

Shrub Litter Production in a Sagebrush-Steppe Ecosystem: Rodent Population Cycles as a Regulating Factor

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Abstract

This study examines the impact of long-tailed vole (*Microtus longicaudus*) and deer mouse (*Peromyscus maniculatus*) population changes and their feeding behavior on shrub populations and the resulting litter production in a shrub-steppe ecosystem in southwestern Wyoming. Rodent populations were monitored on 3 replicate plots over a 3-yr period. Populations peaked in autumn 1983 and declined to lower levels in 1984-86. Damage to shrubs (in the form of bark-stripping and girdling) was observed after the winter of 1983-84, but not after the winters of 1984-85 and 1985-86. We assessed damage to shrubs on 4 sites. Extent of damage, mortality, and biomass-to-litter transformations were quantified. We found that: (1) 21% of all shrubs and 28% of the big sagebrush (*Artemisia tridentata*) sustained rodent damage; (2) 1% of all shrubs were killed as a result of girdling; (3) mean biomass lost from shrubs that suffered damage was 36%; (4) total above-ground biomass loss occurring on big sagebrush was 231 kg/ha or 4% of the standing crop. These results indicate that rodents feeding on big sagebrush can periodically increase annual rates of litter production by as much as 69% above "normal." Rodents in the sagebrush-steppe ultimately influence ecosystem-level nutrient cycles by accelerating shrub litter production, and may affect plant species composition via feeding-induced shrub mortality.

Key Words: *Artemisia tridentata*, herbivory, *Microtus longicaudus*, *Peromyscus maniculatus*, rodents

The role of herbivorous animals in determining the structure and functioning of ecosystems has generally been appraised on the basis of trophic interactions, i.e., the proportion of net primary production (NPP) actually consumed by the herbivores. For most ecosystem-level analyses, the amount of NPP handled by herbivores (both vertebrate and invertebrate) is less than 20% (Chew 1974, Bormann and Likens 1979, Swift et al. 1979, Zlotin and Khodashova 1980). Rather than being important as consumers of energy, herbivores may act as ecosystem regulators, influencing not only plant species composition (via selective herbivory), but also the rates at which energy transfers take place (Chew 1974, 1978, Swift et al. 1979, MacMahon 1981). Such regulatory functions may involve very meager energy expenditures, but can have dramatic and far-reaching effects on the ecosystem. Examples of such animal-plant interactions include pollination of flowers, dispersal of seeds, transmission of diseases, alteration of soils, inoculation of fungal-spores, and so on. These phenomena have what Odum and Odum (1976) term a "high energy quality ratio;" that is, the amount of energy flow affected by the interaction is far greater than the amount of energy spent during the interaction.

In contrast to their relatively minor role in energy consumption, herbivores may dramatically affect the rates of nutrient cycling (Kitchell et al. 1979). Herbivores normally feed on living plant parts that contain a disproportionately high concentration of

essential nutrients (compared to woody parts or detritus), and therefore can consume a large percentage of the vegetation's nutrient stores (Swift et al. 1979). Some herbivores also induce non-consumptive wastage of plant parts (e.g., meristem feeders, stem borers, and bark ringers), that cause pulses of nutrients to be added to the decomposition process via release of nutrients stored in normally long-lived plant parts (e.g., tree trunks or shrub stems) (Crawley 1983).

The role of rodents as consumers of primary production in many ecosystems appears to be minor, although impacts on vegetation during population outbreaks can be severe. In a review of the literature, Golley (1973) reported that in 12 of 17 studies, rodents consumed less than 5.5% of the available primary production. He further suggested that, because of the rapid turnover rates exhibited by rodent populations, rodents may influence nutrient cycling and decomposition rates via litter production and fecal deposition (Golley 1973). In support of this hypothesis, results of studies in the meadow-steppe of the USSR have demonstrated that the presence of voles (*Microtus arvalis*) causes a substantial increase in litter production and an even greater increase in litter mineralization, resulting in overall faster nutrient cycling (Zlotin and Khodashova 1980).

