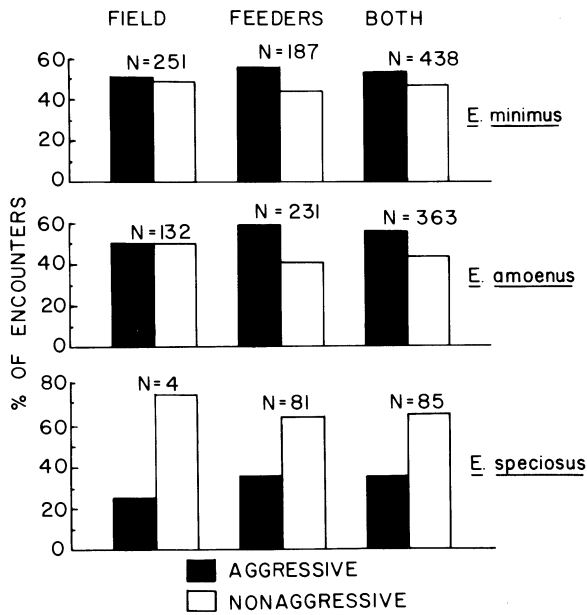


FIG. 9. Intraspecific aggression in each of the 3 species. Bars represent the percentage of total observed encounters that were aggressive (black) or nonaggressive (open).

cating that microhabitat selection did not change greatly with the removal of competing species. However, the number of observations was small, especially of *E. minimus* in woodlands.

The budgeting of various types of behavior also varied with habitat type (Fig. 8). All 3 chipmunks spent more time feeding in sagebrush areas than in woodlands. There was very little overall difference between the activity budgets of *E. minimus* and *E. amoenus*, but *E. speciosus* spent considerably more time feeding than the other species.

TABLE 3. Frequency of encounters in chipmunks, *Eutamias* spp.

Parameter	<i>E. minimus</i>	<i>E. amoenus</i>	<i>E. speciosus</i>
Total of single-animal observations	14,662	13,868	2,272
Total hours of activity observed	40.7	38.5	6.31
Total of intraspecific encounters	251	132	4
Frequency of intraspecific encounters (encounters per hour of chipmunk activity)	6.16	3.43	.63
Total of interspecific encounters	52	59	19
Frequency of interspecific encounters (encounters per hour of chipmunk activity)	1.28	1.53	3.01

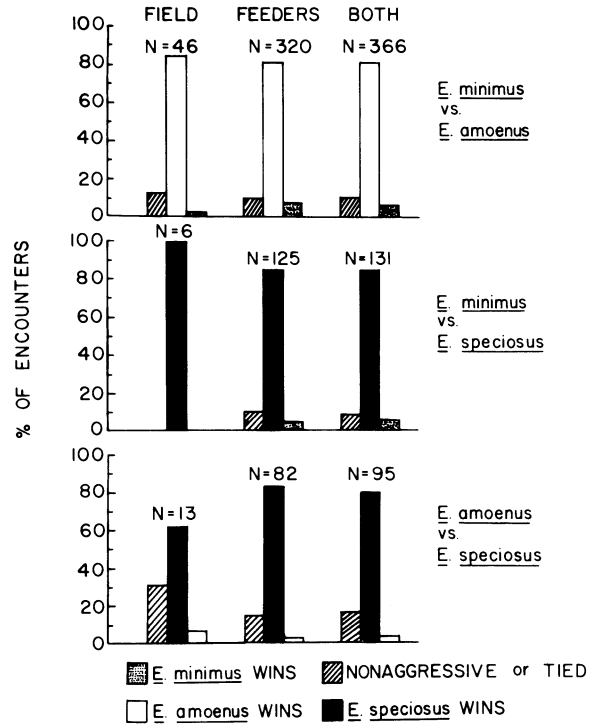


FIG. 10. Interspecific aggression between the 3 *Eutamias* species. Bars represent the percentage of total observed encounters won, lost, or tied by each species.

