

Vole-Driven Restoration of a Parariparian Meadow Complex on the Colorado Plateau, South-Central Utah

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Abstract—Rapid and substantial reductions in the local density of invasive rubber rabbitbrush (*Chrysothamnus nauseosus*) have been achieved on a shrub-infested meadow complex solely by manipulating grazing so as to benefit the native meadow vole, *Microtus montanus*. The key adjustment has been a shift from spring-summer to late season grazing, thereby allowing sufficient growth of herbaceous vegetation to offer suitable vole habitat. We hypothesize that voles were instrumental in defending many historic western meadowlands against woody shrub encroachment, but have now been widely displaced by livestock competition. This suggests that voles could prove an important restoration tool on certain shrub-dominated rangelands.

Introduction

Woody shrub encroachment into grassland is a worldwide phenomenon and often attributed to poor land management practices (Archer 1994). In the arid rangelands of the Western United States, the transition from grassland to shrub-dominated vegetation often began soon after the introduction of livestock (McPherson and others 1988). Excessive grazing together with a reduction in fire frequency is thought to have been a primary driver of the grassland to shrubland transition in many parts of the region. Among the most heavily impacted areas have been the grass and sedge dominated meadow complexes that flank the riparian zones in many parts of the Intermountain West. These “Parariparian Meadow Complexes” (PMCs) vary considerably in size, extending from just a few tens of meters to over a kilometer to either side of the riparian zone. They also vary in vegetation type and according to water availability. Thus, PMCs range from wet through mesic to dry meadow complexes,

with the gradients between them usually correlated with distance and elevation away from the riparian zone. The extent of a PMC is strongly influenced by the local hydrology, geomorphology and soil characteristics (Jewett and others 2004). Regardless of size, these areas are typically among the most heavily disturbed of all rangeland habitats, owing to their ability to provide reliable sources of forage and water, both in close proximity. For the same reason, the PMCs were the first to feel the pressure of livestock introductions in the mid 1800s and most have continued to be impacted by livestock to some degree ever since (Belsky and others 1999). At the same time, the PMCs are among the most valuable of all rangeland environments in the arid West because they typically harbor the greatest biotic diversity and function as important dispersal and breeding corridors for a host of animals, including migrating neotropical birds (Martin and Finch 1996). Restoration of degraded PMCs, therefore, deserves to be among the highest priorities on western rangelands.

Woody shrub invasion into western PMCs is often so extensive that most of the original cover of grasses, sedges, and forbs has been lost through shrub competition and persistent grazing pressure. Among the most common woody shrubs to invade these environments are big sage (*Artemisia tridentata*), rubber rabbitbrush (*Chrysothamnus nauseosus*) and, where soils are alkaline, greasewood (*Sarcobatus vermiculatus*). Whereas sage is readily controlled by a variety of common brush treatment strategies (for example; burning, cutting, herbicides), this is not true of rabbitbrush and greasewood. Both of these shrubs are very resistant to most standard brush control measures due to their capacity to re-grow from the root crowns (Whitson and others 1996). Such resistance generally assures that, in the absence of considerable effort and expense, a PMC dominated by these shrubs will likely remain so. Moreover, as with some other shrub-invaded rangelands in the West (Archer 1994), many transformed PMCs have probably reached a new alternate stable state with respect to vegetation structure and would not return to their original condition even if grazing were discontinued.

In this preliminary study, we report extraordinary success in reducing brush domination in a former meadow complex without resort to conventional control techniques. Rather, we have relied exclusively on biological control using native small mammals as the primary agents of our restoration program. In a surprisingly short time, this strategy has substantially shifted vegetative structure away from a brush-dominated complex to one that is beginning to resemble the original

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mesic and dry meadow to savannah-like vegetation that appears to have occupied the site prior to the introduction of livestock.

Background

Site History and Characteristics—The South Hollow study site occupies approximately 200 acres in the Upper Valley region of Garfield County in south-central Utah. It has a mean elevation of approximately 7,100 ft (2,165 m) and an average annual precipitation of between 12 to 14 inches (30.5 to 35.6 cm). Roughly 30 to 40 percent of the precipitation arrives as monsoonal rains between mid July and mid September. The site consists of an original 160-acre (~65-ha) homestead patented in 1911 plus roughly 60 acres (~24 ha) of rangeland belonging to the Dixie National Forest. The rangeland acres are included within the homestead fences due to water rights on nearby Upper Valley Creek. The site is almost entirely surrounded by an active grazing allotment administered by the Escalante District of the Dixie National Forest. The whole of the Upper Valley region was subjected to intense unregulated livestock (cattle and sheep) grazing beginning in the early 1880s and continuing until about 1910 when a USFS grazing permit system was established (Hall 1954). According to historic records, the Upper Valley had no defined creek, but instead displayed a system of meadows dotted by numerous seeps and short spring runs (Webb 1985). Present day Upper Valley Creek, which resides within a deeply entrenched arroyo (fig. 1), appears