In the shrub-steppe ecosystem of the Intermountain Basin of North America, the ubiquitous deer mouse (*Peromyscus maniculatus*) is usually the numerically dominant rodent species. By virtue of their numbers, deer mice can potentially account for a substantial proportion of the NPP normally consumed by rodents. Voles (*Microtus* spp.) constitute only a small proportion of the total rodent fauna (e.g., Rickard 1960, Brown 1967, Maxwell and Brown 1968, Parmenter and MacMahon 1983) and are patchily distributed (Long 1965, Lechleitner 1969, Randall 1978). Consequently, their contribution to total NPP consumption should be minimal. Microtines, however, are renowned for their tremendous population irruptions (Piper 1909, Murray 1965), peaking at reported densities of 7,000-29,000 voles per hectare (Piper 1909, Spencer 1959). When rodent populations reach cycle peaks, extensive damage to both herbaceous and woody vegetation occurs (Piper 1909, Hubbard and McKeever 1961, Mueggler 1967, Phillips 1970, Frischknecht and Baker 1972, Sturges 1983). Rodent consumption of woody vegetation is generally restricted to the plant's cambium and phloem layers (after having stripped off the dry, outer bark). The amount of plant material consumed is relatively small; but if the rodents' feeding activity completely surrounds a stem, then the remaining plant above the "girdling" site dies. This type of feeding activity results in a biomass-to-litter transformation which is orders of magnitude greater than the amount of biomass actually eaten. Hence, an important aspect of the rodents' influence in the shrub-steppe ecosystem may be to periodically increase litter production, which ultimately accelerates nutrient cycling.

The purpose of this study was to determine the extent and distribution of nonconsumptive damage to shrubs by long-tailed voles (*Microtus longicaudus longicaudus* [Merriam]) and deer mice (*Peromyscus maniculatus nebrascensis* Coues), and to estimate the amounts and proportions of aboveground shrub biomass converted to litter.

Study Site

The study site was located 8 km southwest of Kemmerer, Wyo.,

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(Lat. 41°43'30"N, Long. 110°38'15"W) (T.20N, R.117W, Sec. 9) at an elevation of 2,255 m. Terrain was characterized by rolling hills with a north-south strike. Precipitation (mostly snow) averages 22.6 cm/yr, but is highly variable. Mean monthly temperatures range from -8° C in January to 17° C in July (Parmenter and MacMahon 1983).

Vegetation in the area was shrub-steppe (West 1983), and was composed of 2 physiognomically distinct plant associations. The first, with which this paper deals, was dominated by big sagebrush (*Artemisia tridentata* Nutt.), antelope bitterbrush (*Purshia tridentata* DC.) and Utah serviceberry (*Amelanchier utahensis* Koehne). Understory vegetation was predominantly grasses (*Oryzopsis* spp., *Poa* spp. and *Bromus* spp.) and a variety of forbs. This association of plants was patchily distributed throughout the area, occurring most frequently in moister areas (e.g., along ephemeral stream courses and the leeward side of hills and ridges where deep winter snowpacks accumulate). These patches of tall shrubs were surrounded by areas of much shorter vegetation, dominated by the diminutive low sagebrush (*Artemisia arbuscula* Nutt.), cushion plants (*Arenaria congesta* Nutt., *Artemisia frigida* Willd., and *Phlox hoodii* Richards) and grasses (*Oryzopsis* spp. and *Poa* spp.).

Methods

Shrub-feeding Rodent Species

Direct observations of rodent shrub-feeding behavior could not be made, because the feeding activity took place beneath the winter snowpack. In addition, we were unable to ascribe shrub damage to a particular rodent species, because stems damaged by different rodent species were identical in appearance (see below). Therefore, we combined published natural history reports and documented incidences of rodent damage to shrubs with our own field and laboratory observations to identify the potential shrub-feeding rodent species. Our field observations included the presence and patterns of rodent tracks in the snow, as well as winter activity and nesting data on deer mice obtained during a 1983-84 radio-telemetry study (data provided by L. Broome, Department of Biology, Utah State University, 1985).

