Seasonal and Altitudinal Variations in Populations of Small Mammals on Rattlesnake Mountain, Washington

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ABSTRACT: Small mammals were live-trapped for 2 years at four elevations in shrub-steppe vegetation of S-central Washington to determine seasonal and altitudinal changes in populations. Species trapped included: Perognathus parvus, Peromyscus maniculatus, Onychomys leucogaster, Lagurus curtatus, Spermophilus townsendii; Neotoma cinerea and Mustela frenata. Perognathus parvus was the most numerous, and widespread species, reaching peak densities in the Artemisia/Poa association at 500-ft elevation. Its density declined with increasing elevation. Perognathus was most numerous on a site with a high frequency of seed-producing annuals, and less numerous in perennial grasslands or where soil temperatures below 40 F were prolonged in the spring. Peromyscus maniculatus were most numerous in the Artemisia/Agropyron association above 2000 ft. Peromyscus appeared to be limited by lack of succulent vegetation or free water at lower, more arid sites. Perognathus was most active and breeding between spring and autumn. Peromyscus favored the period between autumn and late spring. Interspecific competition was not apparent. Perognathus employed periods of torpor during the winter, and some evidence indicated that Peromyscus may have used hypothermia during the driest part of summer and midwinter. Average weights of male Perognathus increased with increasing altitude: this was not apparent in Peromyscus.

INTRODUCTION

After the U.S. Atomic Energy Commission set aside the 120-sq-mile Arid Lands Ecology Reserve (Project ALE), a preliminary survey of the mammalian fauna was conducted (O’Farrell, 1975). Eight species of small mammals were live-trapped in seven vegetation associations at seven elevations. Great Basin pocket mice, Perognathus parvus, and deer mice, Peromyscus maniculatus, were the most widespread as well as the most numerous species captured. Pocket mice, which have evolved in arid environments, dominated the mammalian fauna at lower elevations in the Artemisia/Poa association. Their numbers declined with increasing altitude. Deer mice were most numerous in the more mesic Artemisia/Agropyron associations at higher elevations. Their densities declined sharply below 2000 ft.

The altitudinal clines presented an opportunity to examine niche fit and habitat overlap of Perognathus and Peromyscus as a means of testing for interspecific competition. Between April and September 1969, Kritzman (1970, 1974) investigated populations of Peromyscus and Perognathus at four elevations between 500 and 3500 ft to deter-

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mine the influence of substrate and microclimate on their distribution. She also studied food habits and agonistic behavior. She concluded that substrate conditions were most important in partitioning the niches: *Perognathus* was most successful in deep, sandy soils; *Peromyscus* was most successful in the cooler, rocky soils of the upper elevations. There was little dietary overlap between them since pocket mice were almost exclusively granivorous while deer mice were predominantly insectivorous.

Kritzman's study was conducted in spring and summer; thus she obtained limited data on temporal variation during the periods of activity aboveground and during breeding. It was also possible that her results were unusual since the winter of 1968-1969 was severe and populations of small mammals were no doubt depressed; also, productivity in 1969 was near maximum as a result of excellent winter precipitation. Increased vegetation, in turn, stimulated maximum reproduction in rodents. The present study was initiated to examine constancy of populations over a period of years to better understand the seasonal as well as altitudinal influences on distribution, abundance and reproductive potential in the two dominant species.

**METHODS**

*Description of study area.*—The ALE Reserve occupies the portion of the U.S. Atomic Energy Commission's Hanford Reservation lying W of State Highway 240 (Fig. 1). The southeastern boundary is approximately 9 miles (14 km) NW of Richland, Benton Co., Wash. The altitudinal range is between 432 ft (132 m) in Cold Creek Valley to the crest of Rattlesnake Mountain, 3581 ft (1091 m). There is a gradual upslope to the 1200 ft (366 m) elevation, followed by a steep rise to the rocky summit of the ridge. Dry Creek separates Rattlesnake Mountain from Yakima Ridge (1665 ft; 507 m) on the N.

Soils in the valley are mostly coarse-textured sands and silt sands. These integrate with finer-textured Warden and Ritzville silt loams over most of the area above 1000 ft (300 m) elevation. Creek beds, outwash plains and exposed ridges are generally underlain by Scootney or Lickskillet stony silt loams (Hajek, 1966).