Aggression.—More than 1400 encounters were observed in the field and at the feeders (886 intraspecific, 592 interspecific). High levels of both inter- and intraspecific aggression occurred in all of the chipmunk species. There was essentially no difference between the outcomes of field and feeder encounters (Figs. 9 and 10). More than half of the intraspecific encounters of *E. minimus* and *E. amoenus* ended aggressively. Levels of aggression were lower in *E. speciosus*, but even in this animal, almost a third of intraspecific encounters were aggressive. There was a very clear-cut dominance hierarchy in interspecific interactions. Almost all ended aggressively (Fig. 10) with few neutral or friendly outcomes. *Eutamias speciosus* clearly dominated the other species, winning almost 90% of all encounters and losing <5%. Though subordinate to *E. speciosus*, *E. amoenus* dominated *E. minimus* almost completely. A sign test (Sokal and Rohlf 1969) of the interspecific dominance results showed them to be highly significant ($P < .01$ that each species had an equal probability of dominating interactions).

The frequency of interactions could be estimated from the number of single-animal observations and encounters. Because 360 single-animal observations equal 1 h of chipmunk activity (1 observation = 10 s), the number of observations divided by 360 gives the hours of activity. Dividing the number of encounters by the hours of activity gives the frequency of inter-

actions (encounters per hour of activity). These estimates for the 3 species are shown in Table 3. Encounters are surprisingly frequent; intraspecific interactions occurred every 10–20 min, and interspecific interactions every 40 to 50 min. Since it is uncommon, *E. speciosus* engaged in more inter- than intraspecific encounters (due simply to the higher probability of encountering a member of another species than of their own species).

DISCUSSION

Although the 3 chipmunk species in the study area are contiguously allopatric, it is incorrect to assume a priori that this spatial distribution is a direct result of competitive exclusion. The lines of contact between the species may also result from environmental discontinuities presenting physical or physiological barriers to the animals, or from habitat selection evolved in response to these or other selective pressures. To evoke competitive exclusion as a primary cause of contiguous allopatry, it is necessary to demonstrate that the presence of one species has reduced the realized niche of another species to less than its fundamental niche (Hutchinson 1957; Miller 1964, 1967; Heller 1971). Fundamental niches are difficult to measure accurately, but several lines of evidence can be used to speculate on their degree of overlap. These include the spectrum of habitats occupied by each species in other parts of its range, comparison of differential adaptations to major sources of environmental stress, removal experiments, and habitat selection tendencies.

Distributional evidence

Examination of the distributional patterns of *E. amoenus*, *E. minimus*, and *E. speciosus* across North America, especially where they are not in contact with congeners, suggests that their fundamental niches overlap considerably. The habitat types occupied by *E. minimus* include all of those found on the east slope of the Sierras. It occurs in open and closed deciduous and coniferous forests (Soper 1947, 1953), alpine fell fields and talus slopes (Sheldon 1932, Willems and Armitage 1975), and semiarid scrub (Whitlow and Hall 1933, Willems and Armitage 1975). *Eutamias amoenus* can be found in areas ranging from alpine tundra and dense coniferous forest (Johnson 1943, Shaw 1944; Larrison 1947) to the open semiarid woodland of the study area, although it is not found in treeless shrublands as is *E. minimus*. It is possible that local populations may have lost the ability to utilize all of the habitats inhabited by the species. However, in both *E. minimus* and *E. amoenus*, a single subspecies may occupy the species' full habitat spectrum. For example, *E. minimus scrutator* ranges from the sagebrush shrublands at the east base of the Sierras throughout most of the Great Basin. It is found in alpine areas in the White Mountains of California (<150 kilometres

from the study area), and can also inhabit piñon pine woodlands wherever *E. amoenus* is absent.

Eutamias speciosus has a more restricted distribution than *E. minimus* or *E. amoenus* (Johnson 1943). It is invariably found in coniferous forests, although it may penetrate more arid habitats along the margins of streams where the riparian growth is dense enough (as at the study site). In some areas, where the vegetational zonation is not as sharply defined as on the Sierran scarp, these 3 species occur sympatrically. An example is the Sagehen Creek Research Station in the northern Sierras (Byrne 1972). The vegetation in this area is a mixture of Jeffrey pine forest, dense undergrowth, and open sagebrush, without discrete borders.