We conducted feeding experiments in the laboratory to determine if voles and deer mice would eat sagebrush stems. Three long-tailed voles and 3 deer mice were housed in glass cages, with each cage having a 5-cm-deep layer of sand across the bottom. The rodents were provided with nest boxes and bowls of water. We first placed stems (20-30 cm long) of big sagebrush in the rodents' cages (6 stems/rodent) in the presence of other foods (native seeds and green vegetation) for 5 days, and periodically checked the stems for evidence of feeding activity. We then deprived the rodents of all food except the sagebrush stems for 48 h, and again inspected the stems for evidence of feeding activity.

Rodent Trapping

Rodents were trapped on three 2-ha grids of Sherman live traps. Each grid consisted of 225 traps arranged in a 15 × 15-station square (10-m station interval) with a single trap at each station. Traps were baited with peanut butter and rolled oats and left open continuously for 4 consecutive days and nights during each trap period. Traps were checked daily; and captured rodents were identified, toe-clipped, and then released. Trap periods occurred at approximately 6-wk intervals (May through September) during 1983-85 and in early May 1986.

Vegetation Sampling

Preliminary inspection of shrubs in both plant associations revealed that instances of shrub damage were confined to the patches of tall shrubs. For this reason, we restricted our plant sampling efforts to the tall shrub patches. To ascertain the areal proportion of tall shrub patches on the study site, we used a planimeter to measure the sizes of all tall shrub patches on a 1:4800 scale aerial photograph of the area. Tall shrub patches delineated on the aerial photograph were verified by ground-truth examination.

Vegetation surveys took place during midsummer (July and August) in 1984 and 1985, and in May 1986. Four 30-m transect lines were arbitrarily chosen based on the criterion that lines were enclosed within the tall shrub patches. Relative abundance and percentage cover of shrub species on each line was determined using the line intercept method (Canfield 1941). Shrub canopy area was estimated by assigning a particular geometric configuration (circle, triangle, or ellipse) to each individual shrub and measuring the appropriate dimensions. Shrub height was also recorded.

Each shrub along the transect line was inspected for rodent damage. Damage to shrubs ranged from small areas (<10 cm²) of stripped bark along the main stem to complete girdling of branches. This latter type of damage resulted in parts of the shrub being killed. These dead parts were cut off at the girdling point with pruning shears and weighed in the field using Pesola® scales. After removing and weighing all dead parts on a shrub (attributable to rodent feeding), the remaining parts of the shrub were cut off at ground level and weighed. Through this procedure we were able to determine the total aboveground biomass of the damaged shrub and the proportion of the shrub killed by girdling. [Note: Our shrub biomass measurements were all fresh weights, although the dead shrub parts had dried out considerably and lost most of their leaves by the midsummer sampling time. Hence, our values represent conservative estimates of shrub-biomass losses.]

Results and Discussion

Shrub-feeding Rodent Species

Only 3 species of rodents on our plots were active during the winter: the long-tailed vole, the deer mouse, and the sage vole (*Lagurus curtatus levidensis* [Goldman]). Long-tailed voles, along with other microtines, have been implicated in bark-stripping, particularly during periods of winter snowpack (Bailey 1900, Piper 1909, Hubbard and McKeever 1961, Mueggler 1967, Frischknecht and Baker 1972). The long-tailed vole also inhabits the tall shrub patches in which all of the observed shrub damage occurred (Long 1965, Lechleitner 1969, this study [see below]). We believe the long-tailed vole was a major participant in the shrub-feeding activity on our study plots.