to have been the result of major erosion linked to a series of catastrophic floods between 1909 and 1932 (Webb and Baker 1987). The depth of the arroyo system on and adjacent to the study site varies from approximately 6 to 30 feet and has resulted in a substantial drop in the original water table. In the West, stream incision and the resulting changes in geo-hydrological processes can have profound effects on riparian corridors and their associated meadow complexes, chiefly by reducing water availability through lowering the water table (Jewett and others 2004). Though several factors, including climatic change, may have contributed to arroyo formation in the Upper Valley, severe overgrazing of the surrounding rangelands and their watersheds was likely an important ingredient. Local soil types within the South Hollow study area are highly varied and range from deep sandy loams to heavy alkaline clays.

Historic Land Office reports indicate that by the 1890s greasewood was already beginning to take hold on eroded soils in the Upper Valley (Webb 1985). Sage dendrochronology (D. Bramble unpublished data) confirms that the invasion of South Hollow by big sage was already underway by at least 1910. Prior to a 1988 prescribed burn by the former owner, the vegetation on the study site consisted chiefly of dense stands of mature to senescent basin big sage (*A. tridentata* ssp. *tridentata*); the graminoid community was overwhelmingly represented by a single introduced bunch grass, crested wheatgrass (*Agropyron cristatum*). The fire, which was patchy, succeeded in killing virtually 100 percent of the sage where it burned, but left many areas untouched.

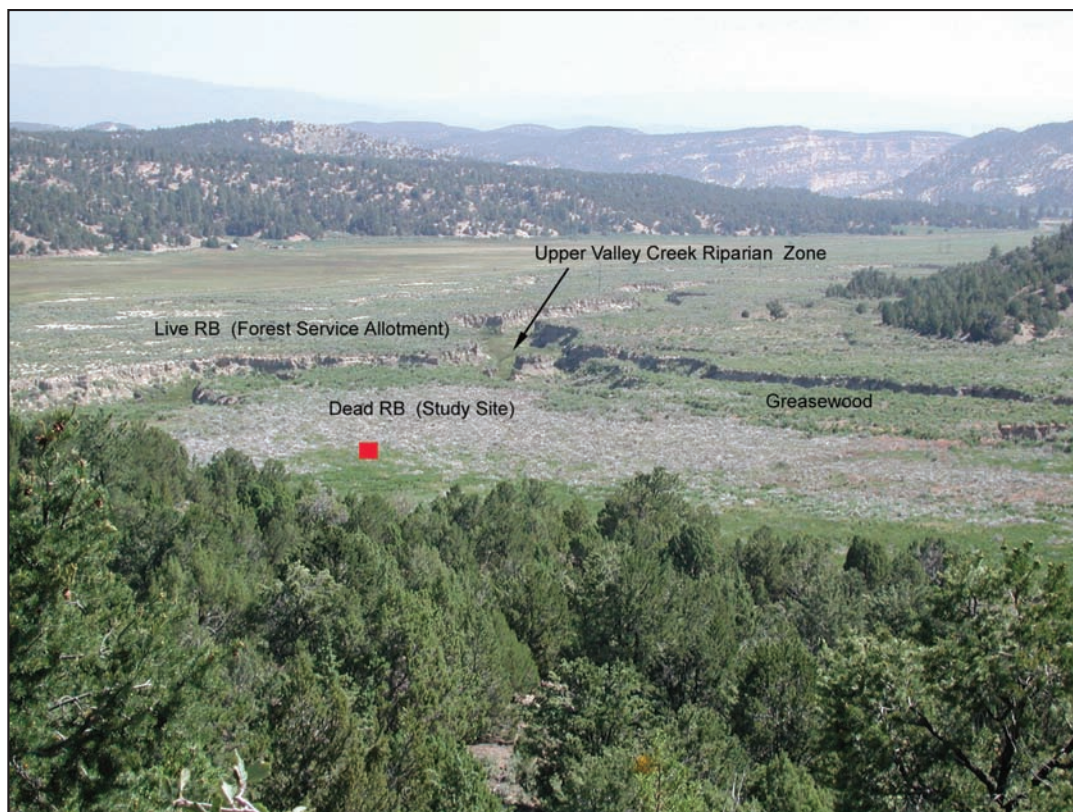


Figure 1—View of north end of South Hollow study site showing extent of most recent shrub kills in this area as well as untouched rabbitbrush (RB) on Forest Serve range on the opposite side of the riparian zone. The red square marks the approximate location of study Plot II (photographed on July 4, 2005).