The region is characterized by hot, dry summers and cool, moist winters. At the lower elevations the average annual temperature is 53.1 °F (11.7 °C) with an average annual high of 68.4 °F (18.2 °C) and an average annual low of 41.4 °F (5.2 °C). Temperatures above 100 °F (37.8 °C) and below 32 °F (0 °C) are not uncommon. The average annual precipitation is 6.25 inches (15.9 cm) with 42% of the annual precipitation falling between November and January. With increasing altitude, precipitation increases. Near the summit the average annual precipitation is between 10 inches (25 cm) and 12 inches (30 cm). Average temperatures are inversely related to elevation except during parts of the year when a well-developed inversion effects warmer temperatures at mid-elevations (Stone *et al.*, 1972).

The changes in elevation, soil and microclimate provide suitable
conditions for a mosaic of shrub-steppe vegetation that can be classified in a few broad categories (Daubenmire, 1970). The *Artemisia/Poa*, big sagebrush/Sandberg bluegrass association covers most of the lower elevations on the drier sandy soils. Some parts of the *Artemisia/Poa* association might be described as *Artemisia/Grayia/Poa* due to the significant contribution of hopsage to the shrub cover.

At approximately 1000 ft (300 m) elevation large bunch grasses become the dominant ground cover; this *Artemisia/Agropyron*, big sagebrush/bluebunch wheat grass association covers most of the remaining portions of the ALE Reserve. Where periodic wildfires have destroyed the shrubs, the physiognomy looks much like the *Agropyron/Poa* association. The lithosolic phase of the *Artemisia/Agropyron* association or the *Eriogonum sphaerocephalum/Poa*, roundheaded buckwheat/bluegrass, or *Eriogonum thymoides/Poa*, thyme-leaved buckwheat/bluegrass associations can be found on rocky outcrops or ridge lines.

**Trapping grids:**—Trapping grids were established at 500, 1500, 2500 and 3500 ft at the southern end of Rattlesnake Mountain (Fig. 1). The 500-foot plot lay on the floor of Cold Creek Valley. The soils were mainly Ephrata sandy loam with virtually no stones. The vegetation was *Artemisia/Poa* although disturbances over the years allowed alien...
weeds such as *Bromus tectorum*, *Salsola kali* and *Descurainia pinnata* to invade and become important floristically. Except for the association dominants, over 75% of the flora were annuals.

The 1500-ft site was situated on a gentle plateau near the base of Rattlesnake Mountain. The soil was aeolian Ritzville silt loam that was also stoneless in the upper horizons. The plant association would be *Artemisia/Agropyron*, but a range fire in 1957 destroyed all shrubs except a few scattered rabbit brush, *Chrysothamnus nauseosus*. *Agropyron spicatum* dominated the landscape, which in physiognomy resembles the *Agropyron/Poa* association.

There was a mixture of soil and vegetation types at the 2500-ft grid. The western edge consisted of Lickskillet silt loams with numerous surface stones and rocks and the *Eriogonum sphaerocephalum/Poa* association. This graded into *Artemisia/Agropyron* over the deeper Ritzville silt loams on the eastern part of the site. This and the former site had 11-14 species of plants, mostly perennials.

The 3500-ft grid lay just below the summit along the western face of the mountain. Lithosolic plant associations (*Eriogonum thymoides/Poa*) grew in the upper corner of the grid, but the majority of the site was *Artemisia/Agropyron* on deeper silt loams. This site had the greatest species diversity of flowering plants (21), predominantly perennials.

At each site, 25 Sherman live traps (8 × 9 × 30 cm) were arranged in a 5 × 5 grid with 15-m spacing. Traps were shielded by a large can (10 × 10 × 30 cm) and placed under a 24-gauge galvanized steel tent (30 cm wide, 50 cm long and 25 cm at the peak). These helped protect trapped animals from extreme temperatures and precipitation, thus extending the morning trapping period an additional 1 1/2 to 2 hr without stressing the mice. Each trap contained a sufficient quantity of seeds to prevent torpor in animals, as well as Dacron batting for use as a nest during confinement. After late September 1969, an additional trap was placed at each station bringing the total to 50 traps per site.

