Chapter 6. Beavers, Livestock, and Riparian Synergies: Bringing Small Mammals Into the Picture

Jennifer K. Frey

Introduction

Riparian ecosystems provide the anchor for their associated aquatic habitats and the structure for a unique assemblage of life found in these exceptionally productive ecosystems. Much of upland life also is tied to this zone, particularly in arid regions. For instance, on National Forest lands in the Southwest Region, 57 percent of all vertebrates occur in riparian ecosystems, but these systems make up <2 percent of these lands (Rickel 2005a). However, it has been estimated that 90 percent of riparian ecosystems have been lost or degraded in parts of the western United States through human-mediated factors (Ohmart and Anderson 1986). The inception of much of this degradation occurred during the 1800s when trappers flooded into the West exploring each river and tributary in pursuit of the American beaver (*Castor canadensis*; hereafter beaver). The pelts of these animals were made into felt that was used for the manufacture of gentlemen's top-hats. Trade in the pelts of these and other furbearers constituted a major economic export to Europe, which helped fuel the economy of the young country (Weber 1971). As a consequence, beavers were extirpated from many streams and the population of beavers in North America fell from more than 60 million before the arrival of Europeans to near extinction by 1900 (Naiman et al. 1988). Prior, beavers were an important force that influenced the hydrology and hence overall ecology of streams and rivers. Beavers cut trees to build dams on smaller streams and on side channels of larger rivers. Beaver dams and the coarse woody debris introduced into the waterways due to beaver activities are a strong force that alters the stream planform by spreading the water into a multitude of smaller channels and by creating ponds, pools, and backwaters (Polvi and Wohl 2013). With the loss of beavers, there was a simplification of the complex hydrology maintained by beavers resulting in single channels of water with relatively high stream power and erosive force, as well as reduced storage of water that otherwise would be released to sustain riparian plants during dry periods and droughts. This resulted in the inception of stream channel incision and a narrowing and simplification of the riparian zone (Naiman et al. 1988).

Of course, other factors besides the demise of beaver also have contributed to the loss of riparian habitats. Nearly all western rivers have had natural flow regimes altered by dams and diversions. Free water is an essential limiting factor for human survival and hence most human settlements are located along streams and rivers. Agricultural areas were initially developed in the fertile valleys along low gradient reaches of streams and rivers where water could be harnessed for irrigation. In turn, the larger of these valuable agricultural areas helped to fuel the growth of cities, which in turn are run by a complex infrastructure of water delivery and waste often originating and ending in rivers. Exotic species have been introduced, either intentionally or by accident, some of which, such as saltcedar (*Tamarix* spp.), have nearly wholly displaced native riparian communities in some areas in favor of novel systems consisting of near monotypes of the alien species (Shafroth et al. 2005).

Another agricultural product that exerts an influence on riparian ecosystems is domesticated livestock, such as cattle, horses, sheep, and goats. In the American West, livestock grazing is one of the few economic uses of much of the land and hence they are nearly ubiquitous on larger tracks of private lands and on the extensive tracks of public lands managed for multiple uses (e.g., U.S. Forest Service [USFS]; Bureau of Land Management [BLM]). These exotic animals were introduced into western North America in the late 1500s and hence some areas have been grazed by these animals for over 400 years (Bowling 1941). The behaviors and managed distributions of livestock are substantially different from native ungulates such as elk (*Cervus elaphus*) and deer (*Odocoileus* spp.). The long-term and differential use of riparian zones by livestock has substantially changed the composition and structure of riparian plant communities, typically resulting in an overall drying and simplification of the ecosystem (Belsky et al. 1999). And lastly, the world has embarked on a period of rapid climate change that is just beginning to exert its influence. In the American West, the future is expected to bring periods of prolonged drought as well as intense flooding. How riparian zones will respond to these changes is not precisely known, but it is likely to cause the continued deterioration of riparian ecosystems.

Water is vital for human interests and ecosystem function. Consequently, there is increasing interest in restoring riparian ecosystems and their associated aquatic habitats. Regardless of the goal (e.g., restore stream hydrology to improve fish habitat, improve specific riparian habitat elements) and regardless of the mechanics (e.g., use of big machinery to recontour streambeds, installation of instream structures, planting specific species), nearly all such restorations ultimately consider aspects of the riparian plant community. It is the deep-rooted riparian plants that ultimately stabilize the riparian and aquatic habitats and provide habitat for associated animals. However, to a large extent, these efforts focus on woody plants and their associated bird communities. This narrow perspective may fail to result in projects that restore full ecosystem function.

Thus, the ultimate purpose of this chapter is to call attention to an overlooked but vital element of riparian zones: the small mammal community, which is associated with herbaceous vegetation near ground level. I argue that taxonomic biases in the study of riparian ecosystems and frequent goals of riparian restoration have resulted in overlooking one of the most important elements of the riparian zone. Abundant and diverse small mammal communities support a vast array of ecosystem services. However, such communities are only fully expressed when riparian zones support a productive and diverse herbaceous riparian community. This may be maximally expressed through a synergism between healthy native riparian vegetation and beaver activities. However, this synergism can be disrupted, especially by livestock grazing, which ultimately can cause a loss of diversity and function to these ecosystems. I conclude by making recommendations on needed research to help improve understanding of these relationships and the management of these systems. Riparian restorations that fail to consider these aspects are not likely to reap full ecosystem benefits.