The northern portion of the study site, and that containing our study plots, was the most thoroughly burned. Following the fire, and depending on local soil characteristics, either rubber rabbitbrush (RB) or greasewood, quickly invaded this area (fig. 1). By the time the property was acquired in the fall of 1992, both shrubs were already established in dense stands.

Methods

Grazing

Our restoration project was initiated in 1993 and continues at this time. It has utilized only a single restoration tool—the manipulation of grazing. Our grazing program departs from that traditionally employed on the South Hollow study site in three important ways:

1. A reduction in grazing intensity and duration. We estimate that our AUMs (Animal-Unit Months), which have ranged between 22 and 60, are at least 50 percent lower (and very likely more) than that of the historic grazing pattern on our study site. There are no actual records of the stocking rate on the property. Our cattle have remained on the property from 4 to 8 weeks depending on range conditions. Traditionally, the property appears to have been continuously grazed from late spring or early summer until fall.

2. Deferred grazing. With a single exception (1999), we have elected to shift to late season grazing. Under our plan, cows are not allowed onto the property until late August or September, and sometimes not until the end of September.

3. No grazing in drought years. Thus, the property was not grazed in 1996 and 2000. Limited grazing took place (late September to early November) in 2002, after summer rains broke severe drought conditions.¹

Vegetation Monitoring

We have periodically monitored the vegetation through field observation and repeat photography since 1993. Our only quantitative measurements have come from two study plots established in the summer of 2002. Each plot is a cattle exclosure 22.9 m (75 ft) square. Plot II is the lower of the two and closest (~83 m or 275 ft) to the Upper Valley Creek riparian zone. It is also the more mesic plot. Sedge (*Carex* sp.) is a common and increasing element of the herbaceous vegetation within Plot II. Sedge appears to be a good indicator of reliable soil moisture at the study site. Plot I is located approximately 210 m (700 ft) south of Plot II and thus farther (~210 m or 1,000 ft) from Upper Valley Creek. It is slightly higher in elevation (~25 feet) and drier; *Carex* has not been recorded from this plot. Since plot establishment in 2002, there have been several brief instances of trespass grazing on Plot II, but Plot I has remained free of cows.

¹ Additionally, the property was not grazed in 2005 owing to an exceptionally wet winter and spring that eliminated the need for our lessee to rent our pasture.

From 2002 to 2005 the study plots were protected from cattle by portable electric fencing. In 2006 permanent post and wire fencing was installed around each site.

The shrub composition of the plots has been surveyed at three points in time: July 2002, September 2005, and October 2006. Each plot was divided into 10 equal sections within which all established shrubs (>15 cm or 6 inches in height) were counted and then added to obtain the total for the plot. The species identity of each shrub was noted, but only three species of woody shrub occur within these plots (RB, big sage, mountain snowberry). Both plots were thoroughly burned in the 1988 fire, resulting in 100 percent mortality of the existing sage population. In the initial 2002 census, we counted all burned sage stumps to determine pre-fire shrub density. We also scored all established shrubs (RB) with respect to the following categories: (1) live or killed, (2) rodent damaged or not, and (3) if damaged, then by girdling or burrowing (tunneling beneath the shrub). In the 2005 census all established shrubs were scored according to two categories: (1) killed or alive, and (2) rodent damaged or untouched. In the 2006 survey, shrubs were scored only as to killed or alive; at this time all dead shrubs exhibited clear evidence of rodent damage, including burrowing around their bases. Moreover, all RB within the plots were counted because by 2006 all plants exceeded 15 cm in height.

The first indication of widespread shrub mortality associated with rodent activity occurred during the period of 1997 to 1999. The 2002 census reflects this event, because there was no detectable vole herbivory on shrubs during the dry period of late 1999 to 2003. The second episode of vole predation on woody shrubs began with the exceptionally wet winter of 2004 to 2005 and continued into 2006 (fig. 2).