In our laboratory feeding trials, all 3 long-tailed voles and all 3 deer mice exhibited identical behavior: they ate none of the big sagebrush stems when seeds and green vegetation were present but ate the bark and cambium layers of all 6 sagebrush stems when alternative foods were absent. The results indicate that although big sagebrush is not a preferred food, it is readily eaten when better foods are not available. The stripped pieces of stem appeared identical to damaged shrubs observed in the field. Stems damaged by voles were indistinguishable from those damaged by deer mice.

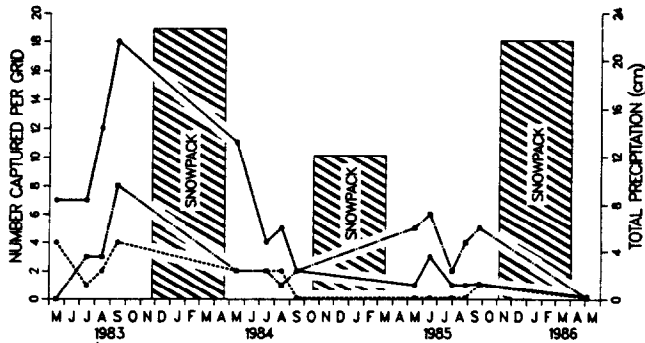
The deer mouse is not known to regularly eat shrub parts (Williams 1959, Johnson 1961, Becker 1977), although it may shift its diet during periods of food shortage. This was demonstrated in our laboratory feeding experiment. Winter field observations of deer mouse tracks and radio-telemetry data collected during the winter of 1983-1984 showed that deer mice were active in patches of tall shrubs. Inspection of deer mouse nests revealed that they were made almost entirely from strips of big sagebrush bark (L. Broome, personal communication, 1985). While we do not know for certain if the deer mice in the study area were feeding on shrub stems or simply collecting bark for nesting material, it seems probable that deer mice contributed to the damage inflicted on the shrub population.

The sage vole is active all year and feeds predominantly on green vegetation, especially sagebrush (Walker 1975). However, the trap-capture locations of this species, combined with radio-telemetry data on microhabitat use (R. Parmenter, unpublished data), indicate that sage voles on our study plots stayed in areas of short vegetation which did not suffer any observable shrub damage. Therefore, we do not believe that sage voles contributed to the winter shrub damage.

Rodent Population Changes

The populations of both long-tailed voles and deer mice were greater during the winter of 1983-84 than in subsequent periods (Fig. 1). Rodent populations peaked in September 1983, and had declined somewhat by May 1984. The populations continued to decline during the summer of 1984 and began the winter of 1984-85 at considerably reduced levels. [Note: We did not measure population sizes during periods of snowpack; hence, the true form of the winter population changes depicted in Figure 1 may not be linear.]

Microtus longicaudus



Peromyscus maniculatus



Fig. 1. Rodent population changes on 3 trap grids (solid, dashed, and dash-dot lines) near Kemmerer, Wyo. Shaded columns represent periods of permanent winter snowpack: column width corresponds to duration of snowpack; column height corresponds to the total amount of precipitation received during the snowpack period (precipitation data from S. Smith, Department of Biometeorology, Utah State University).

Captures of long-tailed voles were restricted to traps located in the tall shrub associations, and the areal amount of tall shrub vegetation varied among plots; therefore, differences in absolute population sizes among grids were partially attributed to differing quantities of suitable habitat. Vole populations on all 3 replicate grids, however, exhibited similar fluctuations over time.

Rodent Impacts on Vegetation

The patches of tall shrub vegetation in the sample areas were dominated by big sagebrush (Table 1). Sagebrush density in the patches, measured in 1981, was approximately 16,000 shrubs/ha (Alan Carpenter, Department of Range Science, Utah State University, unpublished data). Based on the aerial photo measurements, the tall shrub association comprised 43% (86 ha) of the total land area (200 ha) covered in the photograph.