Taxonomic Bias in Riparian Restoration

There appear to be taxonomic biases in our knowledge about riparian ecosystems and the typical goals and monitoring of riparian restoration. People often seem to assume that birds are the group of animals most impacted by loss and degradation of riparian systems, perhaps with the exception of the impact to fishes by the concomitant degradation of the aquatic systems. Many references on riparian restoration explicitly link vegetation restoration with the needs of birds or use birds as the basis for understanding existing or future conditions (e.g., Eubanks 2004; Gardner et al. 1999). Monitoring the success of riparian restorations typically involves birds, and sometimes other taxa such as reptiles or bats, but rarely includes small mammals (e.g., Bateman et al. 2008; but see Queheillalt and Morrison 2006).

For instance, a USFS riparian restoration guide, while noting the importance of riparian systems for all wildlife, singles out only the analysis of threatened and endangered species and bird communities for establishing existing conditions of a riparian zone (Eubanks 2004). Furthermore, bird communities are often promoted as an index for planning and monitoring riparian condition and restoration, to the exclusion of other taxa (Bryce et al. 2002; Rich 2002; Young et al. 2013). As an example, it has been proposed that evaluation of breeding bird communities should be used as a means to assess "Proper Functioning Condition," which is the main method that Federal land management agencies, including the USFS, BLM, and Natural Resources Conservation Service, use to evaluate riparian health (Rich 2002).

I believe there are numerous reasons for this seeming taxonomic bias, although few have a biological basis. First, birds are viewed as charismatic and valuable animals. Besides the human fascination with flight, most birds are relatively easy to observe due to their flight, diurnal behavior, and repertoire of often loud, beautiful, and distinctive vocalizations. Pronounced morphological and plumage variation in this diverse group allows for relatively easy identification of species and often identification of different genders and ages, allowing even casual observers to understand something a bit deeper about their biology. As a consequence, birds are enormously popular with the public, which has led to formation of powerful lay advocacy groups (e.g., National Audubon Society). Such organizations convey numerous tangible and intangible benefits to birds by bringing attention to issues, garnering resources, and influencing legislation.

Further, the accessibility of birds allows citizens to participate in the collection of biologically meaningful data (e.g., winter bird count, rare bird alert, eBird) that help to expand the knowledge base of these organisms. Just as birds are popular with the public, they also are popular study organisms for scientists. For instance, consider that in North America there is only a single professional society dedicated to the study of mammals (American Society of Mammalogists), while in contrast there are at least four professional societies dedicated to the study of birds (American Ornithologists Union, Cooper Ornithological Society, Association of Field Ornithologists, Wilson Ornithological Society). One important consequence of this heightened attention and knowledge is that birds might be more likely to be listed as threatened or endangered than other taxonomic groups, and the perceived bar for "endangerment" might be lower. In turn, threatened or endangered listing can stimulate research and management focuses.

While there is no doubt that birds can be impacted by changes to riparian habitats and that they provide ecosystem services (Whelan et al. 2015), the taxonomic bias focuses attention on a suite of species that are primarily associated with the woody components of riparian ecosystems. This approach parallels another apparent bias in how humans tend to perceive ecosystems. Although trees and shrubs are usually a minor component of the diversity of riparian zones, they are usually the largest species present and hence they receive our differential attention. As an example, most vegetation classification schemes are based, in large part, on the woody species present (e.g., U.S. National Vegetation Classification). In addition, because these plants are relatively long-lived, they are used as a benchmark or proxy for assessing the "health" of a riparian system or success of a restoration project. The main focus of many riparian restoration projects is planting woody species or adjusting hydrology to encourage their natural regeneration (e.g., Dreesen et al. 2002). Thus, a focus on avian species seems to dovetail nicely with a corresponding viewpoint of the importance of the woody component of riparian habitats.

Although birds are diverse, their influence on the structure and function of riparian ecosystems may be relatively weak compared to other taxonomic groups. There are several reasons for this. First, due to territoriality and high vagility, birds tend to be relatively sparsely distributed. As a result of this rarity, and in combination with their relatively small body size, birds usually account for but a minor proportion of the animal biomass in a given area (Turner and Chew 1981). Consequently, birds have relatively little influence on higher trophic levels. On the other hand, due to the relatively high diversity of birds, their greatest ecosystem influence might be a consequence of some foraging behaviors (Whelan et al. 2015). For instance, granivores are considered important agents of seed predation and dispersal, even though when compared directly with rodents, the impacts of birds are relatively weak (e.g., Hulme and Benkman 2002; Mares and Rosenzweig 1978). Some birds, such as hummingbirds, transfer pollen that benefits some plants. Insectivores may help regulate invertebrate communities, while raptors may help regulate some rodent communities (Whelan et al. 2015). Other services provided by some kinds of birds, such as creating cavity holes in trees by woodpeckers, while important, are of more minor impact to the overall ecosystem.

Although the restoration of riparian habitats is considered important for the maintenance of bird diversity (Gardner et al. 1999), the taxonomic bias on birds focuses attention on species that may be only weakly linked to overall ecosystem function or may cause other important aspects of ecosystem function to be missed. In contrast, other elements of the riparian zone, in particular small mammals, have been mostly overlooked and yet they may have more strong influence on overall ecosystem structure and function. Consequently, riparian habitat restorations without consideration of small mammals, and the riparian habitat elements they require, will be incomplete and may not provide the full range of ecosystem services.