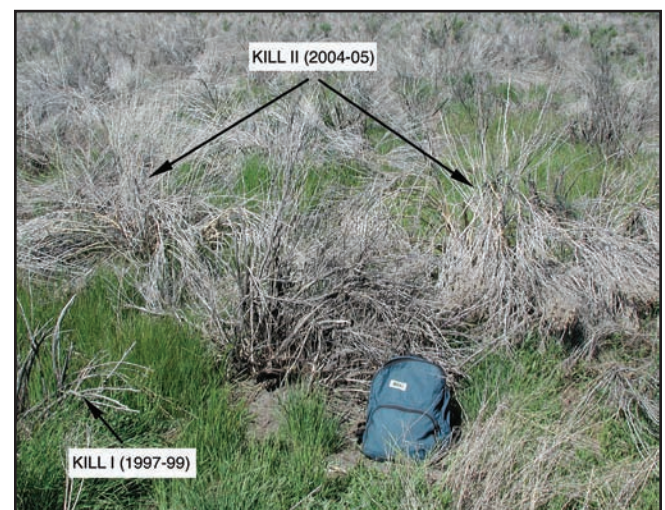


Figure 2—Closer view of vole-killed and damaged RB in June 2005. Shrub skeletons from first shrub kill (1997-99) are weathered and lack terminal branches. Most of the skeletons in this picture represent shrubs killed by voles during the winter of 2004 to 2005. Notice re-growth on some severely damaged but surviving plants in the background. With the removal of the shrub canopy, herbaceous vegetation is expanding in this area. The backpack rests on freshly disturbed soil from a vole burrow system.

Results

The 2002 census shows that prior to the 1988 fire both plots had been dominated by dense, pure stands of basin big sage. The fire killed all sage shrubs within the plots, but their burned stumps remained and were readily identifiable in 2002. By 1993 a large percentage of these stumps had become sites of RB establishment and dense stands of this shrub, most of which exceeded 3 feet in height (~0.9 m), were already beginning to form a substantially closed canopy.

The overall trend in shrub numbers on the two study plots is illustrated in figure 3. Pre-fire sage densities, as reflected in burned sage stumps, differed on the two sites, being greater on the drier site, Plot I (fig. 3A). However, the replacement of sage by RB following the 1988 fire resulted in a larger fraction of stumps being occupied by RB in Plot II (76.77 percent) than in Plot I (62.06 percent). There was no significant difference, however, in the absolute number of established (>15 cm height) RB shrubs on the two plots by the time of the first survey in 2002 (table 1).