We observed damage to shrubs only after the winter of 1983-84; extensive inspections of shrubs on the plots following the winters of 1984-85 and 1985-86 produced no observable evidence of rodent shrub-feeding activity. The 1984 damage was confined to the tall shrub patches and was evident in the spring, after snowmelt. Rodents had stripped the bark primarily from big sagebrush

Table 1. Percentage cover of shrub species in tall shrub vegetation on sample transects near Kemmerer, Wyoming.

Shrub species	Transect Number			
	1	2	3	4
<i>Artemisia tridentata</i>	34.7	54.1	27.0	11.4
<i>Chrysothamnus viscidiflorus</i>	0.8	0	13.2	10.8
<i>Purshia tridentata</i>	7.2	1.5	0	0
<i>Symphoricarpos</i> sp.	3.1	0	0.3	0

(Table 2), although several antelope bitterbrush (4 of 6 shrubs sampled) and a single rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.) were also damaged. Shrubs in Transect 4 did not sustain any damage by rodents. Although both voles and deer mice had been trapped in the area of Transect 4 during the summers of 1984 and 1985, we do not know for certain if the rodents remained in this area during the winter months. When the data from Transects 1-4 are combined, 28% of the big sagebrush population and 21% of the total shrub population suffered some degree of damage. Only 1% of the big sagebrush individuals were completely killed by the girdling.

Table 2. Assessments of rodent damage to big sagebrush (*Artemisia tridentata*) near Kemmerer, Wyoming, during the winter of 1983-84. No damage was observed after the winters of 1984-85 or 1985-86.

Transect number	Number of shrubs sampled	Percentage of shrubs damaged	Percentage with biomass losses	Mean (\pm SE) percentage of biomass lost per damaged shrub
1	23	39	17	25 \pm 4
2	37	22	11	48 \pm 21
3	16	38	6	19 \pm 0
4	5	0	0	0

Comparison of our results with previously published estimates of shrub damage and/or mortality during rodent population irruptions (Hubbard and McKeever 1961, Mueggler 1967, Phillips 1970, Frischknecht and Baker 1972) are difficult because concomitant values of rodent population sizes were not included in those studies. The percentage of damaged shrubs reported by these authors, however, is quite comparable to our value of 21% (28% of big sagebrush). Hubbard and McKeever (1961) observed that 15% of the bitterbrush on their plots in northeastern California was damaged by voles in 1957-59. Phillips (1970) reported damage of 10-20% of bitterbrush in southern Idaho during 1958 and 1963. Frischknecht and Baker (1972) estimated that 28% of the big sagebrush on their central Utah plots was damaged in 1969.

While these damage estimates appear similar, the shrub mortality reported in those same studies was considerably higher than our estimate of 1%. Mortality estimates for bitterbrush ranged from 5% (Hubbard and McKeever 1961) to 38% (Phillips 1970), while big sagebrush mortality varied from 10-84% in Montana during 1962-64 (Mueggler 1967) and 36-73% in Utah (Frischknecht and Baker 1972). The discrepancy between our estimate of mortality and those in other reports may be due to different rodent densities in the study area. Vole densities during the other studies must have been quite high for those authors to discern a population irruption without comparative trapping data. The vole and deer mouse populations during our study were not particularly large, and without extensive trap data we would have had difficulty detecting population changes between years. The magnitude of shrub mortality may reflect rodent densities, although several mediating factors (discussed later) may also be involved.

On our sites (4 Transects combined) 11% of the shrubs lost some biomass due to girdling. If a shrub lost biomass, then the average

amount lost was 36% of its wet weight (actual mean biomass loss per shrub = 305 g ± 106 (SE), range = 18–1015 g). The big sagebrush plants in the area had a mean wet weight of 849 g ± 177 (SE) (range = 371–1750 g). Combining these values, the total amount of big sagebrush biomass lost via rodent girdling was 231 kg/ha, or approximately 4% of the total aboveground standing crop of sagebrush.