Terrestrial Small Mammal Riparian Communities

In western North America, terrestrial small mammals strongly associated with riparian zones include members of the order Eulipotyphla (e.g., shrews [Soricidae], moles [Talpidae]); Rodentia (e.g., deer mice [Cricetidae], cotton rats [Sigmodontidae], voles [Arvicolidae], jumping mice [Zapodidae]); and some small members of the orders Carnivora (e.g., short-tailed weasel [*Mustela erminea*; Mustelidae]) and Lagomorpha (e.g., some *Sylvilagus*). These species can be categorized into two groups: those that are relatively specialized on riparian ecosystems and those that become disproportionately abundant within riparian ecosystems. Examples of species in the first category, the riparian specialists, include: marsh shrew (*Sorex bendirii*), cordilleran water shrew (*Sorex navigator*), water vole (*Microtus richardsoni*), muskrat (*Ondatra zibethicus*), and some jumping mice (e.g., *Zapus luteus luteus* and *Z. hudsonius preblei*). Examples of species in the much larger second category include: montane shrew (*Sorex monticola*), Townsend's mole (*Scapanus townsendii*), white-footed deermouse (*Peromyscus leucopus*), North American deermouse (*Peromyscus maniculatus*), western harvest mouse (*Reithrodontomys megalotis*), hispid cotton rat (*Sigmodon hispidus*), tawny-bellied cotton rat (*S. fulviventer*), California vole (*Microtus californicus*), long-tailed vole (*Microtus longicaudus*), montane vole (*Microtus montanus*), meadow vole (*M. pennsylvanicus*), white-footed vole (*Phenacomys albipes*), western heather vole (*Phenacomys intermedius*), western jumping mouse (*Zapus princeps*), Pacific jumping mouse (*Zapus trinotatus*), brush rabbit (*Sylvilagus bachmani*), and short-tailed weasel.

In addition, other species that are more typical of other vegetation types may also occur in the riparian zone when the communities closely abut (e.g., small order stream in coniferous forest), such as the cinereus shrew (*Sorex cinereus*), mountain cottontail (*Sylvilagus nuttalii*), least chipmunk (*Neotamias minimus*), red squirrel (*Tamiasciurus hudsonicus*), Botta's pocket gopher (*Thomomys bottae*), northern pocket gopher (*T. talpoides*), Mexican woodrat (*Neotoma mexicana*), and southern red-backed vole (*Myodes gapperi*). In the Mountain West, riparian small mammal communities become more unique in comparison with uplands as elevation increases (Olson and Knopf 1988). Finally, it should be recognized that many species exhibit geographic variation in their habitat associations such that a species may be a riparian associate in a more mesic region, but become more of a riparian specialist in a more xeric region (e.g., California vole; Conroy et al. 2016).

Although terrestrial small mammals are important members of riparian communities, they have been mostly overlooked both in terms of knowledge of their ecology and focus in riparian restorations (but see for example Rickel 2005b and Golet et al. 2008). There are a number of reasons for this. First, small mammals tend to be relatively difficult to study. Most are nocturnal and live in burrows or other hidden places such that they are not easily observed. Study usually requires capturing individuals, which is labor intensive and necessitates specialized equipment, permits, and expertise. Because most small mammals have generalized, nondescript body plans, accurate identifications can be difficult, often requiring examination of cranial characters (necessitating collection and preparation of series of museum specimens) or DNA (which is expensive and requires specialized equipment).

These difficulties largely preclude the public, and even many scientists, from informal or formal study of these organisms. Thus, relative to some other taxonomic groups, such as birds, fishes, and big game mammals, there are relatively few scientists that specialize on studying small mammals. Perhaps more importantly, most of these species, with the exception perhaps of some squirrels, simply lack charisma or perceived value (e.g., few are considered game species). To many people, these "rats and mice" are simply vermin. Consequently, no public organizations that promote these species exist and there is limited funding and political will. Taken together, these factors cause knowledge about riparian small mammals to lag far behind other species. For instance, the recent comprehensive Beaver Restoration Guidelines reference manual (Pollock et al. 2015), which reviewed the ecological impacts of beavers on other organisms, included sections on birds, fishes, and invertebrates, but did not include mention of ecological impacts to other mammals.

Ecological Roles of Riparian Small Mammals

The ecological roles of most small mammals have been poorly studied. Yet, limited research indicates that the ecosystem services provided by small mammals are strong and important to diverse ecosystems, including riparian zones. By way of example, I highlight four essential aspects of the role of small mammals in riparian ecosystems, including: (1) dominance of animal biomass, (2) prey base for diverse carnivore communities, (3) influence on soil condition, and (4) influence on plant composition and succession.

Animal Production and Biomass

Although data are limited, small mammals likely constitute the dominant proportion of vertebrate animal production and biomass in healthy riparian systems. For instance, Turner and Chew (1981) found that production of terrestrial small mammals in arid environments of southwestern North America far outweighed production by other groups of animals (in contrast, birds were among the lowest). In part, this is because small mammals, while having small body size compared with other mammals, are on average larger than most other kinds of organisms. In addition, terrestrial small mammals are year-round residents and they have relatively small and overlapping home ranges. For example, home ranges of the meadow vole may be as little as 160 m^2 (Van Vleck 1969).

Further, small mammals are prone to population irruptions that can produce extremely high densities and biomass. Generation of exceptionally high biomass is particularly true for the graminivorous (grass eating) riparian species, including the cotton rats at lower latitudes and elevations and the voles at higher latitudes and elevations; both groups may display population cycles or strong annual variation in population densities (Fagerstone and Ramey 1996; Grant et al. 1982; Rickel 2005b; Taitt and Krebs 1985). For instance, densities during population highs for these species can exceed 369 cotton rats/ha (Guthery et al. 1979) and 7,400 voles/ha (Spencer 1958). Production of small mammals in vole-dominated communities can exceed 5,000 kcal/ha in high quality habitats (Grant et al. 1982).

Small mammal populations are renowned for their volatility (Witmer and Proulx. 2010). Whitford (2002) identified episodic species as those that respond to periods of high primary production with high rates of reproduction and population growth, and hence driving high rates of secondary production. Riparian zones may serve as important refugia for episodic species in arid environments. During wet periods, episodic species experience population growth and immigration into marginal habitats, where they can exhibit explosive growth relative to corresponding dry periods. Thus, population dynamics of small mammals in riparian ecosystems can have far reaching and direct impacts on adjacent terrestrial ecosystems.