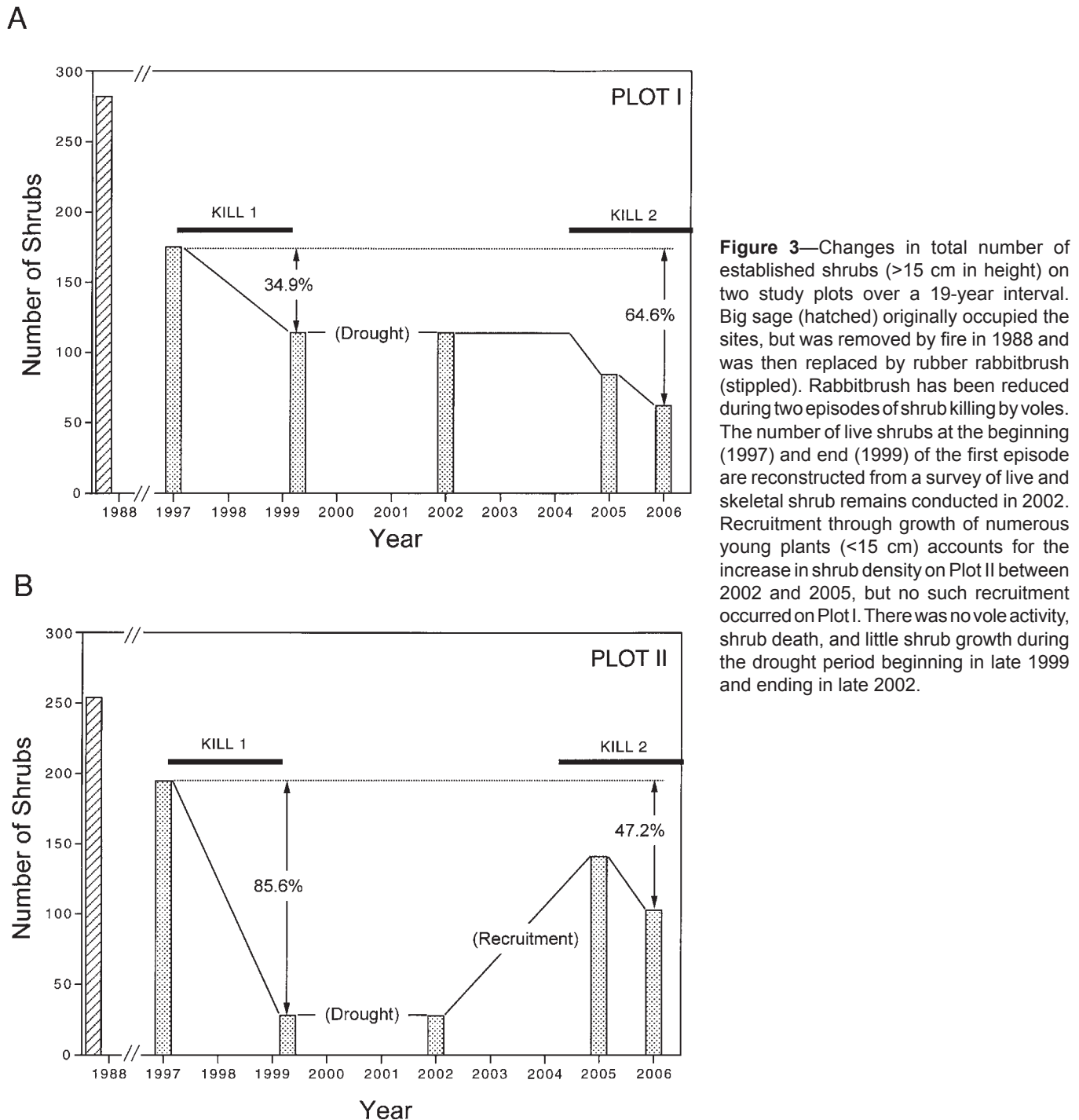


Table 1—Results of surveys of established (> 15 cm ht.) rubber rabbitbrush (RB) on two 22.9 m (75 ft) square plots conducted in July 2002 (top), together with observed shrub densities in September 2005 and October 2006 and reconstructed earlier densities of big sage (1988) and RB (1997).

	PLOT I	Percent	PLOT II	Percent
Total Rabbitbrush (RB)				
(2002)	175	100.00	195	100.00f
Killed ^a	61	34.86	167	85.64***
Damaged	64	36.57	17	8.72***
Untouched	50	28.57	11	5.64***
Girdled	124	70.86	159	81.54
Burrowed ^b	73	41.71	160	82.05***
RB density (1997) ^{c,d}	3350	—	3732	—
RB density (2002)	2182	—	563	—
RB density (2005)	1608	—	2699	—
RB density (2006)	1187	—	1971	—
Sage density (1988) ^e	5397	—	4862	—

^aAll “killed” shrubs exhibited positive signs of rodent attack. Girdled = stripping of bark from lower stems; Burrowed = excavation and gnawing of root crowns.

^bThere is no significant difference ($P > .05$; χ^2 test) between the number of RB burrowed and killed within the same plot, reflecting the fact that the two are correlated.

^cDensities are given as shrubs per hectare.

^dDensity of RB in 1997 reconstructed from census of live and dead shrubs in 2002.

^eSage densities in 1988 reconstructed from burned stumps recorded in 2002.

^fThe total number RB on the two plots was not significantly different in 2002.

*** Values for which the differences between plots are highly significant ($P < .001$; χ^2 test).

The impact of the first episode of rodent predation on RB produced strikingly different levels of shrub mortality on the two sites, with nearly 86 percent of the established shrubs killed on Plot II compared to just 35 percent on Plot I. Beginning with the second episode of rodent predation in the fall of 2004, shrub density on Plot I continued to decline during the 2005 and 2006 surveys. In Plot II, however, there was actually a large increase in RB density between 2002 and 2005 (fig. 3B). This was almost entirely attributable to the growth of a large cohort of very young plants that were too small to be counted as “established” in 2002. These shrubs grew rapidly afterward, having been “released” by the near elimination of large canopy forming RB during the initial round of rodent activity. Compared to 2005, shrub numbers had once more declined on Plot II in 2006, and again due entirely to rodent predation. Thus, despite the temporary spike in shrub numbers in 2005, the total reduction of established RB between the initial (1997) and 2006 density is still impressive (47.18 percent). That on Plot I was even more dramatic (64.57 percent) (fig. 3A).

Closer examination of the 2002 data offers additional insight into rodent-shrub interactions (table 1). When scored for status, the shrubs on our plots were again significantly different in several categories: percent killed, damaged by girdling, and burrowed. Vole-driven mortality of established plants was much higher in Plot II. However, in both plots the number of killed shrubs was not significantly different from the number having rodent burrows beneath their crowns (table 1). This statistic simply confirms what has been obvious in our field observations: RB damaged by the girdling of their stems and base, even when extensively so, are rarely killed. But once serious digging begins under a

shrub, its eventual death is nearly certain. While burrowing was specifically scored only in 2002, it is clear that essentially all subsequent RB mortality, both within and external to our study plots, has been associated with rodent burrowing.