A fourth species, *Eutamias alpinus*, is present on the east slope of the Sierras and is contiguously allopatric with *E. speciosus* at timberline. This animal is only found in alpine communities in south-central California, and never occurs in areas where it is not in contact with other species. Hence, examination of its distribution does not yield much information of the possible extent of its fundamental niche beyond the alpine zone.

Physiological evidence

Investigation of the physiological adaptations of these 4 *Eutamias* species to environmental stresses (primarily high temperatures and aridity) also indicate that broad overlaps exist in their fundamental niches. The steady-state climate spaces (conditions of ambient temperature, wind speed, and absorbed radiation under which the animals can maintain body temperature) are almost identical (Heller and Gates 1971). The water budgets of the animals, and their resistances to imposed H₂O stress, were also quite similar. The largest differences were between *E. minimus* and the other species. This animal had a slightly greater tolerance for high heat loads, and a lower H₂O loss rate under these conditions (Heller and Poulson 1972). Further investigations of thermoregulatory adaptations in *E. minimus*, *E. amoenus*, and *E. speciosus* (Chappell et al. 1978) revealed pronounced differences in the heat storage capabilities of the 3 species. Heat storage is a transient excursion beyond the steady-stage limits of the climate space, followed by a retreat to within these limits to dissipate stored heat passively. It allows animals to remain active during conditions that are intolerable under steady-state limitations, and thereby extends the limits of fundamental niches. Heat storage is extensively developed in *E. minimus*, which can tolerate a 7°C range in euthermic body temperatures (T_b) and withstand an elevated T_b as high as 43°C. *Eutamias amoenus* is also capable of heat storage, but within a much narrower T_b range (3.5°C) than *E. minimus*. *Eutamias speciosus* does not seem to have evolved this adaptation to heat stress (T_b range <2°C). Laboratory measurements were supported by field recordings of T_b from animals equipped with thermo-

sensitive telemeters. Although the data were limited, they demonstrated that both *E. minimus* and *E. amoenus* tolerated hyperthermia during normal activities and environmental conditions, and that *E. minimus* withstood a considerably higher T_b than *E. amoenus* (mean T_b of 41.2°C, maximum 43.1°C for *E. minimus*; mean T_b of 39.7°C, maximum 40.8°C for *E. amoenus*).

Removal experiment

Removal experiments, despite the many technical and interpretive problems associated with them, are perhaps the most direct and convincing evidence of the nature of the line of contact between 2 species. They have been used in studies of species ranging from barnacles (Connell 1961) through many kinds of rodents (Koplin and Hoffmann 1968, Grant 1970, Schroder and Rosenzweig 1975) including chipmunks (Shepard 1971). Results from this study suggest that *E. minimus* can occupy the piñon pine–mountain mahogany woodlands in the absence of *E. amoenus*, but that *E. amoenus* is precluded from occupying vacant sagebrush areas. Not only did a significantly higher proportion of *E. minimus* invade vacant *E. amoenus* habitat than *vice versa*, but there was a very important difference in the movements and types of individuals. *Eutamias amoenus* trapped in the sagebrush were transient visitors, but *E. minimus* often remained permanently in woodlands, and several breeding females (probably the most sedentary age–sex class) were included in these new residents (Fig. 4). These results cannot be explained by interspecific differences in mobility or dispersal, because if this were the case, there would have been no difference between the control and experimental sections. In addition, the mobility of individuals should be revealed by the size of home ranges, and examination of Table 2 reveals little or no difference between the average home range sizes of *E. amoenus* and *E. minimus*; if anything, the latter has smaller home ranges and hence is less mobile. Dispersal is more difficult to quantify; however, there was no interspecific difference in the percentage of young which left the area. Also, *E. minimus* seems to produce slightly fewer young than *E. amoenus* (Table 1) and therefore may have a lower dispersal pressure.