Fuel for Predator Communities

The high density and biomass of small mammals that concentrates in healthy riparian zones provides fuel for supporting a diverse predator community that includes hawks, owls, snakes, and myriad mammalian carnivores such as weasels, minks, bobcats, foxes, and coyotes (Hamilton et al. 2015). Starvation is a real and constant threat for many kinds of predators. Consequently, a high threshold of prey abundance is required for many kinds of predators to persist in an area. For instance, weasels have particularly high energy demands due to their active lifestyle and their lean, narrow body plan. Meals pass through their short digestive tracks in just a few hours, meaning they must eat frequently. It has been estimated that long-tailed weasels (*Mustela frenata*) must consume 20−40 percent of their body weight in small mammal prey every day. However, the energetic demands for smaller weasels are even more extreme. For instance, captive least weasels had to eat meals every 2.5 to 3 hours, totaling 5−10 meals per day. Small weasels are not likely to be able to survive more than 24 hours without eating (Gillingham 1984). The energetic demands of females that successfully raise young are even higher. Voles are the main group of small mammals in the temperate zone that can generate the densities and biomass of animal flesh required to support predators that have high energy demands (Frey and Calkins 2013; Rickel 2005b). Thus, it is no surprise that many species of owls also specialize on voles preferential to other kinds of small mammals (e.g., Colvin and McLean 1986).

Exceptionally high abundance of suitable prey is thought to be necessary to permit coexistence of some predators. For instance, short-tailed weasels and long-tailed weasels are sympatric across much of the western United States. However, models indicate that it might not be possible for both species to coexist in a local habitat unless the prey populations are high and diverse (Powell and Zielinski 1983). Riparian zones also provide an important source of alternate prey for more specialized predators such as Canada lynx (*Lynx canadensis*), river otters (*Lontra canadensis*), martens (*Martes* spp.), fishers (*Pekania pennati*), wolverines (*Gulo gulo*), and wolves (*Canis lupus*). Alternate prey serves as a critical resource for these predators during certain seasons or years or by certain demographic groups (e.g., nursing mothers). Thus, small mammals contribute to the diversity of riparian zones, not only through the presence of a unique assemblage of riparian small mammals, but also by supporting diverse predator communities. By supporting diverse predator communities, riparian small mammals provide an important link between the riparian zone and adjacent upland communities.

Soil Condition

Soil is formed over time primarily through the interactions of the parent material, topography, climate, vegetation, and invertebrate animals. However, small mammals also play an important role in the structure and function of soils through their burrowing activities, underground caching of seeds and other plant parts, and decomposition of latrines and carcasses. Most terrestrial small mammals construct subterranean burrows or modify and utilize the burrows constructed by other species of small mammals, at least for some aspects of their life cycle (e.g., hibernacula, maternal nest chambers). Some species, such as the pocket gophers and moles, spend most of their lives within these burrows. Burrowing activity has an important role in improving soil structure by loosening soil particles and in mixing soils by bringing soils from lower strata to the surface, to the extent that sometimes this mixing can obliterate the upper soil horizons (Hendricks 1985). For instance, estimates of soil excavated by pocket gophers can exceed more than 100 Mg/ha (Cox 1990; Grinnell 1923).

Burrow systems also affect the soil climate by enhancing infiltration of oxygen and water. Subterranean chambers made by small mammals to store food caches, or serve as nest sites or latrines, create local concentrations of key limiting nutrients such as salts, nitrogen, phosphorus, and potassium (Hendricks 1985). Finally, like woodpeckers creating tree cavities that may be used by other species, the burrows constructed by small mammals can harbor an array of non-burrowing organisms such as fungi, spiders, amphibians, and snakes, thus supporting overall biodiversity (Scheffer 1945).

Plant Community Composition and Succession

Although understudied, terrestrial small mammals may have a profound impact on the structure and function of plant communities. For instance, Bryce et al. (2013) demonstrated that the long-term impacts of vole burrowing activities and herbivory result in a patchwork of different plant successional stages in riparian systems. Further, small mammals impact the structure and function of plant communities through their predation on seeds and seedlings and concomitantly through the dispersal of seeds and mycorrhizal fungi. Seeds are an important part of the diet of most small mammals, including species such as shrews, which are normally thought of as strictly insectivorous (Hallett et al. 2003). Small mammal seed predators include species such as harvest mice and jumping mice that specialize on harvesting seeds from grasses and other herbaceous plants prior to seed dispersal (e.g., Wright and Frey 2014), as well as species such as chipmunks, pocket mice (e.g., *Chaetodipus* spp.), and deer mice that forage on a wide range of seed types from both herbaceous and woody plants in the seed rain or seedbank.

In the temperate zone, most seed removal is due to small mammals (Hulme and Benkman 2002; Mares and Rosenzweig 1978). Thus, granivory by small mammals can have a profound impact on seed populations, and hence plant communities (Hulme and Benkman 2002). For instance, the extent of small mammal seed predation can be so high (>95 percent of seeds sown) that it can hamper efforts to restore forests and other ecosystems via direct seeding (Hallett et al. 2003). Similarly, seedlings and saplings are also vulnerable to predation by rodents, including those of conifer trees that are especially vulnerable under cover of snow when herbaceous plants are less available (Hallett et al. 2003). Thus, small mammal herbivory tends to impede succession, thereby maintaining early successional habitats that provide favorable food and cover (Davidson 1993).

Few studies have examined the role of mammals in seed dispersal. However, the number of fruit seeds dispersed into a plant population by medium-sized mammals, such as foxes, may be twice that mediated by frugivorous birds (Jordano et al. 2007). Further, although small mammals are efficient predators on some seeds, many also gather, move, and store these seeds in underground burrows. Unrecovered seeds cached by these rodents may be essential to the establishment of some plants (e.g., Hallett et al. 2003; Longland and Ostoja 2013).

