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VEGETATIVE AND EDAPHIC FACTORS AFFECTING ABUNDANCE AND DISTRIBUTION OF SMALL MAMMALS IN SOUTHEAST OREGON

George A. Feldhamer¹

ABSTRACT.— The relationships between vegetative and edaphic habitat factors and the local distribution and abundance of small mammals on Malheur National Wildlife Refuge, Harney County, Oregon, were examined between July 1973 and June 1975. Of 16 species of small mammals captured, deer mice (*Peromyscus maniculatus*), montane voles (*Microtus montanus*), Great Basin pocket mice (*Perognathus parvus*), and least chipmunks (*Eutamias minimus*) comprised 90.1 percent of the individuals. The physiognomy of the vegetation was a factor in the distribution of rodent species other than deer mice. Pocket mice and chipmunks were restricted to the communities dominated by sagebrush (*Artemisia tridentata*) or greasewood (*Sarcobatus vermiculatus*). Population densities of pocket mice and chipmunks were significantly related to edaphic factors such as soil depth, texture, and strength, which may have affected the construction and stability of burrows. Montane voles occurred only in marsh or grassland communities. Population densities of voles were directly correlated with the amount of cover and inversely correlated with its patchiness. Deer mice were the most common species encountered and occurred in all but the grassland communities. The density of this species was related to vegetative or edaphic factors only seasonally or in certain habitats, and few generalizations could be made.

The general habitat preferences of many species of small mammals have been documented by several generations of natural historians, and often can be attributed to food preferences and associated morphological adaptations (Baker 1971). Many other extrinsic factors affect populations of small mammals, including vegetation, soils, predation, competition, and weather. Intrinsic factors, such as genetic and behavioral changes, also are of significance (Krebs 1964:63–67). However, the quantitative relationships between many environmental factors and the distribution and abundance of small mammals usually are considerably less well known than their general preferences.

This study was initiated to provide quantitative information concerning the effect of vegetative and edaphic factors on the local distribution and abundance of small mam-

mals inhabiting four community types on the Malheur National Wildlife Refuge.

DESCRIPTION OF THE AREA

Malheur National Wildlife Refuge is primarily a resting and breeding area for migratory waterfowl and is located in the Harney Basin, Harney County, Oregon, between 118.5° and 119.5° W longitude and 42.7° and 43.4° N. latitude (Fig. 1). The refuge is at an elevation of approximately 1250 meters (m). The climate is characterized by dry summers with temperatures rarely exceeding 32.2 C and cold winters with average temperatures of -6.6 C. The average annual precipitation is 22.9 cm, much of which occurs as snowfall (Meteorology Committee, Pacific Northwest River Basin Commission 1969).

Much of the refuge consists of valley wet-

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lands vegetated primarily by hardstem bulrush (*Scirpus acutus*), cattail (*Typha latifolia*), baltic rush (*Juncus balticus*), sedges (*Carex* sp.), and submerged and emergent wetland flora. Rimrock areas above the valley floor support mainly big sagebrush, greasewood, and grasses, principally the exotic annual, cheatgrass (*Bromus tectorum*). Grassland areas were dominated by bluegrass (*Poa secunda*), saltgrass (*Distichlis stricta*), bluestem (*Agropyron smithii*), and numerous other graminoid species, as well as sedges.

METHODS AND MATERIALS

Eighteen study plots were established among the four predominant types of terrestrial plant communities on the refuge. Five plots each were in sagebrush and greasewood areas and four plots each were in marsh and grassland communities. Areas designated as marsh were characterized by habitat factors that generally conformed to the "inland shallow fresh marsh" category of Shaw and Fredine (1956:21). Areas designated as grassland conformed to the "inland fresh meadow" category. Live-trapping on all plots was conducted once during 1973 (July-September), twice in 1974 (June-August, September-November), and once in 1975 (April-June). Each trapping period roughly corresponded seasonally to either spring, summer, or fall, except in 1973. Vegetative and edaphic parameters were measured during each trapping period.



Fig. 1. Location of Malheur National Wildlife Refuge, Harney County, Oregon.

Small Mammals

Trapping grids consisted of 49 Sherman live-traps at 15.0 m intervals in a square grid of 1.1 ha (2.7 acres). This area included a border of 0.3 ha (0.7 acres), from which it was assumed animals would be captured (Faust et al. 1971).

Traps were operated for 10 consecutive days, except during 1973, when grids were operated for 3- or 4-day periods. Traps were baited with rolled oats, contained Dacron batting for nesting material, and were covered with aluminum shields to minimize heat stress (Feldhamer 1977). Animals were removed from traps as soon after dawn as possible.

Trapped animals were individually marked by toe clipping, following the procedure outlined by Taber and Cowan (1971), and released at their respective points of capture. The species, sex, reproductive condition, age class, weight, and trap locality of each captured animal were recorded.