Habitat selection

If physiological constraints or other factors are preventing *E. amoenus* and *E. speciosus* from occupying open sagebrush (as indicated by the removal experiment), we would expect them to show strong tendencies to avoid these stressful areas during their daily activities. Such avoidance could occur as a result of direct physiological strain, from conditioning by experiences early in life, or through genetically determined habitat selection (Wecker 1963). The eventual evolution of habitat selection is to be expected if the environment is fairly stable, because such selection

would prevent the animals from subjecting themselves to unfavorable habitats (Schroder and Rosenzweig 1975). As predicted, *E. amoenus* does show strong selection of areas near trees (Fig. 7). In sagebrush areas, it spends almost 5× as much time in this microhabitat as expected on the basis of random orientation.

The microhabitat orientation of *E. speciosus* presents an enigma: although this species is (according to laboratory data) the most vulnerable of the 3 to heat stress and should strongly avoid open areas, it shows the weakest orientation of all to trees. This apparent paradox could be due to the fact that most observations of *E. speciosus* were on cloudy days or early in the morning, when heat stress was minimal. Also, direct limitation of *E. speciosus* by heat stress may have been reduced in importance in the study area by the availability of riparian lodgepole forest, a refuge to which the animals could retreat during the hottest parts of the day.

From the evidence discussed above we can speculate on the limits of the chipmunks' fundamental niches (shown diagrammatically in Fig. 11). It is clear that *E. minimus* has a fundamental niche which includes the entire spectrum of habitats available on the eastern Sierran scarp, because (a) it occurs in similar habitats elsewhere in its range, and (b) it readily colonizes vacant *E. amoenus* habitat. It is also apparent, from distributional evidence, that the fundamental niche of *E. amoenus* includes lodgepole forests and alpine areas. However, the lower fundamental limits of *E. amoenus* and *E. alpinus*, and the upper and lower limits of *E. speciosus*, are less obvious.

Despite their limited heat-storage capabilities, *E. amoenus* and *E. speciosus* may not be absolutely prevented by physiological limitations from occupying open, arid habitats on a short-term basis. However, they would be seriously impaired in foraging efficiency if they did so, especially during the crucial summer months when the food supply for hibernation is gathered. It is unclear if these species (especially *E. speciosus*) could successfully overwinter and reproduce in sagebrush areas, even if not subjected to competition from a more efficient, heat-tolerant animal such as *E. minimus*. Thus it is unlikely that the sagebrush zone is included within the fundamental niches of *E. amoenus* or *E. speciosus*. In woodlands, the scattered trees provide patches of shade and cool, elevated perches—refuges which tip the balance in favor of the larger, less heat-tolerant species. Results of the removal experiment support this view, because they indicate that *E. amoenus* is incapable of colonizing vacant sagebrush. However, Schroder and Rosenzweig (1975) have proposed that, under certain circumstances, the optimal strategy would be to use only the most suitable habitat, even if survival (at reduced population densities) might be possible in other areas. Under such conditions, a powerful habitat selection