These results indicate that rodents can have a substantial influence on rates of litter production in the sagebrush-steppe ecosystem. Measurements of "normal" annual litter production from big sagebrush in the Great Basin Desert indicate that between 5.8% (West and Gunn 1974) and 13.4% (Mack 1977) of total aboveground standing crop biomass is converted to litter each year via senescence, drought, winter-kill, insects, pathogens, etc. Leaves and inflorescences comprise a vast majority of the litter; only 0.2% of the standing crop biomass annually converted to litter is woody material (calculated from data in Mack 1977). Assuming that the big sagebrush on our sites produces comparable annual amounts of litter, then the amount of aboveground standing crop biomass killed by rodents (4%) represents a 30–69% increase in total annual sagebrush litter production. In addition, because almost all of the biomass from killed shrub parts was woody stems, the rodent damage equates to about a 20-fold increase in annual production of wood litter from big sagebrush. These values would be substantially larger in situations where extensive shrub mortality occurs, such as those in areas studied by Mueggler (1967) and Frischknecht and Baker (1972).

Given that even moderate densities of rodents can inflict substantial damage and mortality on shrub populations, a potential influence of rodents on the nutrient cycling processes of the shrub-steppe ecosystem is apparent. The large amounts of unconsumed detritus produced by the rodents' feeding activity enters the decomposer food chain and provides a new source of essential nutrients to the remaining plant community. The leaves on shrubs girdled during the winter wither and drop from their branches in the spring, and are quickly decomposed. In our study areas, big sagebrush leaves on the ground beneath shrubs lost 75% of their dry weight in only 4 months (May to September) (M. Allen, Department of Biology, Utah State University, unpublished data, 1985). The remaining twigs and branches are not immediately available to the decomposers, as they persist as "standing dead" shrubs of several years. Eventually, though, they too are incorporated into the litter layer.

Rodent-induced mortality of shrubs influences the population age structure of the target species, as well as the species dominance relationships in the plant community. Mueggler (1967) found that voles preferentially selected mature and "decadent" (senescent) big sagebrush over young individuals. Analysis of damaged and undamaged shrub size classes on our sites revealed that rodents generally selected shrubs without preference to height or canopy coverage (Table 3). While rodents on Transect 1 fed on shrubs with

Table 3. Heights (cm) and canopy areas (cm²) of undamaged and damaged big sagebrush (*Artemisia tridentata*) from sample areas near Kemmerer, Wyoming. All values are means ± 1 SE.

Transect number	Shrub Height		Shrub Canopy Area	
	Undamaged	Damaged	Undamaged	Damaged
1	50 ± 6	71 ± 8	1950 ± 255*	4213 ± 743
2	77 ± 5	86 ± 9	3532 ± 664	2906 ± 846
3	85 ± 10	55 ± 8	4824 ± 1113	2473 ± 531
4	98 ± 19	None	5669 ± 2186	None
		Damaged		Damaged

* = Significantly different, t-test, P ≤ 0.05.

significantly greater canopy areas, no such phenomenon was observed on Transects 2 or 3. Our data suggest that shrub selection based on shrub height and canopy area is generally random,

although our tall shrub patches were dominated by mature individuals. Elimination of large shrubs from the population exposes new areas of land for colonization by individuals of the same and other plant species, thereby altering the community structure. If shrub mortality were extensive (e.g., Mueggler 1967, Frischknecht and Baker 1972), dramatic and persistent changes could occur in both the floral and soil components of the shrub-steppe ecosystem (Sturges 1983).

Because shrubs are damaged only periodically by rodents, and then only during the winter months, we hypothesize that bark-stripping by rodents is initiated when (1) population densities become so great as to exhaust the supply of palatable grasses, forbs and seeds, and/or (2) the accessibility of subnivean food resources is reduced by structural changes (ice or crust formations) in the lower levels of the winter snowpack (Langham 1981, Male and Gray 1981). Winters characterized by deep, long-lasting snowpacks would presumably exacerbate the food shortage situation. While these hypotheses have yet to be experimentally tested in the field, they are certainly consistent with the observations reported here (Fig. 1) and in previous studies (e.g., Mueggler 1967, Frischknecht and Baker 1972).