Reproductively active males had descended testes. Females were termed pregnant if their abdomens were visibly swollen or if developing young were detected by palpation. Nursing females were recognized by lacking fur around the teats or by large and protruding mammae.

Individuals were classified as juvenile or adult on the basis of body size and weight. All deer mice (*Peromyscus maniculatus*) with grey pelage or an incomplete postjuvenile developmental molt were considered juveniles (Layne 1968). The estimated mean densities during each trapping period, and associated estimates of variance, were calculated using a Mean Peterson Estimate (Seber 1973:138). The trap-revealed distribution of the four common species inhabiting the study plots were classified as uniform, random, or clumped by Southwood's (1966:36) index of dispersion (X^2).

Vegetation

Percentage cover was estimated on each plot using a Gossen Tri-Lux photoelectric cell. Light intensity was measured between 1100 and 1300 hours at ground level and immediately above the vegetation at each of 10

points. The percentage differences between readings represented the amount of cover at each point. Measurements were made at 20 m intervals along two diagonal transects on each plot and the average considered an index to the cover present during that trapping period. In addition, in 1975 each plot was visually "divided" into 49 quadrats, each 15.0 m² with a trap-site at the center. The percentage of cover in each quadrat was estimated and rated as follows: 0-20 percent = 1; 21-40 percent = 2; 41-60 percent = 3; 61-80 percent = 4; and 81-100 percent = 5 (Myton 1974). For each species of small mammals, a chi-square ratio test was used to determine if the number of captures were equal for each of the five ratings. Expected values were calculated as—

$$E(\text{captures/ rating } i) = \frac{\text{total captures on plot} \times \text{(number of sites with rating } i)}{\text{trap sites}}$$

These distributions were considered separately for each plot.

Although an average cover value was calculated for each plot, individual portions often differed substantially in the amount of cover present. Therefore, the same five-division rating system (Myton 1974) was used to calculate a cover diversity index ("patchiness") from the 10 photometric cover readings made on each plot. The formula $1/\sum q_i^2$ was used (M'Closkey and Fieldwick 1975) where q_i was the proportion of readings within each of the five cover rankings.

During the initial trapping period on each plot in 1974, the foliage height diversity (FHD) of the vegetation was measured using general methods described previously (MacArthur and MacArthur 1961, Rosenzweig and Winakur 1969, M'Closkey and Lajoie 1975). Vegetative density was measured in a different direction from each of the eight central trap-stations at heights of 7.6, 15.0, 30.0, 46.0, and 61.0 cm above the ground (q_i). The FHD was computed using $1/\sum q_i^2$, with $i = 1, 3, \text{ and } 5$ only. Thus, the vegetation was considered to occupy three distinct layers: below 15.0 cm, between 15.0 and 46.0 cm, and above 46.0 cm.

The percentage of vegetative moisture (succulence) was determined each trapping period beginning in 1974. Ten samples were

collected at 20 m intervals along two diagonal transects and an average succulence value per plot computed. The procedure involved clipping vegetation from an approximate 1-m² area, placing samples in airtight cans, and weighing each sample before and after oven drying at about 63 C to determine the weight of water in the material. The ratio of water weight to dry weight was considered the percent moisture content (Dawson 1972).

Soils

The soil texture of each study plot was determined once in 1973 and was considered to remain constant for the duration of the field work. Ten soil subsamples were collected from depths of approximately 15.0 cm along diagonal transects. Subsamples were combined to form a single sample that was analyzed for composition of sand, silt, and clay using the Bouyoucos method (Dawson 1971).

The mean soil depth on each plot was estimated by forcing a sharpened steel probe, 1.0 cm in diameter, into the ground to a depth of 102.0 cm. If an obstruction was met prior to this depth, the distance from ground surface to the obstruction was recorded. An average depth was determined from 10 probings made along diagonal transects.

The soil shear stress ("strength") on each plot was measured once during the initial trapping period of 1974, using a Soil Test pocket penetrometer. The index value, measured in kg/cm², was in direct proportion to the soil strength. Ten measurements, made along diagonal transects, were averaged to obtain a mean value. Diversity values for both soil depth and soil strength were calculated using $1/\sum q_i^2$. For soil depth, diversity was computed on the basis of four equal rankings (q_i) of 25.4 cm each. Diversity for soil strength also was computed on the basis of four rankings: 0-1.12, 1.12-2.25, 2.26-3.39, and 3.40-4.50 kg/cm².

The percentage soil moisture on each plot was estimated each trapping period following the procedure described to estimate vegetative succulence. Ten samples were collected from a depth of 15.0 cm along diagonal transects and an average value computed.

Regression Analyses

Linear regression analyses were used to determine the relationship between the estimated mean density of each species of small mammal and concurrently measured independent habitat parameters. Habitat variables and associated densities of small mammal species in each of the four community types were analyzed in three groupings: (1) for the entire study period; (2) for all periods exclusive of 1973, so that the effects of vegetative succulence and patchiness could be evaluated; and (3) for the initial trapping period of 1974, because foliage height diversity and soil strength were measured only during this period. Correlations were considered to be statistically significant if $P < 0.05$.