Perhaps even more important than the role mammals play in seed dispersal and germination is their crucial relationship with mycorrhizal fungi. Mycorrhizal fungi form symbiotic relationships with the roots of most vascular plants. Growth and survival of many plants is dependent on this relationship, which provides for the uptake of water and nutrients (Molina 1994). Concurrently, mycorrhizal fungi are an important component of the diet for many small mammals, but the spores of these fungi pass through the digestive tracts of the small mammals with no loss in viability (Maser et al. 1978). Thus, small mammals have been implicated as the dominant means for dispersal of mycorrhizal inocula, which in turn must be present to support plants. Small mammals, therefore, may control some aspects of succession.

For instance, an interesting study by Terwilliger and Pastor (1999) concluded that small mammals regulated the succession of trees into "beaver meadows." Beaver meadows are herbaceous dominated ecosystems that form in the silt that is left behind after a beaver dam has been breached and the pond drained. These are exceptionally important habitats, especially in coniferous forest dominated regions, and they can persist for many decades, although an explanation for their longevity was lacking. Terwilliger and Pastor (1999) found that the soils of beaver meadows lacked the mycorrhizal fungi necessary for the growth of conifers and attributed that to long-term inundation of the soils by the former pond. In their study system, the primary consumer of mycorrhizal fungi associated with conifers was the red-backed vole (*Myodes gapperi*), which mostly occurs in forested habitat. In contrast, they speculated that meadow voles, which are associated with the graminoid habitats of the beaver meadows, competitively excluded red-backed voles and their spore containing feces from the meadows. Thus, it was speculated that reestablishment of conifers in the beaver meadows was limited both by patterns of mycorrhizal fungal distribution and by use by small mammals and the competitive interactions among them.

Terrestrial Small Mammal Community Habitat Relationships

Terrestrial small mammals serve as prey for a host of predators, such as snakes, hawks, owls, minks, foxes, bobcats, and bears. Consequently, appropriate concealment cover from predators is one of the most important overriding microhabitat component required for the production of abundant and diverse small mammal communities (e.g., Longland and Price 1991). In riparian ecosystems, these communities are mainly associated with early seral plant communities typified by tall, dense herbaceous ground cover, often in conjunction with riparian shrubs such as willow and alders (e.g., Dickson and Williamson 1988; Golet et al. 2008).

Because these communities are often associated with riparian shrubs, vegetation maps are likely to underestimate the extent of this vegetation type and there are no estimates for the proportion of riparian systems that support herbaceous riparian vegetation. These herbaceous plant communities also provide necessary food for small mammals. Small mammals have high energetic demands and utilize a wide range of foods. Many small mammals eat the seeds of grasses and forbs. Other small mammals, such as the voles and cotton rats, eat the vegetative parts of graminoids, while pocket gophers utilize the roots of herbaceous plants.

In well-developed herbaceous riparian habitats, graminoid food is not limiting, which contributes to potential for exceptionally high biomass of voles and cotton rats. Invertebrates are supported by diverse and abundant riparian vegetation and these are utilized as food by shrews and moles, and to a lesser extent by many rodents. In contrast, late seral riparian vegetation types are dominated by trees (e.g., cottonwood gallery forest) and consequently may have lower densities and diversity of mammals due to the drier soils and lack of adequate ground cover (Andersen and Nelson 1999). Furthermore, in late seral riparian habitats that have been substantially degraded, such as via conversion to monotypes of saltcedar, small mammal communities may be indistinguishable from upland communities (i.e., due to loss of riparian adapted species and invasion by upland species) or become dominated by disturbance adapted species such as deer mice (e.g., Ellis et al. 1997).

Riparian habitats that offer tall, dense, diverse herbaceous vegetation are maximally developed in locations with relatively low topographic relief, low gradient, broad floodplains, high soil moisture, and high exposure to solar radiation (low tree canopy cover or lack of shading by adjacent mountainsides; Dickson and Williamson 1988). To a large extent these characteristics are determined by local landscape features. However, beavers are unique in that their activities can increase the distribution and abundance of riparian characteristics that support early seral stage herbaceous communities. Beavers increase these habitats through a variety of mechanisms, including felling trees, creating dams that retain sediments, creating ponds that kill trees (due to submergence), increasing the area of sub-irrigated soils, storing water that is released as base flows during dry periods or drought, and creation of beaver meadows following abandonment of ponds (McMaster and McMaster 2000; Naiman et al. 1986, 1988; Rosell et al. 2005). For instance, Naiman et al. (1986) found that beaver dams increased the wetted surface area of the channel by several hundred-fold, while in Wyoming the width of riparian zones was 33.9 m in streams with beaver ponds but only 10.5 m in streams without such ponds (McKinstry et al. 2001).

Although research is limited, studies indicate that beaver activities can have a profound impact on small mammal communities. For instance, in Idaho, Medin and Clary (1991) compared riparian small mammal communities in an area within a complex of beaver ponds versus a control reach that did not have beaver ponds. They found that the standing crop biomass (g/ha) of small mammals was about 2.7 times higher at the beaver complex. This was due to exceptionally higher density of shrews and voles in the beaver modified habitats. In addition, the western jumping mouse was only found in the beaver modified habitat. Medin and Clary (1991) attributed differences in small mammal communities to the dense and structurally complex vegetation created by beavers, which provide food and cover. Similarly, in Oregon, Suzuki (1992) found significantly more deer mice (*Peromyscus*), voles in genus *Microtus*, Pacific jumping mice, and certain species of shrews (*Sorex*) on stream reaches occupied by beavers compared to stream reaches lacking beavers. In the American Southwest, beaver dams were implicated as important for the occurrence of the short-tailed weasel, which is of conservation concern (Frey and Calkins 2013), and the Federally endangered New Mexico meadow jumping mouse (*Z. l. luteus*), which is a riparian obligate (Frey and Malaney 2009).