Discussion

Our restoration project has produced large reductions in RB density in a short period of time (Bramble and Bramble 2003). Moreover, this success has been achieved without resort to any of the traditional methods of shrub control (such as burning, disking, herbicide application). Our data suggest that local densities of woody shrubs may now be approaching pre-grazing levels. Nearly all the reductions in invasive woody shrubs, and especially RB, appear to be directly linked to the activities of a single species of native rodent, the montane meadow mouse or vole (*Microtus montanus*). This phenomenon, in turn, appears to be a response to the manipulation of a single variable, the pattern of livestock grazing.

Our grazing protocol compared to the historic pattern at the site involves both a reduction in grazing intensity as well as a shift in timing. Of the two, timing seems the most important. Grazing on the study site has been deferred until the fall. Traditionally our pastures, like elsewhere in the Upper Valley, have been grazed from late spring/early summer until fall. With deferred grazing, both cool and warm season components of the grass flora have ample time to grow, mature, and set seed. In the process, the herbaceous cover attains densities and heights that would not otherwise be realized. This change in vegetative structure is critical to montane voles. During the warm season this

rodent appears to be limited by environmental conditions, especially adequate food, cover, and humidity close to the ground. Grazing related reductions in grass density and height on the pastures of the Upper Valley during the spring and summer generally preclude occupation by voles. There has, for example, been little indication of vole activity on the Forest Service grazing allotment immediately adjacent to our property (fig. 1). This range, which is primarily dense sage with crested wheat in the interspaces but also containing locally dense stands of RB in close proximity to the north end of the study site, continues to be grazed in late spring and summer. Montane meadow voles are chiefly grazers and hence dependent on the availability of grasses, sedges, and forbs. Their food requirements overlap those of livestock to a considerable degree. Unlike livestock, however, individual voles have a restricted foraging range and are consequently more dependent on the local availability of plant resources. For these reasons, and despite immense differences in size, voles and livestock actually compete for much the same vegetation during the warm season. Such ecological overlap may help to explain the endangered or threatened status of several species of *Microtus* (including races of *M. montanus*) in various parts of the Western United States, most of which appear to be associated with rangelands altered by livestock utilization (Nowak 1999).

The exact mechanism by which voles kill otherwise healthy, mature RB is unclear. Girdling of the basal stems is almost always the first outward signal that voles have begun to target a particular shrub. But, as previously mentioned, RB is noted for its ability to re-sprout from the root crowns and thus girdling alone is unlikely to prove fatal. Burrowing around the base of the shrub, which is generally initiated only after girdling has started, virtually assures the death of the shrub (table 1). Our initial observations indicate that voles feed on the rootstock, which may contribute directly to a shrub's death. However, burrowing through or near the rootstock may promote shrub mortality in other ways, including the introduction of fungal pathogens or increasing the plant's vulnerability to water stress. Voles clearly prefer larger shrubs and generally ignore small, young RB plants (<15 cm in height). Small shrubs are sometimes girdled but rarely burrowed. This suggests that beyond providing access to underground food, the burrows built beneath an established shrub have other important functions, including shelter and protection from aerial predators. Burrowing also creates a disturbed area surrounding each dead RB that frequently becomes a germination site for native and exotic annual weeds (such as tansymustard, lambsquarters, and cheat grass). However, our observations suggest that this is a transitory condition and that native graminoids and forbs typically replace the weedy annuals within a few years. Importantly, these disturbed sites have not been re-populated by either RB or sage despite ample seed availability and the sorts of climatic perturbation (severe drought followed by an exceptionally wet period) that favor woody shrub establishment (Archer and Smeins 1991).

The two major episodes of vole predation on RB are related to climatic conditions. Both the 1997 to 1999 and the 2004 to present intervals are associated with above average precipitation in south-central Utah (Region 4). During both episodes, positive indicators of vole activity (such as surface

runways, burrow systems, fecal pellets, grass cuttings) were extremely abundant, and daytime sightings of these normally nocturnal to crepuscular rodents became commonplace. The greatest damage to shrubs, especially from stem girdling, corresponded to periods of deep winter snow pack (for example, 2004 to 2005). At these times the rodents took advantage of the snow to strip bark as far up the plant as the surface of the snow allowed. (When feeding, voles remain beneath the snow surface.) There was no apparent sign of vole activity or shrub predation during the dry period lasting from fall 1999 to late summer 2002. Rodent numbers declined dramatically and the animals became either very rare or altogether absent from the shrub-dominated PMCs in South Hollow, including our study plots. Small populations of voles did persist in the riparian zones along Upper Valley Creek (fig. 1) where locally dense stands of grass, sedge, and rush (*Juncus* spp.) remained despite drought conditions. Riparian areas thus appear to act as refugia, serving to buffer vole populations against local extinction when unfavorable conditions render adjacent environments uninhabitable. The much higher rates of vole-killed RB on Plot II (table 1) may be related to the fact that it is located closer to the riparian staging area from which voles reentered the South Hollow meadows following a return to wetter conditions.