RESULTS AND DISCUSSION

During the field work, 26,460 trap-nights on the study plots produced 4,717 captures of small mammals. These captures involved 1,580 individuals and represented four mam-

malian orders (Table 1). Three orders were represented by single species and were considered incidental to the study because traps were not set for them. Although 13 species of rodents from four families were captured, deer mice, montane voles (*Microtus montanus*), Great Basin pocket mice (*Perognathus parvus*), and least chipmunks (*Eutamias minimus*) comprised 90.1 percent of the small mammals captured and were considered in detail in the analyses and discussion. All four species had trap-revealed sex ratios significantly biased toward males ($P < 0.05$). Male-to-female ratios were: deer mice, 1.7:1.00; montane voles, 2.12:1.00; Great Basin pocket mice, 1.7:1.00; and least chipmunks, 1.9:1.00.

Perognathus parvus

Density.—Great Basin pocket mice were resident only in sagebrush or greasewood communities. In sagebrush communities, among-plot variation in the density of pocket mice differed seasonally only by a factor of about 4. Within-plot variation did not exceed

TABLE 1. Total number of individuals of each mammalian species captured on study plots in the four predominant types of terrestrial plant communities on Malheur National Wildlife Refuge from July 1973 through June 1975.

Order	Species	Community Type				Total ¹
		Sagebrush ^a	Greasewood ^b	Marsh ^c	Grassland ^d	
Rodentia	<i>Peromyscus maniculatus</i>	153	231 (245) ^e	59 (86)	1 (2)	444
	<i>Microtus montanus</i>	0	7 (7)	330 (478)	100 (171)	437
	<i>Perognathus parvus</i>	206	72 (76)	5 (7)	0	283
	<i>Eutamias minimus</i>	101	159 (169)	0	0	260
	<i>Reithrodontomys megalotis</i>	1	13 (14)	36 (52)	21 (36)	71
	<i>Dipodomys ordii</i>	30	11 (12)	0	0	41
	<i>Dipodomys microps</i>	9	2 (2)	0	0	11
	<i>Onychomys leucogaster</i>	7	0	0	0	7
	<i>Microtus longicaudus</i>	0	0	3 (4)	0	3
	<i>Microdipodops</i>					
	<i>megacephalus</i>	3	0	0	0	3
	<i>Spermophilus townsendii</i>	2	1 (1)	0	0	3
	<i>Neotoma lepida</i>	2	0	0	0	2
<i>Thomomys talpoides</i>	1	0	0	0	1	
Carnivora	<i>Mustela frenata</i>	0	1 (1)	2 (3)	0	3
Insectivora	<i>Sorex vagrans</i>	0	0	10 (14)	0	10
Lagomorpha	<i>Sylvilagus nuttallii</i>	1	0	0	0	1
	TOTALS	516	497 (528)	445 (645)	122 (209)	1,580
	H ¹ (6)	0.605	0.549	0.389	0.207	

^aInvolves 5 plots and 8,232 trap nights.

^bInvolves 5 plots and 7,742 trap nights.

^cInvolves 4 plots and 5,684 trap nights.

^dInvolves 4 plots and 4,802 trap nights.

^eBecause unequal effort was expended in each habitat type, numbers in parenthesis represent relative totals for animals captured in greasewood, marsh, and grassland habitats, based on a total effort comparable to that made in sagebrush areas.

^fCalculated as $H^1 = 1/N(\log_{10}N! - \sum \log_{10}n_i!)$ according to Lloyd et al. 1968, for the rodent species in each community type.

a factor of 5 seasonally. In the greasewood areas, however, among-plot differences in the density of pocket mice differed by as much as a factor of about 7; there was an equivalent difference in density within plots (Table 2). Although densities were generally lower on the greasewood than the sagebrush plots ($t=4.29$, $df=37$, $P<0.001$), in both habitat types peak numbers of pocket mice were trapped from late April to early June. The lowest population densities occurred from late June through mid-August. These fluctuations in population density were similar in both timing and magnitude to those of a population of *P. parvus* studied by O'Farrell et al. (1975) in shrub-steppe habitat in southeast Washington. Densities of pocket mice apparently increased on most plots in the fall. This was probably the result of increased activity as temperatures cooled.

Reproduction.— Male pocket mice were in breeding condition from early May until early August. Peak breeding activity probably occurred in early June, a period not adequately represented by trapping data. Males were believed to be reproductively active about a month before the females, based on the percentage in reproductive condition in May (56 percent of males, 8 percent of females). Pregnant females were trapped almost exclusively in June, although sample size was small ($n=4$), and no reproductively active pocket mice were trapped after 29 August in either habitat type.