From April through September 1969, all traps were opened for 2 or 3 consecutive nights each month depending upon weather conditions. After October, traps were prebaited (peanut butter/oatmeal mixture) once each month, and then operated the following night. The 500-ft grid was not operated in October and November 1969, but estimates of the numbers were extrapolated from nearby larger trapping grids. The lowest site was then operated each month for the remainder of the study.

Trapped animals were removed early in the morning. Species, sex, age class, reproductive condition, pelage, general condition and location of capture were recorded. Between April and September 1969, all animals were marked by amputation of the distal portion of the tail to mark a segment of the population. After October only deer mice were marked as individuals with metal ear tags. Pocket mice were not marked individually to avoid confusing them with pocket mice marked during studies in the valley. In April 1971 all animals were weighed.
with small spring scales. Animals were immediately released at the point of capture after data were recorded.

Juvenile *Perognathus* and *Peromyscus* can be easily separated from adults during the 1st 4-6 weeks after weaning by body size, and pelage color and condition. All animals were considered to be adults unless juvenile conditions were obvious. Males were considered to be reproductively active when they had scrotal testes. Females were recorded as reproductively active if they were obviously pregnant or their vaginas or mammae were enlarged.

Climatological data were gathered by the Atmospheric Resources Department using maximum-minimum thermometers located in small shelters 1 ft above the soil, and 5-inch-capacity rain gauges. The latter contained oil to minimize evaporation and antifreeze in the winter.

**Results**

*Species composition and relative abundance.*—Trapping effort, expressed as trap nights, numbers of small mammals captured and trapping success per 100 traps are presented in Table 1 as a function of altitude and year. Captures included Great Basin pocket mouse, *Perognathus parvus*; deer mouse, *Peromyscus maniculatus*; sagebrush vole, *Lagurus curtau*; Townsend’s ground squirrel, *Spermophilus townsendii*; grasshopper mouse, *Onychomys leucogaster*; bushy-tailed wood rat, *Neotoma cinerea*; and the long-tailed weasel, *Mustela frenata*. Most captures were of *Perognathus* (1133) and *Peromyscus* (844): the other five species accounted for less than 5% of the total captures. For this reason the bulk of the synthesis is concerned with the populations of pocket mice and deer mice.

*Perognathus* and *Peromyscus* were caught at all elevations throughout the study (Table 1). Of 1133 pocket mice, 37% were captured at 500 ft; the remainder were evenly divided between the other three trapping sites, at higher elevations. A total of 844 deer mice were taken: 31, 20, 7 and 3 per 100 trap nights at 3500 ft, 2500 ft, 1500 ft and 500 ft, respectively. Like the previous study (O’Farrell, 1975), and during each year of this study, *Perognathus* were more dense at lower elevations and *Peromyscus* were much more numerous at higher elevations.

Information for these dominant species was graphed to illustrate changes in numbers, breeding condition, presence of juveniles and new individuals as a function of time and altitude (Fig. 2). At 500 ft an average of 21 pocket mice were trapped each month they were active, compared with an average of 11-12 per month at the higher elevations. There was a twofold difference (32 vs. 14) in the total number trapped per 100 trap nights at 3500 ft, 2500 ft, 1500 ft and 500 ft, respectively. Like the previous study (O’Farrell, 1975), and during each year of this study, *Perognathus* were more dense at lower elevations and *Peromyscus* were much more numerous at higher elevations.

Pocket mouse populations at higher elevations did not show such
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<th>Trap nights</th>
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<th><em>Peromyscus maniculatus</em></th>
<th><em>Lagurus curtatus</em></th>
<th><em>Spermophilus townsendii</em></th>
<th><em>Ochthomys leucogaster</em></th>
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clear annual fluctuations, partially due to the dampening in expression resulting from reduced population sizes. In 1969 they all showed a similar peak in captures during September although the differences at 2500 ft were not great. The 1970 peaks in captures also occurred during the breeding season before the appearance of juveniles, but the difference in annual amplitude was more obvious at 2500 ft and almost unrecognizable at the highest elevation. The 3500-ft population showed a remarkable degree of stability as regards trapping success compared with the other locations.

*Peromyscus maniculatus* populations maintained a tenuous foothold in the *Artemisia/Poa* association. Individuals were trapped in only 13 months during the study, with an average of three captures per month when they were trappable. Most captures were made between December 1969 and March 1970, and from September 1970 until the termination of the project. None were trapped during the summer months.