How frequently do rodent populations damage shrub stands? The published reports suggest major, widespread destruction occurs about once every 5 to 10 years, although localized incidences of shrub damage can be observed in virtually every year (Walter Mueggler, Forestry Sciences Laboratory, Logan, Utah, personal communication, 1985). Because many shrub species in the Intermountain Basin have life spans of 80 years or more (Roughton 1972), they may be exposed to as many as 10–15 rodent population cycles. Therefore, rodent feeding activity can be a very important source of litter production and shrub mortality in areas providing suitable rodent habitat.

Literature Cited

- Bailey, V. 1900. Revision of American voles of the genus *Microtus*. N. Amer. Fauna 17:1-79.
- Becker, E.L., II. 1977. Plant food preferences of 2 sympatric rodents and their estimated impact on a Great Basin shrub-bunchgrass community. M.S. Thesis, Utah State Univ., Logan.
- Bormann, F.H., and G.E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York.
- Brown, L.N. 1967. Ecological distribution of mice in the Medicine Bow Mountains of Wyoming. *Ecology* 48:677-680.
- Canfield, R. 1941. Application of the Line Interception method in sampling range vegetation. *J. Forest.* 39:388-394.
- Chew, R.M. 1974. Consumers as regulators of ecosystems: An alternative to energetics. *Ohio J. Sci.* 74:359-370.
- Chew, R.M. 1978. Impact on the ecosystem. p. 167-180. In: D.P. Snyder, ed. Populations of small mammals under natural conditions, A symposium held at the Pymatuning Laboratory of Ecology, May 14–16, 1976, Vol. 5, Spec. Publ. Series. Univ. of Pittsburg, Pa.
- Crawley, M.J. 1983. Herbivory, the dynamics of animal-plant interactions. *Studies in Ecology*, Volume 10. Blackwell Scientific Publications, Boston.
- Frischknecht, N.C., and M.F. Baker. 1972. Voles can improve sagebrush rangelands. *J. Range Manage.* 25:466-468.
- Golley, F.B. 1973. Impact of small mammals on primary production. p. 142-147. In: J.A. Gessaman, ed. Ecological energetics of homeotherms. A view compatible with ecological modeling. Utah State Univ. Press Monogr. Series Vol. 20, Logan.
- Hubbard, R.L., and S. McKeever. 1961. Meadow mouse girdling—another cause of death of reseeded bitterbrush plants. *Ecology* 42:198.
- Johnson, D.R. 1961. The food habits of rodents on rangelands of southern Idaho. *Ecology* 42:407-410.
- Kitchell, J.F., R.V. O'Neill, D. Webb, G.W. Gallepp, S.M. Bartell, J.F. Koonce, and B.S. Ausmus. 1979. Consumer regulations of nutrient cycling. *BioScience* 29:28-34.
- Langham, E.J. 1981. Physics and properties of snowcover. p. 275-337. In: D.M. Gray and D.H. Male, eds. Handbook of snow. Pergamon Press, New York.
- Lechleitner, R.R. 1969. Wild mammals of Colorado. Pruett Publ. Co., Boulder, Colo.