Juvenile pocket mice were trapped from early May to early September on plots in sagebrush areas, although the majority were found from June through August. In greasewood areas, juveniles were trapped only from June through August (Fig. 2). Recruitment of juveniles was greatest in both habitat types during July.

Dispersion.— The trap-revealed dispersion of pocket mice on all plots differed significantly from random, and a clumped distribution pattern was evident. On each of three plots where 60 or more capture records of pocket mice were obtained, a significant relationship was evident between pocket mouse distribution and cover density. Significantly fewer pocket mice than expected were trapped in quadrats with less than 40 percent cover, but more pocket mice than expected

were trapped in quadrats with greater than 40 percent cover ($X^2=26.33$, $df=8$, $P<0.001$).

The preference of pocket mice for areas of relatively dense cover undoubtedly was a response to the interaction of several factors. Increased vegetation possibly reduced the rate of predation (Rosenzweig and Winakur 1969, Brown and Lieberman 1973) and increased forage availability (O'Farrell 1975). It also probably beneficially affected micro-habitat evaporation rates, humidity, and air temperature (Beatley 1976).

Habitat.— Although vegetation was of obvious importance in the local distribution of pocket mice, the abundance of this species in

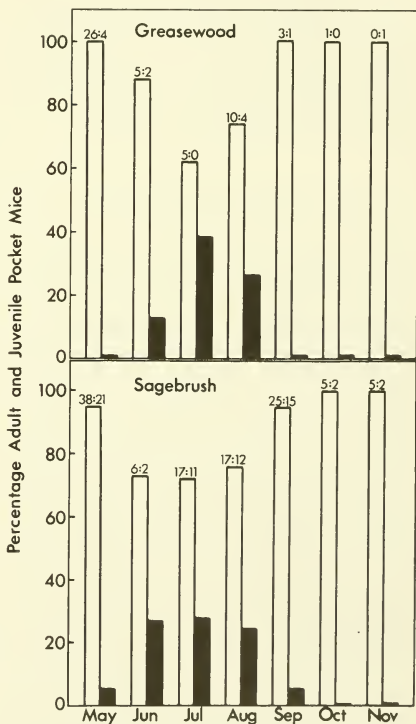


Fig. 2. Percentage of captures of pocket mice each month comprised of adult (open rectangles) and juvenile (solid rectangles) animals. Numbers atop open rectangles denote male:female sex ratios.

all sagebrush or greasewood areas was significantly correlated only with edaphic factors. A direct correlation between the population density of pocket mice and the percentage of sand on each plot was evident ($P < 0.05$ —Fig. 3A). The ability of pocket mice to dig through the surface layer of the soil is of obvious importance to their fossorial activities. The general importance of edaphic factors was further suggested by an inverse relationship between density and the percentage of clay in the soil ($P < 0.05$ —Fig. 3B). These factors probably affect burrow construction and stability. For example, soil texture has a direct influence on several aspects of soil moisture, including depth and rate of percolation, retention, and evaporation rates (Krynine 1947, Beatley 1976). In greasewood areas the mean soil moisture was inversely correlated with percentage of sand ($r^2 = 0.92$, $P < 0.005$). However, Rosenzweig and Winakur (1969) found the distribution and abundance of five other species of pocket mice in Arizona showed no correlation with soil texture.

Eutamias minimus

Density.—Least chipmunks also occurred only in sagebrush or greasewood communities. In the sagebrush community type, among-plot differences in the density of chipmunks generally were less than a factor of 3. Within-plot fluctuations in population density varied by an equivalent amount. In greasewood, among-plot variation in population density varied seasonally by a factor of about 6, with the exception of the 1973 trapping period. There was an equivalent variation within-plot seasonally (Table 2). In neither shrub community type was there a season during which peak numbers were evident. Vaughan (1974) also noted a fairly stable population density for this species in northern Colorado.

Reproduction.—Male chipmunks may have been reproductively active in both community types about one month before the females, as suggested by the percentage of each sex in breeding condition in May (91 percent of males, 40 percent of females). Breeding apparently was confined to a fairly brief period, with peak activity in late April and

May. The number of chipmunks in breeding condition declined rapidly in both community types throughout the summer. No reproductively active chipmunks were trapped after 31 July in the greasewood areas or after 29 August in sagebrush areas. Davis (1939) and Gordon (1943) reported that this species mated from early to midspring in the northern part of its range, and Negus and Findley (1959) reported no sexually active least chipmunks occurring after late June in northwest Wyoming.