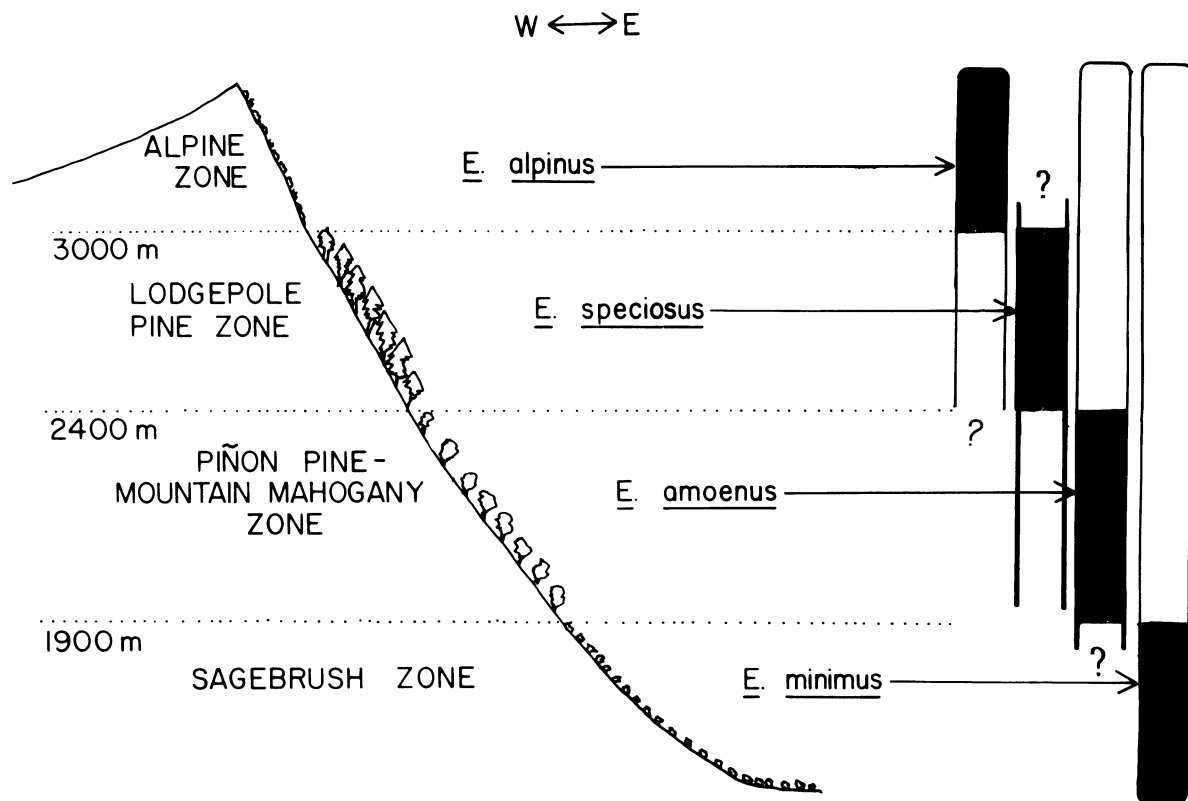


FIG. 11. Stylized transect of the Sierra Nevada, California, near the study site, showing vegetational communities, the zonation of the 4 *Eutamias* species, and their fundamental (entire bars) and realized (black portions of bars) niches. Question marks denote uncertainties in the extent of fundamental niches (see text for details).

should evolve, which might complicate interpretation of short-term removal experiments. This habitat preference would be maintained as long as competition, or its potential, were present. Removal experiments would have to be maintained long enough to allow natural selection to alter habitat preferences before a species would begin to use a physiologically tolerable, though suboptimal, habitat. *Eutamias amoenus* does show a distinct orientation to trees. However, it is doubtful that habitat selection alone prevented *E. amoenus* from entering *E. minimus* habitat, in view of the large differences in heat tolerance between the 2 species and their quite dissimilar habitats.

Schroder and Rosenzweig's (1975) ideas are more applicable to *E. amoenus*–*E. speciosus* line of contact. These species are fairly similar physiologically and their preferred habitats are not strikingly different. It is unlikely, then, that strict physiological constraints prevent *E. speciosus* from colonizing piñon pine–mountain mahogany woodlands and these areas are probably included in its fundamental niche. However, the woodlands are definitely more thermally stressful than lodgepole pine forests (they are hotter, drier, and experience more direct solar radiation), and therefore woodland-dwelling *E. speciosus* may be at a competitive disadvantage to the more heat-tolerant *E. amoenus*. Under these conditions, *E. speciosus*' optimal

strategy might be habitat selection of lodgepoles and avoidance of woodlands. I could not directly test for this in my observations, because an *E. amoenus*–*E. speciosus* removal experiment was not done and there were no lodgepoles in the observation areas. However, *E. speciosus* spent less time near piñons and mountain mahogonies than either of the other 2 chipmunks, which may be indicative of an aversion to these tree species.

The inclusion of alpine areas within *E. speciosus*' fundamental niche is questionable. It is certainly capable of short-term survival above timberline, but due to its relatively large size, it may not be able to gather enough food in the short, unproductive alpine growing season to successfully overwinter. This would effectively restrict *E. speciosus*' fundamental niche to forested areas. The evolution of strong habitat selection is highly likely under these circumstances, even without the presence of competitors. The lower fundamental limits of *E. alpinus* almost certainly include lodgepole forest, because there is no reason to suspect that it is prevented by physiological limitations from occupying forests (Heller and Gates 1971). Nothing is known of *E. alpinus*' heat-storage abilities, so the extent of its fundamental niche into more open, arid habitats is uncertain.