The influence of small mammals on rangeland vegetation structure and health is still poorly understood (Archer and Smeins 1991); however, recent evidence suggests that it might well be more profound than previously assumed. The systematic elimination of prairie dogs, for example, is thought to have altered the local vegetation composition on short-grass prairie, including an increase in woody shrubs (Archer and others 1987). Landscape level impacts by rodents and lagomorphs may have helped produce the vegetation contrasts that mark the United States-Mexican border in parts of the Southwest (Curtin and Brown 2001). Recent experiments have established the importance of voles in shaping vegetation structure and succession in the Midwest. There meadow voles (*Microtus pennsylvanicus*) have been shown to influence the herbaceous composition of synthetic tallgrass prairie (Howe and Lane 2004) as well as to bias the rate and species composition of trees that successfully invade old-field habitats (Mason and others 2001). In California, voles (*Microtus californicus*) likewise alter the structure of grasslands (Batzli and Pitelka 1970) and significantly impact the survival of young redwood trees through their girdling behavior (Guisti 2004).

Our study on the Colorado Plateau extends these findings by offering evidence that small mammal activity may actually reverse the pattern of woody shrub encroachment into grassland and meadow habitats. Net reductions of established RB within our study plots are as high as 68 percent, but some areas outside the plots have realized reductions of nearly 100 percent over the same period of time. Preliminary calculations suggest that more than 10,000 shrubs (mostly RB, but a growing number of big sage and greasewood) have already been killed by voles on the South Hollow study site. Moreover, all documented reductions in invasive woody vegetation have occurred within less than a decade of the first unambiguous signs (spring of 1997) of vole activity within these former meadows. Vole-driven shrub mortality has also been accompanied by a parallel expansion of open habitat

that is increasingly occupied by native grasses, sedges and forbs (fig. 2). The composition of this vegetation is assumed to be similar to that originally occupying the study site, although no direct data bearing on this matter are presently available. Voles appear to shape the composition of vegetation on mid-western prairies over periods of years through selective herbivory and seed predation, the results of which may exhibit a considerable time-lag (Howe and Brown 2001). It will probably be years, therefore, before the exact nature of a stable herbaceous plant assemblage becomes apparent on those areas of South Hollow recently cleared of shrubs. Regardless, we are witnessing a surprisingly rapid shift from a closed-canopy shrub land to an open, graminoid dominated vegetation complex. In effect, *Microtus montanus* appears to be forcing vegetation structure back toward an earlier (pre-grazing?) state on this site and one that, not incidentally, is much closer to its preferred natural habitat.

It is important to note that vole predation on woody shrubs in South Hollow has thus far been highly selective. The greatest shrub losses have been to mature RB. Increasingly, however, basin big sage (*A. tridentata* ssp. *tridentata*) is being targeted, especially on the higher and drier portions of the site where dense stands of this shrub still exist. Girdling readily kills sage, but voles frequently establish burrows under this shrub as well. Greasewood (*Sarcobatus vermiculatus*), which following the 1988 fire, developed very dense stands on exposed alkaline soil, is likewise coming under more frequent vole predation. Like RB, this shrub is very difficult to control due to its propensity to re-sprout from underground rootstock, but it may likewise be vulnerable to burrowing. Since vole activity resumed in late 2004, numerous examples of girdled and burrowed greasewood have appeared on the study site, although to date only a handful of these shrubs have actually died. The voles have, at the same time, ignored other native shrubs including mountain snowberry (*Symphoricarpos oreophilus*), Wood's rose (*Rosa woodsii*), squawbush (*Rhus trilobata*) and bitterbrush (*Purshia tridentata*).² All these shrubs are increasing to varying degrees, but snowberry most obviously. Snowberry, in fact, may have special resistance to voles. This shrub is routinely burrowed without apparent negative effect, and in some instances it has replaced vole-killed RB by establishing directly on the disturbed soil underneath the dead shrub. We think it is significant that the woody shrubs targeted by vole predation (RB, big sage, greasewood) in South Hollow are among the most common, widespread, and aggressive invaders of western grasslands and meadows. Among the shrubs avoided by voles are species that are commonly reduced or eliminated on heavily grazed rangelands. Thus, vole activity is not only reducing the overall presence of woody shrubs on the study site but is also shifting its composition.