Of the 260 chipmunks captured during the study, only one was considered a juvenile. Juveniles were probably most numerous in early June, when no trapping was conducted. This is suggested by the reproductive data

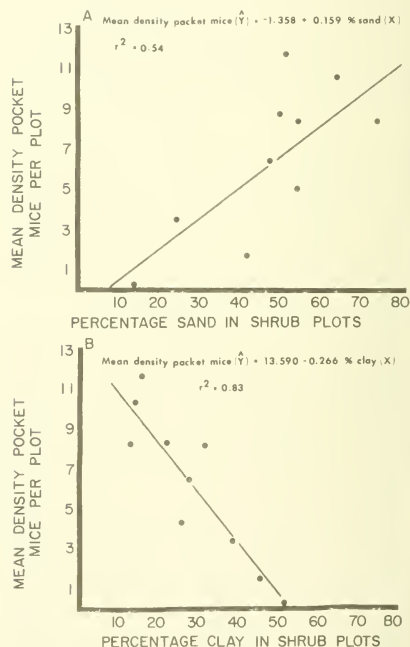


Fig. 3. Relationship between components of soil texture and mean density of pocket mice on 10 study plots in shrub communities on Malheur National Wildlife Refuge from July 1973 through June 1975. (A) Percentage of sand; (B) Percentage of clay.

above and the results of Hall (1946) and Linsdale (1938), who reported parturition in least chipmunks in Nevada occurred during May and early June. Tevis (1958) found gravid least chipmunks during mid-April in north-eastern California. It is possible the age criteria may have been inadequate to distinguish juvenile chipmunks.

Dispersion.—On all plots where more than 23 capture records of chipmunks were obtained, their dispersion was clumped. On none of the plots was there a relationship between dispersion and the amount of vegetation cover. However, on only one plot were there as many as 60 location records.

Habitat.—On both shrub areas, the density of chipmunks was directly correlated with the mean depth of soil ($P < 0.05$, Fig. 4) and with soil strength ($P < 0.05$, Fig. 5). On sagebrush areas, a positive correlation was found between density and diversity of soil strength ($r^2 = 0.88$, $P < 0.01$). Correlations between the density of chipmunks and habitat factors

on the greasewood areas included a direct relationship to the percentage of clay in the soil ($r^2 = 0.72$, $P < 0.05$).

As with pocket mice, the depth, texture, and strength of the soil would directly affect chipmunks in the construction and stability of burrows, and indirectly affect aspects of temperature and humidity. The densities of pocket mice and chipmunks were oppositely related to the percentage of clay in the soil; this suggests that chipmunks did not find it as difficult as the smaller pocket mice to dig through a sometimes hard, consolidated soil surface of high clay fraction.

Peromyscus maniculatus

Density.—Deer mice exhibited the widest local distribution, being resident in sagebrush, greasewood, and marsh community types (Table 1). Deer mice generally were most abundant on the greasewood areas, where among-plot variation differed by a fac-

TABLE 2. Estimated population densities and standard deviation for four species of small mammals common on study plots (1.1 ha) in three community types on Malheur National Wildlife Refuge from July 1973 through June 1975.

Period	Plot	Sagebrush						Greasewood						Marsh			
		<i>P. man.</i>		<i>P. parvus</i>		<i>E. min.</i>		<i>P. man.</i>		<i>P. parvus</i>		<i>E. min.</i>		<i>P. man.</i>	<i>M. mont.</i>		
		$\bar{N} \pm Sd$	$\bar{N} \pm Sd$	$\bar{N} \pm Sd$	$\bar{N} \pm Sd$	$\bar{N} \pm Sd$	$\bar{N} \pm Sd$	$\bar{N} \pm Sd$	$\bar{N} \pm Sd$	$\bar{N} \pm Sd$	$\bar{N} \pm Sd$	$\bar{N} \pm Sd$	$\bar{N} \pm Sd$	$\bar{N} \pm Sd$			
1973 July- Sept.	1	4.8	0.4	5.5	0.9	7.7	3.2	9.3	2.0	8.7	2.7	1.7	0.7	5.6	0.9	0.0	—
	2	13.7	2.4	5.5	0.5	2.3	0.3	9.2	1.9	0.0	—	16.9	1.7	b	—	b	—
	3	2.3	0.3	8.4	0.4	2.0	0.6	6.2	1.2	0.7	0.7	6.5	2.6	0.0	—	169.5	30.0
	4	1.0	0.0	9.0	2.0	0.0	—	2.0	1.0	0.0	—	14.3	0.3	0.0	—	252.8	82.2
	5	3.2	0.2	9.5	1.5	0.0	—	5.3	0.3	2.0	—	0.0	—	—	—	—	—
1974 June- Aug.	1	2.8	0.4	9.3	0.9	7.9	1.1	6.5	0.9	8.3	0.9	2.1	0.7	5.2	1.0	0.0	—
	2	6.9	0.5	12.5	1.4	9.7	1.6	10.1	1.8	0.0	—	9.8	0.9	0.0	—	0.0	—
	3	0.8	0.3	5.8	0.8	3.6	0.4	9.1	0.7	1.3	0.2	10.7	1.6	4.7	0.8	46.6	5.4
	4	0.8	0.1	6.0	0.5	0.0	—	4.4	0.4	0.0	—	9.8	0.5	1.3	0.6	36.5	4.7
	5	2.9	0.1	4.4	0.7	0.0	—	4.4	0.5	4.0	0.3	0.0	—	—	—	—	—
1974 Sept.- Nov.	1	6.3	0.5	15.1	2.6	6.4	0.6	7.2	0.4	11.9	0.8	5.1	0.8	8.2	1.1	0.0	—
	2	5.7	0.3	11.6	1.6	9.4	0.7	20.1	1.7	0.0	—	13.6	2.3	0.0	—	0.1	—
	3	3.0	0.0	5.4	0.2	5.9	0.7	17.0	1.0	1.8	0.2	6.6	0.8	6.4	0.5	33.9	6.7
	4	8.5	0.6	5.0	0.2	0.0	—	7.8	0.9	1.0	—	11.6	1.2	5.4	1.6	40.2	13.9
	5	24.4	0.4	6.7	0.3	0.0	—	4.3	0.9	0.7	—	0.0	—	—	—	—	—
1975 April- June	1	0.8	0.1	10.8	0.9	13.9	1.0	3.5	0.5	3.4	0.3	5.9	0.7	a	—	a	—
	2	2.9	0.3	16.3	0.6	6.0	0.6	a	—	a	—	a	—	0.0	—	0.0	—
	3	3.0	0.3	4.8	0.2	2.2	0.4	18.2	1.1	8.7	0.3	4.4	0.5	1.4	0.2	4.2	0.8
	4	14.8	0.8	12.0	0.8	0.0	—	15.0	0.9	3.9	0.8	3.5	0.4	a	—	a	—
	5	11.8	0.9	12.3	0.3	0.0	—	20.5	1.9	10.7	0.7	0.0	—	—	—	—	—