At 1500 ft, an average of five deer mice were trapped each month they were active. There were no captures for the 1st 5 months, but from then on at least one deer mouse was taken each month except for November 1969. At this elevation there was the first suggestion of an annual cycle in the apparent abundance of *Peromyscus* with peak numbers recorded during March each year. Unlike the lower site, some deer mice were trapped during the summer months, albeit in low numbers.

There was a significant threefold increase in the total number of *Perognathus parvus* and *Peromyscus maniculatus* populations maintained a tenuous foothold in the *Artemisia/Poa* association. Individuals were trapped in only 13 months during the study, with an average of three captures per month when they were trappable. Most captures were made between December 1969 and March 1970, and from September 1970 until the termination of the project. None were trapped during the summer months.

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![Graph showing captures of Perognathus and Peromyscus at four elevations on Rattlesnake Mountain, Benton Co., Washington, 1969-1971. New individual Peromyscus are also shown.](image-url)
captures between the 1500- and 2500-ft sites. An average of 11 *Peromyscus* were trapped each month at 2500 ft. There was a well-defined annual cycle in trappability, with increased numbers being taken between autumn and spring with a depression in numbers during the summer. In 1969 more than 10 deer mice were taken each month between September and May, and in 1970 between October and April.

The greatest numbers of deer mice were trapped at the 3500-ft site with an average of 17 captures per month and a high of 33 in April 1970. A total of 427 captures were logged, 50% more than the total for the 2500-ft grid and 10 times the total number trapped at the lowest elevation. Deer mice were available every month of the year, but there was an annual cycle of abundance that peaked during the winter-spring of 1970, and between autumn and spring in 1971.

*Breeding season.*—Pocket mice were reproductively active through August 1969 at the two lower elevations but only through July at the higher sites. In 1970 breeding adults were trapped between March and August on the lower two sites, March and July at 2500 ft, and April through July at 3500 ft. This indicated that the duration of the breeding season was approximately 4 months at the highest elevation and 6 months at the lower elevations.

Juveniles were observed at different frequencies across sites and between years (Fig. 2). Juvenile *Perognathus* were trapped on the 500-ft grid during 4 months (June-September) in 1969 with a peak success in July. At 1500 ft they were trapped between June and August 1969, with equal numbers appearing in July and August. Juveniles were taken in July and August only at 2500 ft; and in June and between August and September at 3500 ft. Both reached peak trapping success in August. In 1970 the breeding season appeared shortened compared with 1969: juveniles were trapped between May and July at 500 ft, during July only at 1500 and 2500 ft, and during July and August at 3500 ft.

The small sample size at the lowest site only permitted the observation that most of the *Peromyscus* trapped during the colder months were reproductively active. Subadults were trapped only during the months of December 1969 and 1970, and March 1969. Deer mice were breeding in December 1969 on the 1500-ft plot as well, but most of the mice bred between February and April with new juveniles appearing in January, March and May, with the greatest number in March. In 1970-1971, *Peromyscus* bred from October until the end of the study. Juveniles were trapped in December, January and March.

Above 2000 ft there was an obvious increase in the duration of breeding. On the 2500-ft plot reproductively active animals were observed in June 1969 and from October through the following June. Breeding resumed between November 1970 and April 1971. Juveniles appeared in December, January and April the 1st year, and in December and April the following year. Peak numbers were recorded during either December or January.

The breeding season was most protracted at the highest elevation:
breeding adults were observed in June and July, and from October through the following July; and after a summer break breeding resumed from December to April. Juveniles were trapped during nine of the first 14 months of the study with the largest numbers appearing in April.

**Torpor.**—Pocket mice were not trapped for varying lengths of time during the winter and were presumably in some state of torpor. During the first winter, data indicated that with increasing altitude the number of months pocket mice were inactive was 1, 2, 2 and 3, respectively; and in 1970-71 they were inactive for 2, 2, 3, and 4 months (Fig. 2).

New *Peromyscus* entered the trapping population every month (Fig. 2). At 3500 ft an average of seven new *Peromyscus* were caught each month, and at 2500 ft an average of four per month. During the breeding season most of the new individuals were juveniles, but in the other months they were adults, presumably emigrants or transients. In October 1970 several new adults were trapped months after the last juveniles had appeared and immediately after the summer depression in population size. One explanation might be that *Peromyscus* were not active for periods of time during the hotter months of the summer, even at the higher elevations. MacMillen (1964) observed that *Peromyscus* were trappable for about 2-5 months, but that 8% of a marked population reappeared at the same trap sites in autumn after varying absences from the trappable population.