- Long, C.A. 1965.** The mammals of Wyoming. Univ. of Kansas Publications Museum of Natural History 14:493-758.
- Mack, R.N. 1977.** Mineral return via the litter of *Artemisia tridentata*. Amer. Midl. Natur. 97:189-197.
- MacMahon, J.A. 1981.** Successional processes: comparisons among biomes with special reference to probable roles of and influences on animals. p. 277-304. In: D.C. West, H.H. Shugart, and D.B. Botkin, eds. Forest Succession. Concepts and Application. Springer-Verlag, New York.
- Male, D.H., and D.M. Gray. 1981.** Snowcover ablation and runoff. p. 360-436. In: D.M. Gray and D.H. Male, eds. Handbook of snow. Pergamon Press, New York.
- Maxwell, M.H., and L.N. Brown. 1968.** Ecological distribution of rodents on the high plains of eastern Wyoming. Southwestern Natur. 13:143-158.
- Mueggler, W.F. 1967.** Voles damage big sagebrush in southwestern Montana. J. Range Manage. 20:88-91.
- Murray, K.F. 1965.** Population changes during the 1957-1958 vole (*Microtus*) outbreak in California. Ecology 46:163-171.
- Odum, H.T., and E.P. Odum. 1976.** Energy basis for man and nature. McGraw-Hill Book Company, New York.
- Parmenter, R.R., and J.A. MacMahon. 1983.** Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystem: the role of shrubs. Oecologia 59:145-156.
- Phillips, T.A. 1970.** The status of antelope bitterbrush in the Cassia Mountain area of southern Idaho. Range Improvement Notes Vol. 15, No. 4, 15 p., Forest Service, USDA, Intermountain Region, Ogden, Utah.
- Piper, S.E. 1909.** The Nevada mouse plague of 1907-8. USDA Farmer's Bulletin 352:1-23.
- Randall, J.A. 1978.** Behavioral mechanisms of habitat segregation between sympatric species of *Microtus*: habitat preference and interspecific dominance. Behav. Ecol. Sociobiol. 3:187-202.
- Rickard, W.H. 1960.** The distribution of small mammals in relation to the climax vegetation mosaic in eastern Washington and northern Idaho. Ecology 41:99-106.
- Roughton, R.D. 1972.** Shrub age structures on a mule deer winter range in Colorado. Ecology 53:615-625.
- Spencer, D.A. 1959.** The Oregon meadow mouse irruption of 1957-58: biological and control aspects. p. 15-25. Fed. Coop. Extension Service, Corvallis, Ore.
- Sturges, D.L. 1983.** Long-term effects of big sagebrush control on vegetation and soil water. J. Range Manage. 36:760-765.
- Swift, M.J., O.W. Heal, and J.M. Anderson. 1979.** Decomposition in terrestrial ecosystems. Studies in Ecology, Volume 5. Blackwell Scientific Publications, London.
- Walker, E.P. 1975.** Mammals of the world, Third Edition. The John Hopkins University Press, Baltimore.
- West, N.E., and C. Gunn. 1974.** Phenology, productivity and nutrient dynamics of some cool desert shrubs. US/IBP Desert Biome Res. Memo. 74-7.
- West, N.E. 1983.** Western Intermountain sagebrush steppe. In: N.E. West (ed.) Ecosystems of the World, Volume 5. Temperate Deserts and Semideserts, Elsevier Sci. Publ. Co., New York.
- Williams, O. 1959.** Food habits of the deer mouse. J. Mamm. 40:415-419.
- Zlotin, R.I., and K.S. Khodashova. 1980.** The role of animals in biological cycling of forest-steppe ecosystems. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pa. (N.R. French, ed., English translation).

POSITION AVAILABLE RESEARCH SPECIALIST II

North Dakota State University, Central Grasslands Research Station, Streeter, ND. Will assist the station superintendent in developing, executing, analyzing and publishing results of range-livestock research trials, assists in the operation and maintenance of station facilities and equipment. Requires M.S. degree or commensurate experience in range management and be familiar with range-livestock research techniques; must have experience in farm/ranch operations and be able to assist in the day-to-day operation and maintenance of the station. Letter of application, resume, transcripts and 3 letters of reference must be received by **February 6, 1987**. Send to: Paul Nyren, Central Grasslands Research Station, Box 21, Streeter, ND 58483. North Dakota State University is an Equal Opportunity Institution.

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