It seems probable that physiological constraints and

the resulting habitat selection tendencies are critical in determining the lower altitudinal limit of *E. amoenus* and the upper and lower limits of *E. speciosus*. The remaining species borders, the upper range limits of *E. minimus* and *E. amoenus*, and the lower limit of *E. alpinus*, are probably due to aggressive exclusion, as proposed by Heller (1971) and Sheppard (1971). This view contrasts with that of States (1976), who proposed that chipmunk distribution patterns are the result of a "... proximal process, continuous habitat orientation," rather than overt interspecific aggression. Results from the present study, especially the removal experiment, indicate that aggression plays a more direct role than suggested by States (1976).

Field data demonstrate that *E. speciosus* is clearly dominant in aggressive encounters with *E. amoenus* and *E. minimus*, and that *E. amoenus* is dominant to *E. minimus*. Thus, the upper limit of *E. minimus* is the result of aggressive exclusion by *E. amoenus*, and, in turn, the upper limit of *E. amoenus* is due to its aggressive inferiority to *E. speciosus*. Other members of this laboratory have done extensive fieldwork on *E. alpinus* and *E. speciosus* at timberline. In encounters with *E. speciosus*, the small *E. alpinus* is almost always defeated, suggesting that its lower limit is also due to aggressive exclusion.

Further support for the aggressive exclusion hypothesis comes from data on the frequency of encounters in nature. Aggressive exclusion is only possible if the subordinate species' efficiency of foraging and other vital activities is substantially diminished by the cost of aggressive defeats by the dominant animal. Because there is little overt fighting in most chipmunk encounters, the potential cost of defeat is measured less in terms of physical damage than in decreased access to food sources, burrows, or other resources. A high frequency of interactions should be necessary if invading individuals of subordinate species are to be continually denied access to these resources. The data seem to satisfy this requirement. At the *E. minimus*-*E. amoenus* line of contact, individual chipmunks encountered members of the other species every 40 to 50 min (Table 3), or ≈ 15 -20 times per day. Moreover, an individual penetrating deeply into the habitat of the other species should encounter the residents at about the same frequency at which the residents encounter each other. Rates of these intraspecific encounters are even higher than interspecific interactions, approaching 3/h (35-40/day) in *E. amoenus*. Thus, an individual *E. minimus* in *E. amoenus* habitat would suffer up to 35-40 defeats each day in disputes over resources. Encounter rates are likely to be similar for other species, because their population densities are alike.

My data on the interactions between *E. minimus* and *E. amoenus* are in agreement with the laboratory results of Heller (1971) and Sheppard (1971). However, Heller (1971) found that, in laboratory encounters, *E. speciosus* was subordinate to *E. amoenus* and

E. alpinus, in direct contrast to what is seen in the field. Byrne (1972) described laboratory results with *E. speciosus* and *E. amoenus* similar to those of Heller (1971, *E. amoenus* dominant) and field results identical to ours (*E. speciosus* dominant). She proposed that the unnaturally confined laboratory environment inhibited the aggressiveness of *E. speciosus*. This view is supported by the finding that *E. speciosus* dominates *E. alpinus* in natural situations but that the reverse is true in the laboratory.