In contrast to the positive influence of beavers on herbaceous habitat and small mammal communities, livestock (and sometimes overabundant native ungulates such as elk [*Cervus elaphus*]) can have a deleterious influence on herbaceous riparian habitats. Although the specific impacts of livestock grazing on riparian ecosystems are dependent on a number of variables and some studies have been based on poorly designed methods (Milchunas and Lauenroth 1999; Sarr 2002), the vast majority of evidence indicates that riparian systems are especially prone to excessive grazing that can lead to a disruption of ecosystem structure and function (e.g., Belsky et al. 1999; Fleischner 2002; Trimble and Mendel 1995). As large-bodied nonnative grazers and browsers, livestock can negatively impact or obliterate herbaceous riparian vegetation through herbage removal, soil compaction, and trampling (Giuliano and Homyack 2004; Johnston and Anthony 2008; Kauffman and Krueger 1984). Once deep-rooted riparian plants have been reduced or eliminated from riparian communities, stream banks can erode and channels can downcut, further exacerbating changes to the riparian plant and animal communities.

Small mammals are sensitive indicators of disturbances and changes to plant communities, particularly changes that impact the herbaceous layer (Fagerstone and Ramey 1996). For instance, in Oregon Moser and Witmer (2000) found significantly higher abundance, species richness, and species diversity of small mammals in ungrazed areas versus areas grazed by elk and cattle, while no differences were exhibited in similar metrics of the bird or plant community. While abundance of some upland or generalist mammal species, such as the North American deermouse, can increase in riparian areas that are grazed, most studies show a marked decrease in diversity and abundance of small mammals in grazed riparian areas. This pattern is especially pronounced for species that are more restricted to these areas such as shrews, voles, cotton rats, harvest mice, and jumping mice (e.g., Fagerstone and Ramey 1996; Frey and Malaney 2009; Medin and Clary 1989; Schulz and Leininger 1991).

For instance, voles select areas with high vegetation cover, which provides concealment from predators, reduces antagonistic interactions among individuals, provides food, facilitates subnivean spaces during winter, and moderates temperature and humidity. A threshold of vegetative cover may be necessary to support a population and allow for population buildups (Fagerstone and Ramey 1996). Consequently, voles tend to be relatively intolerant of livestock grazing that reduces cover, and their populations may be greatly depressed or extirpated in locations where grazing has greatly reduced herbaceous cover (Sullivan and Sullivan 2013).

Besides causing changes to riparian habitats that directly impact small mammal communities, livestock grazing can also influence suitability of riparian habitats for beavers. Beavers prefer herbaceous plants for food, but will use certain deciduous trees and shrubs for food when herbaceous plants are not available, such as under ice in winter (Müller-Schwarze and Sun 2003). In western North America where there are relatively few species of deciduous trees and shrubs to choose from, beavers exhibit a mutualistic relationship with willows, wherein beavers benefit from willows for food and building material, while willows benefit from beavers via the increased area of wetted soil created by their dams and asexual reproduction by resprouting of cut limbs (Kindschy 1989; Peinetti et al. 2009).

As strict herbivores, beavers enter into direct competition with livestock and native ungulates for food. Livestock preferentially graze on herbaceous vegetation during the early part of the growing season but then switch to browsing on willows during the latter part of the growing season (Pelster et al. 2004). Thus, excessive livestock grazing can result in loss of both herbaceous vegetation and willows, creating depauperate riparian zones that resemble upland communities (e.g., Small et al. 2016). A similar process can occur due to abundant native ungulates when top predators have been removed from an ecosystem. For instance, in Yellowstone National Park an increase in beavers occurred after restoration of wolves, likely due to decreased use of riparian zones by elk, which allowed for increased growth of willows and other riparian plants (Ripple and Beschta 2012).

Beavers are sometimes able to exist, at least temporarily, in marginal habitats that appear to offer scant resources for food and building material. In New Mexico for instance, I have observed beavers building dams and living on small order streams at the opening of a narrow sheer-sided canyon in the Chihuahuan Desert, and occurring in other locations where the only available dam building material was saltcedar, sagebrush (*Artemisia*), or cattails (*Typha*). On the Rio Grande in the Chihuahuan Desert, beavers can persist in small isolated pools of water after river flows are shut off by upstream dams (Barela and Frey 2016).

Given that beavers can exist in marginal environments, if conditions are inadequate for beavers, they also are likely inadequate to support healthy small mammal communities. Thus, the status of beavers may suggest the concomitant status of small mammal communities. For example, in New Mexico, Small et al. (2016) found only 38 active primary beaver dams on Federal public lands throughout the State, despite historical efforts to restore the species. The near absence of beavers was attributed to the loss of riparian habitat as a consequence of nearly ubiquitous cattle grazing. Given that riparian habitat conditions are mostly not adequate to support beavers, this suggests that riparian habitats are also mostly not capable of supporting diverse and abundant small mammal communities. The recent listing of a riparian habitat specialist, the New Mexico meadow jumping mouse, as endangered supports this idea and suggests the need for managers to more carefully consider the needs of riparian small mammals (and beavers) in management plans.