^aPlot was flooded, could not be operated.

^bGrid not operated during 1973.

tor greater than 3 only in 1973 (Table 2). Within-plot fluctuation in the density of deer mice also approached this magnitude. Populations of deer mice in sagebrush areas exhibited fluctuations in density comparable to those on greasewood areas. Both within- and

among-plot variation generally differed by a factor of about 3. The densities of deer mice on sagebrush and marsh plots were about equal, with fluctuations in the marsh areas again relatively minor. There was no season during which the density of this species was

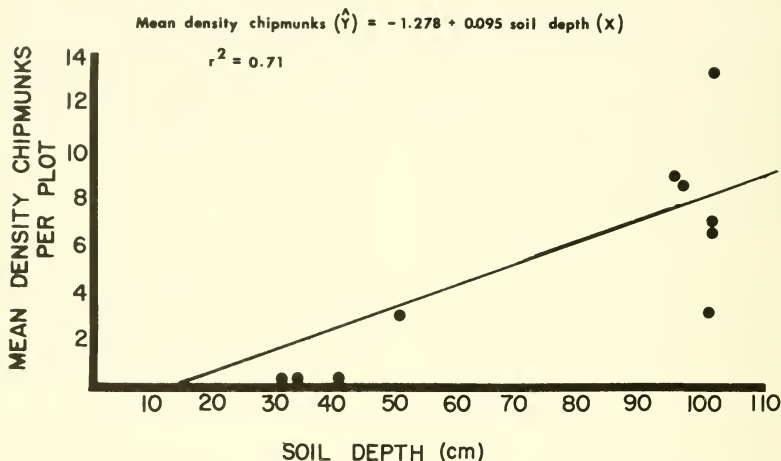


Fig. 4. Relationship between the density of chipmunks and soil depth on study plots in two shrub habitat types on Malheur National Wildlife Refuge from July 1973 through June 1975.

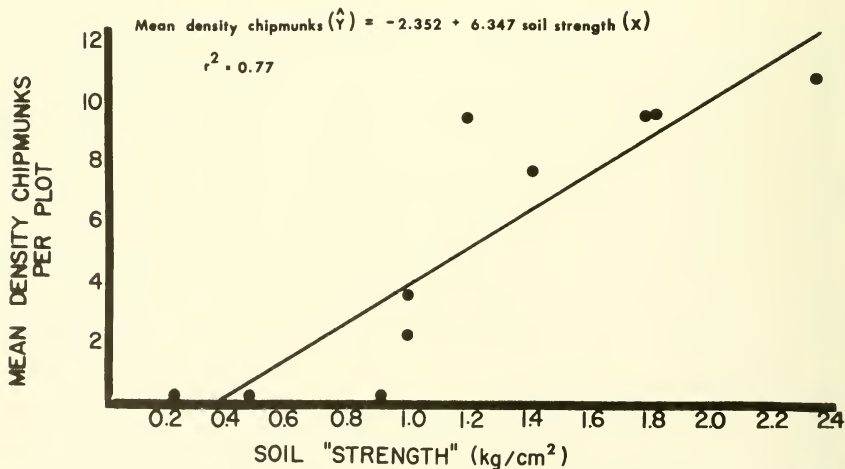


Fig. 5. Relationship between the density of chipmunks and soil "strength" on study plots in two shrub habitat types on Malheur National Wildlife Refuge from July 1973 through June 1975.

consistently highest, although density was generally lowest during the summer.