² Interestingly, voles also ignore "yellowbrush," another native rabbitbrush (*C. viscidifloris lanceolatus*), even when very close to RB shrubs under active predation. However, yellowbrush is a much smaller shrub and is not an aggressive invader of PMC habitats in our area.

We believe that what has occurred on our study site could be reflective of a more general phenomenon affecting the vegetation and ecological health of many similar environments on western rangelands. Specifically, we suggest that small mammals, and especially grazers, may have had a significant but largely unrecognized role in creating and maintaining the types of open meadow complexes and grassy savannahs that historically flanked most riparian zones across the arid West. If so, these species would qualify as keystone elements in such ecosystems, just as heteromyid rodents have been for other western ecosystems (Brown and Heske 1990). Because the western PMCs were among the first to be severely degraded by livestock introductions, and because voles are small and relatively cryptic, these rodents may well have disappeared as functional components of these ecosystems without notice. In this context it is appropriate to raise an important question: What kept aggressive and prolific woody shrubs like RB from dominating western PMCs prior to the onset of grazing? RB, in particular, invades disturbed mesic sites more readily than sage but, unlike sage, will not be removed by fire once it has become established.

Voles and perhaps other herbivorous small mammals provide a possible answer to this question. Through their proclivity to kill invasive woody shrubs these small grazers appear to both defend and promote their preferred natural habitat—open, sunny expanses dominated by a graminoid-rich, herbaceous vegetation. This is in contrast to the apparent role of voles in mid-western and Pacific Coast grasslands, where the rodents act to shape the existing vegetation (Batzli and Pitelka 1970; Howe and Lane 2004) but do not create (or recreate) habitat of this type. It is reasonable to assume that the exact relationship of small mammal activity to vegetation structure and evolution varies considerably from region to region and is influenced by many variables, including the abiotic and biotic history of the area and the specific ecological requirements of the mammalian species involved. It is also possible that the historic absence of large grazing mammals in much of the Intermountain West (Mack and Thompson 1982) may have conferred on small mammalian grazers (such as rodents and lagomorphs) a larger role in structuring rangeland vegetation than in other regions where large grazers were historically present.³ Our findings, therefore, raise the possibility that one of the most biologically important classes of western ecosystems (PMCs) may now be compromised, and widely so, by the absence of a key functional element, microtine rodents. If correct, our success in quickly triggering the initial transformation of a shrub-infested site into one probably more like the historic pre-grazing meadow and grassland vegetation is unlikely to prove an isolated anomaly. More likely, in our opinion, it is the predictable outcome of having reactivated a vital but missing dynamic in a local ecosystem.

³ Elk, while common at the South Hollow study site, appear to have been absent from this region in pre-settlement times (Bryant and Maser 1982). Elk are lacking in faunal collections from local archaeological sites (such as Fremont and Anasazi) and there is no mention of this large native grazer by the early European colonizers of the Escalante region. Present elk populations apparently stem from introductions beginning in the 1970s.

Within the Intermountain West, *Microtus montanus* is most often recognized for its ability to damage or kill young trees and shrubs in agricultural and suburban settings (Askham 1988). But our data clearly imply that such destructive behavior, which involves both girdling and burrowing, is merely a negative manifestation of the same natural tendencies that, until quite recently, assigned these rodents a central role in maintaining some of the West's most biologically rich ecosystems. This rodent is very widely distributed in the West (Zeveloff 1988) and small populations likely persist along most riparian zones where water is permanent and degradation from livestock has not been too severe. Therefore, it is probably safe to assume that many shrub-infested PMCs in the interior West are in close proximity to relict populations of *M. montanus* within nearby riparian corridors. During both major episodes of vole population expansion in South Hollow, vole dispersal and shrub-killing activities have extended to the fence-line marking the extreme southern end of our property, at least 1.64 km from their ultimate dispersal source on Upper Valley Creek. This portion of the study site is nearly 200 feet higher in elevation and distinctly drier than either of our study plots. The prevailing vegetation is similar to that of sage-steppe and related temperate savannah types (McPherson 1997), consisting of mature stands of big sage with bunch grasses (*Agropyron cristatum*, *Stipa comata*, *Sporobolus cryptandrus*) and blue grama (*Bouteloua gracilis*) in the interspaces. This fact demonstrates that the shrub control effects of these voles are not necessarily restricted to the mesic meadow environments close to riparian zones. All of these observations, in our view, strongly suggest that the montane meadow vole could be a new and potentially important restoration tool on western rangelands and one certainly worthy of additional examination.

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