To examine this possibility, individual trapping records for *Peromyscus* were examined for breaks in continuity. Usually an animal was trappable every month once he entered the trapping population, with only an occasional 1-month gap. Those animals with longer gaps were tabulated. A total of 12 animals on the 3500-ft grid had gaps in their trapping records of 2 months or longer, with a range of 2-4 months. Half (53%) of the gaps occurred between May and September, and the remainder between November and January. On the 2500-ft grid only three animals had disjunct records: one between April and August; one July to September; and one November to January. Whether they were in a reduced metabolic state during these periods is unknown, as was their exact location during the interim.

Morhardt and Hudson (1966) were among the first to demonstrate daily torpor in *Peromyscus* spp. in response to starvation. Since then, others (Gaertner et al., 1973, for example) have shown that *Peromyscus* can enter spontaneous torpor in winter as well as induced torpor in response to stresses such as starvation. It now appears that *Peromyscus*, like *Perognathus* and other genera of small rodents, includes torpor in its strategy to cope with environmental stresses. Demonstration of spontaneous torpor in the field presently depends on indirect evidence such as the trapping records mentioned here.

**Weight.**—Animals were weighed only during the last month of the study. The trappable population consisted primarily of males, both *Perognathus* and *Peromyscus*, and only their weights are summarized in Table 2. The data suggest that the average weight of male
Perognathus increased with increasing elevation; there was no indication of a similar relationship in Peromyscus. Hock (1962) described a significant increase in body weight for Peromyscus maniculatus sonoriensis over an altitudinal gradient of 10,000 ft. The mean weights of ALE deer mice were comparable to the mean weights of animals trapped at 14,175 ft on White Mt., Calif., not to animals trapped in Owens Valley (4250 ft).

Climate.—The maximum and minimum air temperatures recorded at the four sites are taken from Stone et al. (1972) and are summarized in Figure 3. The highest maximums were always recorded at the lower sites with a 10-14°F difference between the maximums of the extreme elevations. The minimum temperatures were more com-

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<td>17.4 ± 0.3 (18)</td>
<td>18.3 ± 0.3 (12)</td>
<td>17.6 ± 0.4 (11)</td>
<td>19.1 ± 0.5 (12)</td>
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<tr>
<td>Peromyscus maniculatus</td>
<td>21.7 (2)</td>
<td>18.0 (2)</td>
<td>21.2 ± 0.7 (6)</td>
<td>20.3 ± 0.5 (11)</td>
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x ± S.E. (N)

Fig. 3.—Maximum and minimum air temperatures recorded at four elevations on Rattlesnake Mountain, Benton Co., Washington, 1969-1971. Thermometers are in small shelters 1 ft aboveground to record temperatures most representative of the vegetation height on the ALE Reserve.
plex. The lowest minimums were recorded at the extreme elevations with more moderate lows observed at the intermediate elevations. The lower minimums at the 500-ft plot are due to an inversion phenomenon resulting from greater radiation loss at lower elevations coupled with cold air drainage to the valleys during the night. As a result, the valley and mountain crest experience similar minimum temperatures. The valley is hottest in summer and cold in winter, while the peak is cool in summer and cold in winter, with intermediate elevations experiencing more moderate temperatures both summer and winter.

Soil temperatures recorded at a depth of 6 dm along this gradient have been summarized by Kritzman (1970) and Rickard (1971). They showed that at this depth (which is below the level of diel variations in soil temperatures) there is an inverse relationship between soil temperature and increasing elevation. Soil temperatures at the crest are about 10 F colder in winter and 12-15 F cooler in summer, with a peak of 80-82 F in August in the valley and a peak of 68-70 F at the crest. By burrowing no more than 5 dm the small mammals could enter a buffered environment as regards temperature extremes.