The absence of *E. speciosus* from piñon pine-mountain mahogany woodlands is somewhat paradoxical, in view of its clear aggressive dominance of the resident *E. amoenus*, and the probable inclusion of this habitat within its fundamental niche. In this case, the dominance of *E. speciosus* may not confer enough benefit to overcome the species' physiological limitations and resultant competitive disadvantage to *E. amoenus* in woodlands. Another possibility is that aggression may be disadvantageous to *E. speciosus* in piñon woodlands because it increases exposure to heat stress. Brown (1971) noted a somewhat analogous situation, where aggression was disadvantageous in some habitats, on isolated mountain peaks in the Great Basin. Here *Eutamias dorsalis*, though dominant over other chipmunks in natural or seminatural (feeding station) circumstances, only extends its range into coniferous forests on peaks where the normal forest-dwelling species (*Eutamias umbrinus*, *Eutamias quadrivittatus*, or *Eutamias cinericollis*) are absent. Brown (1971) suggested the forest-dwelling species could easily elude the aggressive *E. dorsalis* because of the abundant cover; in consequence, *E. dorsalis* wasted so much time and energy on fruitless chases that it had little time left to feed. This line of reasoning is not completely applicable to the *E. speciosus*-*E. amoenus* border for several reasons. In the Sierras, the forest-dwelling *E. speciosus* is behaviorally dominant, but in the Great Basin, the forest dwellers are subordinate. Also, if Brown's (1971) theory applies to the *E. speciosus*-*E. amoenus* border, *E. speciosus* should have been unable to successfully defend food resources in woodlands against encroaching *E. amoenus*, as Brown (1971) noted for *E. dorsalis* and *E. umbrinus*. However, in our observations, *E. speciosus* was able to defend such areas (feeders, shrubs in fruit, etc.) and maintain exclusive control over them quite easily. Finally, in Brown's (1971) study the subordinate species were much less aggressive intraspecifically than the dominant *E. dorsalis*, but in the Sierras all species show high levels of intraspecific aggression (Fig. 9).

It is likely that the common strategy of the 4 chipmunks for dealing with the seasonality of their environment is crucial in determining the selection pressures leading to high levels of aggression, as proposed by Heller (1971). These animals are facultative hibernators (Heller and Poulson 1970) which retire to un-

derground hibernacula during the winter months. They depend on caches of food (seeds, nuts, etc.) for energy supplies during the hibernation season, rather than on stored fat. Because snow cover can last for a considerable portion of the year (up to 9 mo at high altitude), the growing season and therefore the time available to breed and gather sufficient stocks of food for the winter is limited. There is probably very strong selection for strategies that maximize the net yield of winter food supplies, especially during years of severe winters or low food productivity.

Although chipmunks do not hold large, exclusive territories, as assumed by Heller (1971), aggression is an effective means of securing access to food sources. Most of the commonly utilized foods in my study area occur sporadically and in small patches; for example a bush in fruit or a patch of grass with ripe seeds. These compact areas can be effectively defended by an aggressive animal against other chipmunks. Direct defense of food sources is a better strategy for chipmunks than possession of a type-A territory (Brown 1964) for several reasons. Because of the sporadic and dispersed nature of food sources, a very large territory would be needed to maintain a constant food supply. Such a territory would be difficult to defend against trespassers, because visibility is low and the animals are relatively cryptic. A territory holder would need to spend a great deal of time searching out and expelling intruders, thus decreasing foraging activities and increasing exposure to predation (predators are abundant in the study area and include snakes, weasels, foxes, coyotes, and 6 raptor species). Another selective advantage of high levels of aggression may be defense of the food cache, an obvious target for other chipmunks, and the burrow itself, because good nest sites may be uncommon. It is possible that the animals defend the nest-site area of the home range (type-B territoriality), but my trapping grid was not fine enough to resolve such small defended areas.

The value of interspecific aggression is less obvious, because it can be disadvantageous (e.g., Brown 1971; Murray 1971). An examination of the food habits of *E. minimus*, *E. amoenus*, and *E. speciosus* (Fig. 6) shows considerable overlap in food utilization in the limited areas where they cooccur. These animals are generalists in their use of food resources, feeding on whatever is available. Therefore, they would probably compete with each other in any of the different vegetational communities on the eastern Sierra if they were sympatric. Because of this potential for interspecific competition for food, it is very likely that interspecific aggression is as valuable as intraspecific aggression to individuals of an aggressively dominant species in contact with an aggressively subordinate congener.

ACKNOWLEDGMENTS

Many people invested their interest, knowledge, time, and efforts in this project, most notably H. Craig Heller, Gary

Colliver, Jeff Stelzner, John Harris, Ross Slotten, Don Kephart, Tracy Chiarelli, and Jefferson Burch. The work was supported by research grants NSF BMS75-09649 and NIH NS10367 awarded to H. C. H., and an NSF predoctoral fellowship awarded to myself. I am grateful to the U.S. National Forest Service for permission to conduct fieldwork in the Inyo National Forest.

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