Conclusions

Small mammals are an often overlooked but vitally important component of healthy riparian ecosystems. These species provide critical ecosystem services to riparian zones by virtue of their high biomass, support of diverse predator communities, physical alterations of the soil, and regulation of plant communities. Small mammal communities are best developed in riparian systems that provide an abundance of tall, dense, and diverse herbaceous vegetation. Beavers are capable of increasing the capacity of riparian systems to produce these early seral plant communities and hence benefit small mammal communities. In contrast, excessive livestock grazing can disrupt small mammal communities by causing loss of tall, dense, and diverse herbaceous vegetation, and can also limit the capacity of riparian systems to support beavers. This negative synergism can result in riparian ecosystems that are depleted and fail to support critical ecosystem services.

Thus, restoration of full ecosystem services of riparian zones requires consideration of the herbaceous plant and small mammal communities. In contrast, riparian restoration that focuses mainly on woody plants might restore habitats for birds and stabilize stream banks, but may fail to provide full restoration of crucial ecosystem function. Additional research is needed on livestock grazing management that can enhance herbaceous riparian vegetation and thereby support beavers and healthy small mammal communities. In addition, there is need for more research on the roles of small mammals in riparian ecosystem function and the patterns of riparian mammal diversity and abundance in relation to various disturbances and management actions.

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References

Andersen, D.C.; Nelson, S.M. 1999. Rodent use of anthropogenic and ‘‘natural’’ desert riparian habitat, Lower Colorado River, Arizona. Regulated Rivers: Research and Management. 15: 377c393.

Barela, I.A.; Frey, J.K. 2016. Habitat and forage selection by the American beaver (*Castor canadensis*) on a regulated river in the Chihuahuan Desert. Southwestern Naturalist. 61: 286–293.

Bateman, H.L.; Chung-MacCoubrey, A; Finch, D.M.; [et al.]. 2008. Impacts of non-native plant removal on vertebrates along the Middle Rio Grande (New Mexico). Ecological Restoration. 26: 193–195.

Belsky, J.A; Matzke, A; Uselman, S. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. Journal of Soil and Water Conservation. 54: 419–431.

Bowling, G.A. 1941. The introduction of cattle into colonial North America. Journal of Dairy Science. 25: 129–154.

Bryce, S.A.; Hughes, R.M.; Kaufmann, P.R. 2002. Development of a bird integrity index: Using bird assemblages as indicators of riparian condition. Environmental Management. 30: 294–310.

Bryce, R.; van der Wal, R.; Mitchell, R.; [et al.]. 2013. Metapopulation dynamics of a burrowing herbivore drive spatio-temporal dynamics of riparian plant communities. Ecosystems. 16: 1165–1177.

Colvin, B.A.; McLean, E.B. 1986. Food habits and prey specificity of the common barn owls in Ohio. The Ohio Journal of Science. 86: 76–80.

Conroy, C.J.; Patton, J.L.; Lim, M.C.W.; [et al.]. 2016. Following the rivers: Historical reconstruction of California voles *Microtus californicus* (Rodentia: Cricetidae) in the deserts of eastern California. Biological Journal of the Linnean Society. doi: 10.1111/bij.12808.

Cox, G.W. 1990. Soil mining by pocket gophers along topographic gradients in a Mima moundfield. Ecology. 71: 837–843.

Davidson, D.W. 1993. The effect of herbivory and granivory on terrestrial plant succession. Oikos. 68: 23–35.

Dickson, J.G.; Williamson, J.H. 1988. Small mammals in streamside management zones in pine plantations. In: Szaro, R.C.; Severson, K.E.; Patton, D.R., tech. coords. Management of amphibians, and small mammals in North America: Proceedings of the symposium. Gen. Tech. Rep. RM-166. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 375–378.

Dreesen, D.; Harrington, J.; Subirge, T.; [et al.]. 2002. Riparian restoration in the Southwest—Species selection, propagation, planting methods, and case studies. In: Dumrose, R.K.; Riley, L.E.; Landis, T. D., eds. National nursery proceedings—1999, 2000, and 2001. Proc. RMRS-P-24. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 370 p. http://www.nm.nrcs.usda.gov/Programs/pmc/symposium/nmpmcsy03852.pdf

Ellis, L.M.; Crawford, C.S.; Molles, M.C. 1997. Rodent communities in native and exotic riparian vegetation in the Middle Rio Grande Valley of central New Mexico. Southwestern Naturalist. 42: 13–19.

Eubanks, E. 2004. Riparian restoration. Tech. Devel. Prog. 0423 1201-SDTDC. San Dimas, CA: U.S. Department of Agriculture, Forest Service, Technology and Development Program. 136 p. https://wildlife.utah.gov/pdf/riparian.pdf

Fagerstone, K.A.; Ramey, C.A. 1996. Rodents and lagomorphs. In: Rangeland wildlife. Krausman, P.R., ed. Denver, CO: The Society of Range Management. 440 p.

Fleischner, T.L. 2002. Ecological costs of livestock grazing in western North America. Conservation Biology. 8: 629–644.

Frey, J.K.; Calkins, M.T. 2013. Snow cover and riparian habitat determines distribution of the short-tailed weasel (*Mustela erminea*) at its southern range limits in western North America. Mammalia. 78: 45–56.

Frey, J.K.; Malaney, J.L. 2009. Decline of the meadow jumping mouse (*Zapus hudsonius luteus*) in two mountain ranges in New Mexico. Southwestern Naturalist. 54: 31–44.

Gardner, P.A; Stevens, R.; Howe, F.P. 1999. A handbook of riparian restoration and revegetation for the conservation of land birds in Utah with emphasis on habitat types in middle and lower elevations. Publication Number 99-38. Salt Lake City, UT: Utah Division of Wildlife Resources. 48 p.

Gillingham, B.J. 1984. Meal size and feeding rate in the least weasel (*Mustela nivalis*). Journal of Mammalogy. 65: 517–519.

Giullano, W.M.; Homyack, J.D. 2004. Short-term grazing exclusion effects on riparian small mammal communities. Journal of Range Management. 57: 346–350.