Precipitation also varied with increasing elevation although the pattern was not as neat as that for temperatures, partly because of the difficulty in measuring total precipitation at the crest where there was more snow and blowing rain. The most useful measure of precipitation in this winter-wet region is the amount of moisture falling between October and May. In 1968-1969 the totals were 9.02, 9.85, 9.63 and 9.99 inches for the 500, 1500, 2500 and 3500 ft sites, respectively. In 1969-1970 the observed values were 7.95, 8.73, 8.35 and 6.27 inches; in 1970-1971, they were 5.35, 7.44, 6.39 and 4.71 inches. The only obvious pattern was that mid-elevations always received greater precipitation than the valley, and in some years received more moisture than the crest of the mountain.

Except for the quantity and quality of snow at higher elevation, precipitation itself had little bearing on the small mammals. What was more critical was the relationship between precipitation and the stimulation of growth and reproduction in the flora, which was food for the mice or provided food for their prey, especially insects. No attempt was made to measure primary productivity each year; therefore, measurements of precipitation were used as an index to food resources.

Discussion

The information on species composition and relative abundance complements earlier data (Kritzman, 1974; O'Farrell, 1975), which showed that the mammalian fauna of the ALE Reserve consisted of a mixture of species adapted to arid environments and more mesic grasslands (Dalquest, 1948). Environmental parameters along the altitudinal transect encompassed an ecotone between the arid Artemisia/Poa association and the shrub-steppe dominated by large, perennial bunch grasses at higher, more mesic elevations. The distribution of small mammals follows the relationships described earlier and further
supports the speculation that several of the species have strong associations with specific vegetation types. *Onychomys leucogaster* has never been trapped in significant numbers on the ALE Reserve, but it is captured consistently throughout the year mainly in the *Artemisia/poa* association (O'Farrell, 1975). Ground-dwelling beetles are also more abundant at the lower elevations (Rickard, 1971), and I have speculated that the distribution of *Onychomys* may be related to the distribution of their primary prey. The trapping data in this study were the first records of grasshopper mice being taken in the *Artemisia/Agropyron* association and the highest elevation where the species has been trapped on the Hanford Reservation.

Both *Lagurus curtatus* and *Spermophilus townsendii* appear to be associated with the *Artemisia/Agropyron* association at elevations above the valley floor. Sagebrush voles, although never taken in large numbers, are most frequently captured at the highest elevations in this association, and the only ones trapped in the *Artemisia/Poa* association were transients that wandered into pitfalls or live traps near Rattlesnake Springs (O'Farrell, 1972). *Spermophilus* were trapped in the lower *Artemisia/Poa* association for the first time during this study. However, they have been observed at all elevations on the Hanford Reservation, especially along the Columbia River where riparian vegetation or extensive stands of winter annuals in abandoned fields appear to provide sufficient food. The species may prefer the *Artemisia/Agropyron* association because it provides green vegetation from autumn through the following June. In this area, *Spermophilus townsendii* ceases hibernation in late January and commences hypothermia in May or June. Therefore, new herbage, thought to be its major food supply, would be available throughout its period of activity and breeding.

The captures of *Neotoma cinerea* and *Mustela frenata* were incidental since the trapping methods were not designed to sample either. Bushy-tailed wood rats are distributed over the entire reservation, especially around buildings, rocky outcrops, and in the riparian vegetation near rivers and springs. Long-tailed weasels are probably one of the more important predators in the region. They have been observed many times in the *Spermophilus* colonies adjacent to alfalfa fields N of Richland.

Pocket mice are the most numerous, as well as the most widespread, small mammal on the ALE Reserve. They can be found in every vegetation association along the altitudinal cline sampled. Deer mice are second in abundance although they are not found in every habitat type and they do not reach comparable densities at the lower elevations. The shift in dominance between the two species that were observed earlier (Kritzman, 1974, O'Farrell, 1975) remained the same in this study: *Perognathus* was more numerous at lower altitudes, while *Peromyscus* was the more abundant at higher elevations. One of the objectives of Kritzman's thesis (1970) as well as this study, was to
determine whether there was competition between the species that might account for the changes observed in distribution and relative abundance. Direct competition seemed unlikely, based upon these observations. For example, three of the sites were in the *Artemisia/Agropyron* association on related soils. The average number of *Perognathus* trapped each month they were active remained the same at all sites, while the number of *Peromyscus* captured rose abruptly at the higher sites. If direct competition were involved, one would predict a more obvious inverse relationship between abundance of the two species. If direct competition were involved, one would also predict that *Peromyscus* would be more successful since it is more aggressive towards *Perognathus* than vice versa (Kritzman, 1970).