Reproduction.— Deer mice were reproductively active during all months that trapping was conducted, although a decline in breeding activity was evident during the summer. Parturition occurred at least as early as April in the shrub habitats, because juvenile animals were trapped in May (Fig. 6). Peak numbers of juveniles were on the plots in May and in the fall. It was not determined if breeding continued throughout the year, but, considering the usually harsh winter conditions on the study area, it seems doubtful. However, deer mice in sagebrush areas of east-central Washington have bred throughout the year (Scheffer 1924).

Dispersion.— The trap-revealed dispersion of deer mice in all habitat types differed significantly from random, and on 10 of 11 plots a clumped pattern was evident. Relationships between dispersion and cover in the marsh plots could not be evaluated because of too few captures in 1975. The results of this analysis on sagebrush and greasewood plots were equivocal. On greasewood plot 4 and sagebrush plot 5, significantly fewer deer mice than expected were captured in portions of those plots with less than 40 percent cover, but greater numbers than expected occurred in portions with more than 40 percent cover ($X^2=58.59$, $df=8$, $P<0.001$). However, on sagebrush plot 2 the opposite relationship was apparent ($X^2=7.53$, $df=1$, $P<0.01$), and on the remaining five plots, where sufficient capture records were available to allow analysis, there were no significant relationships between the amount of cover and the dispersion of deer mice.

These results reflect the range of relationships relative to cover previously reported for this species. A direct relationship between amount of cover and the local distribution and abundance of *Peromyscus* was described by Allred and Beck (1963). However, the proportion of cover did not exceed 25.0 percent in any of the areas sampled by these authors. An inverse relationship between cover and density was reported for several habitat types, including grassland and cultivated areas (Phillips 1936, LoBue and Darnell 1959, Tester and Marshall 1961), desert shrub (MacMillen 1964), and sites disturbed by

strip-mining (Dusek and McCann 1975). In similar habitats, other researchers found no relationship between amount of cover and local distribution or abundance of deer mice (Rickard 1960, Verts 1957). It may be that no general relationship exists between the local distribution or abundance of deer mice and amount of cover.

Habitat.— There was a direct correlation between the density of deer mice and only one vegetative factor: the amount of vegetation at the three heights used to measure foliage height diversity. This correlation was evident on plots in both sagebrush areas ($r^2=0.98$, $P<0.01$) and greasewood areas ($r^2=0.86$, $P<0.25$). Thus, at least during the

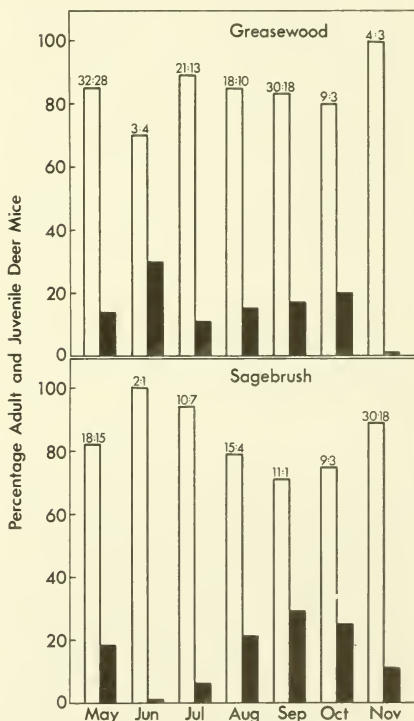


Fig. 6. Percentage of captures of deer mice each month comprised of adult (open rectangles) and juveniles (solid rectangles) animals. Numbers atop open rectangles denote male:female sex ratios.

summer, it appeared that deer mice in shrub communities selected for increased foliage, at least at the measured, interspersed levels of the vegetative profile, rather than a continuum of foliage above or below a particular height. Whether this relationship was of direct adaptive significance in predator avoidance, foraging or general scansorial tendencies (Horner 1954), or was indirectly associated with some other factor, was not readily apparent.

In marsh areas, a slight positive correlation existed between the density of deer mice and the percentage of sand in the soil ($r^2=0.37$, $P<0.05$). On greasewood areas, an inverse relationship was evident between these two factors ($r^2=0.80$, $P<0.025$), as well as a direct correlation between density of deer mice and the percentage of soil moisture ($r^2=0.30$, $P<0.01$). Therefore, deer mice exhibited an opposite response to the percentage of sand on marsh and greasewood areas, and no relationship on sagebrush areas; habitats generally subjected to large differences in the amount of free water associated with them.