There was a temporal partitioning of the annual cycle between the species. *Peromyscus* reached its greatest densities and bred during the period between autumn and spring. Scheffer (1924) reported that *Peromyscus maniculatus* in "central eastern" Washington bred all year. These data do not show this to be true on the ALE Reserve.

There was little dietary overlap between the species in this area (Kritzman, 1970, 1974). *Peromyscus* is an opportunistic feeder (Coggshall, 1928) eating a high proportion of insects, herbage and seeds (Jameson, 1952; Williams, 1959). *Perognathus* is primarily a grazer (Scheffer, 1938), although it consumes some insects (Jameson, 1954). The greatest overlap in diets appears to be in the early spring when both species consume some insects (Kritzman, 1974).

If trapping success reflects adaptability along the altitudinal gradients, then *Peromyscus* must be the more vulnerable species. There was a tenfold increase in abundance of deer mice with increasing elevation. At the lowest elevation, they were not able to maintain numbers through an annual cycle, and few young were recruited to the population. *Perognathus* declined in numbers with altitude, but only by a factor of 2. The species was able to successfully maintain its annual cycle at the highest elevation; it bred, and young animals were recruited.

*Perognathus* were underground during much of the *Peromyscus* breeding season, and the former reached peak numbers either in the spring breeding season or in late summer. Most juvenile *Peromyscus* had already entered the populations before the first litters of *Perognathus* were weaned. Deer mice appeared to be more attuned to increased activity, physiological and behavioral, during the colder months, while *Perognathus* performed best during the spring and hot summers.

Data gathered during this project suggested that *Perognathus parvus* were capable of maintaining adequate populations over the range of environmental parameters sampled. They were more successful in the vegetation associations containing a high frequency of annual plants that consistently produce sufficient quantities of seeds each year to sustain both maintenance and reproductive requirements of the species. Pocket mice were less dense in vegetation associations
dominated by perennial species of flora, even in the absence of other mammals such as *Peromyscus*. The low production of seeds in these associations is postulated as a major cue to population suppression. Although *Perognathus* maintained populations at 3500 ft, their numbers were half that of the valley floor. The relative scarcity of seeds is partially responsible, but soil temperature may be an additional factor. Pocket mice remain underground, presumably in torpor, for a longer duration at the crest. Soil temperatures are 10-14 °F colder and the retarded warming trend in the spring may delay their emergence, thus reducing their annual cycle of aboveground activities and breeding season.

*Peromyscus* appeared to be less capable of adapting to the environmental conditions at lower elevations than *Perognathus* in adapting to conditions at high elevations. The lowest site was hotter in summer, experienced cold minimums throughout the year, and received the least precipitation. *Peromyscus* was able to cope with colder temperatures on the summit; therefore, minimum temperatures in the valley were probably not limiting. *Perognathus* were in torpor when deer mice were most active during the winter and early spring; thus, interspecific competition was reduced. Deer mice can be trapped in abundance all year in the riparian vegetation along Rattlesnake Springs at an elevation of 620 ft. The temperatures in the coulee are equal to those observed on the 500-ft site. However, the mice have a readily available source of water in the spring and the succulent vegetation. Elsewhere at low elevations, vegetation dried in late spring and no abundant sources of free water were available. I suggest that the lack of free water, or aridity, limited the distribution of *Peromyscus* more than the temperature extremes or the condition of the substrate.

The multiplicity of environmental conditions operated to affect the dominant species at different points in their ecological requirements or tolerances. There was a temporal partitioning of the annual cycle so that activities of the two species overlapped to a minimum degree, especially the breeding season. Food resources were not shared to a large degree, but they influenced the species in different ways: *Perognathus* responded negatively to a diminished seed supply in perennial grasslands; *Peromyscus* reacted positively to sustained green herbage and more insects at higher elevations, and negatively to the lack of free water at lower elevations. Direct interspecific competition was not observed, nor did the data suggest that this was an important consideration. Both species may have used periods of hypothermia as a strategy for enduring climatic extremes. *Perognathus* was probably torpid for much of the time it remained underground during the winter. *Peromyscus* known to be alive were not trappable during 2-4 months of the summer and 2-3 months in midwinter. They may have been torpid as well.

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LITERATURE CITED


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