The permeability and drainage capabilities of soils vary directly with their percentage of sand (Krynine 1947). The opposite response of deer mice to the percentage of sand on marsh and greasewood plots may have resulted from an effort by deer mice to select an "optimal" moisture range within the continuum of soil moisture conditions that could be tolerated. That is, "wetter" arid areas and "drier" wet areas.

Microtus montanus

Density.— In marsh areas, montane voles were resident only on plots 3 and 4, which were dominated by burreed (*Sparganium* sp.), as opposed to bulrush (*Scirpus paludosis*) and spikerush (*Eleocharis palustris*) on plots 1 and 2. The density of voles during 1973 was the highest of any small mammal during the study. Densities declined sharply after the initial trapping period. In 1975, the population density of voles on marsh plot 3 was reduced from the 1973 estimate by a factor of at least 20 (Table 2). Although the population densities of voles in grassland areas were generally lower than in marsh areas, the grassland plots were continuously altered by land-use

practices throughout the field work, and trends in the density of voles were difficult to determine.

Reproduction.— The reproductive data for voles were not as complete as those for other species of small mammals. Reproductively active voles were trapped in marsh areas only from July through September. However, montane voles were undoubtedly breeding during the spring months (Bailey 1936), when trapping was not conducted in marsh or grassland communities. Also, considering the short gestation period of this species (Asdell 1964), and that juvenile voles were trapped in early November, breeding must also have occurred in October. There was no period during which the juvenile increment of the population or the percentage of adults in breeding condition was consistently largest.

Dispersion.— The trap-revealed dispersion of voles on all plots differed significantly from random, and a clumped pattern was evident. On the only plot where the analysis could be made, the dispersion of voles was related to the amount of cover. Voles were trapped significantly more often in quadrats where cover was greater than 80 percent ($X^2=15.49$, $df=1$, $P<0.005$).

Habitat.— There was a weak, direct correlation between the estimated population densities of voles and the mean amount of cover on plots in marsh ($r^2=0.41$, $P<0.01$) and grassland communities ($r^2=0.41$, $P<0.025$). In a related manner, an inverse relationship was evident between the density of voles and the patchiness of cover of these habitat types ($r^2=0.41$, $P<0.01$ and $r^2=0.64$, $P<0.01$, respectively). The direct relationship between the occurrence of *M. montanus* and dense cover is well documented (Bailey 1936, Hodgson 1972), and, as Getz (1961) discussed, it is difficult to separate the relative functions of cover, and importance to montane voles, in terms of protection from predators, microhabitat modification, and food resources. That cover is important to this species was further shown by a comparison of vole densities on grassland plots 3 and 4, sampled concurrently in August and November 1974. In August there was no statistical difference in estimated vole densities on each plot (19.1 and 15.4, respectively). Plot 3 was undisturbed prior to the second trapping pe-

riod and the density of voles was unchanged (20.3 per plot). However, plot 4 was mowed two months prior to the second trapping period, and only one individual was caught in November. A similar effect was reported by LoBue and Darnell (1959) for a harvested alfalfa field. No other vegetative or edaphic factor was related with the density of montane voles.

General Vegetative Structure

When each of the four habitat types investigated was viewed in terms of their general physiognomy (Elton and Miller 1954), essentially two structural types were evident, each with a characteristic small mammal fauna. One type consisted of the 10 plots in the sagebrush or greasewood shrub vegetation. This type had relatively few plant species but a relatively large degree of structural diversity. The other physiognomic type, which consisted of the eight plots in marsh or grassland areas, was characterized by a large number of plant species, at least in grassland areas, but a generally low degree of structural diversity.

With the exception of deer mice, each species of small mammal was restricted to one of the two physiognomic types. The small mammal fauna associated with the sagebrush-greasewood type was relatively diverse. It included the four species of heteromyids captured, the only species of chipmunk found on the refuge, and five other rodent species (Table 1). Voles, western harvest mice (*Reithrodontomys megalotis*), and shrews (*Sorex vagrans*) were restricted to the marsh-grassland physiognomic type. Although the small mammal fauna was not as diverse, large population densities were encountered in this type. It should be noted that voles and harvest mice were not considered residents in greasewood areas. The only individuals of these species captured in greasewood habitat were found on plot 5. These 20 individuals were captured while a fire smoldered in dry marsh vegetation 40 m from the plot during September 1974. Presumably, these conditions forced voles and harvest mice from their preferred habitat, as neither of these species were captured on plot 5 during the two trapping periods prior to the fire. Dice

(1931) first suggested that the physiognomy of the vegetation was an important factor in the local distribution of animal species. Since then, this generalization has been corroborated with regard to many species of small mammals (Hardy 1945, Fautin 1946, Pearson 1959, Tester and Marshall 1961, M'Closkey and Lajoie 1975); and the effect of foliage structure on the distribution of species of small mammals was evident in this study.

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