Golet, G.H.; Gardali, T.; Howell, C.A; [et al.]. 2008. Wildlife response to riparian restoration on the Sacramento River. San Francisco Estuary and Watershed Science. 6(2) 1–26. http://escholarship.org/uc/item/4z17h9qm.

Grant, W.E.; Birney, E.C.; French, N.R.; [et al.]. 1982. Structure and productivity of grassland small mammal communities related to grazing-induced changes in vegetative cover. Journal of Mammalogy. 63: 248–260.

Grinnell, J. 1923. The burrowing rodents of California as agents in soil formation. Journal of Mammalogy. 4: 137–149.

Guthery, F.S.; Anderson, T.E.; Lehmann, V.W. 1979. Range rehabilitation enhances cotton rats in South Texas. Journal of Range Management. 32: 354–356.

Hallett, J.G.; O'Connell, M.A.; Maguire, C.C. 2003. Ecological relationships of terrestrial small mammals in western coniferous forests. In: Zabel, C.J.; Anthony, R.G., eds. Mammal community dynamics: Management and conservation in the coniferous forests of western North America. New York: Cambridge University Press: 120–156

Hamilton, B.T.; Roeder, B.L.; Hatch, K.A.; [et al.]. 2015. Why is small mammal diversity higher in riparian areas than in uplands? Journal of Arid Environments. 119: 41–50.

Hendricks, D. 1985. Arizona soils. Tucson, AZ: University of Arizona, College of Agriculture. http://www.library.arizona.edu/exhibits/swetc/azso/index.html.

Hulme, P.; Benkman, C.W. 2002. Granivory. In: Herrera C.; Pellmyr, O., eds. Plant-animal interactions: An evolutionary approach. New York: Blackwell Scientific Publications: 132–154.

Johnston, A.N.; Anthony, R.G. 2008. Small-mammal microhabitat associations and response to grazing in Oregon. Journal of Wildlife Management. 72: 1736–1746.

Jordano, P.; Garcia, C.; Godoy, J.A.; [et al.]. 2009. Differential contribution of frugivores to complex seed dispersal patterns. Proceedings of the National Academy of Science. 104: 3278–3282.

Kauffman, J.B.; Krueger, W.C. 1984. Livestock impacts on riparian ecosystems and streamside management implications…A review. Journal of Range Management. 37: 430–438.

Kindschy, R.R. 1989. Regrowth of willow following simulated beaver cutting. Wildlife Society Bulletin. 17: 290–294.

Longland, W.S.; Price, M.V. 1991. Direct observations of owls and heteromyid rodents: Can predation risk explain microhabitat use? Ecology. 72: 2261–2273.

Longland, W.S.; Ostoja, S.M. 2013. Ecosystem services from keystone species: Diversionary seeding and seed-caching desert rodents can enhance Indian ricegrass seedling establishment. Restoration Ecology. 21: 285–291.

Mares, M.A.; Rosenzweig, M.L. 1978. Granivory in North and South American deserts: Rodents, birds, and ants. Ecology. 59: 235–241.

Maser, C.; Trappe, J.M.; Nussbaum, R.A. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology. 59: 799–809.

McKinstry, M.C.; Caffrey, P.; Anderson, S.H. 2001. The importance of beaver to wetland habitats and waterfowl in Wyoming. Journal of the American Water Resources Association. 37: 1571–1577.

McMaster, R.T.; McMaster, N.D. 2000. Vascular flora of beaver wetlands in western Massachusetts. Rhodora. 102: 175–197.

Medin, D.E.; Clary, W.P. 1989. Small mammal populations in grazed and ungrazed riparian habitat in Nevada. Res. Pap. INT-413. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 6 p.

Medin, D.E.; Clary, W.P. 1991. Small mammals of a beaver pond ecosystem and adjacent riparian habitat in Idaho. Res. Pap. INT-445. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 4 p.

Milchunas, D.G.; Lauenroth, W.K. 1999. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs. 63: 327–366.

Molina, R. 1994. The role of mycorrhizal symbioses in the health of giant redwoods and other forest ecosystems. In: Aune, Philip S., tech. coord. Proceedings of the symposium on Giant Sequoias: Their place in the ecosystem and society; 1992 June 23–25, 1992; Visalia, CA. Gen. Tech. Rep. PSW-GTR-151. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 78–81.

Moser, B.W.; Witmer, G.W. 2000. The effects of elk and cattle foraging on the vegetation, birds, and small mammals of the Bridge Creek Wildlife Area, Oregon. International Biodeterioration and Biodegradation. 45: 151–157.

Müller-Schwarze, D.; Sun, L. 2003. The beaver: Natural history of a wetlands engineer. Ithaca, NY: Cornell University Press. 190 p.

Naiman, R.J.; Johnston, C.A.; Kelley, J.C. 1988. Alteration of North American streams by beaver. Bioscience. 38: 753–762.

Naiman, R.J.; Melillo, J.M.; Hobbie, J.E. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology. 67: 1254–1269.

Ohmart, R.D.; Anderson, B.W. 1986. Riparian habitats. In: Cooperrider A.Y.; Boyd R.J., Stuart, H.R., eds. Inventory and monitoring of wildlife habitat. Denver, CO: U.S. Department of the Interior, Bureau of Land Management: 169–199.

Olson, T.E.; Knopf, F.L. 1988. Patterns of relative diversity within riparian small mammal communities, Platte River Watershed, Colorado. In: Szaro, R.C.; Severson, K.E.; Patton, D.R., tech. coords. Management of amphibians, and small mammals in North America: Proceedings of the symposium. Gen. Tech. Rep. RM-166. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, 379–386.

Peinetti, H.R.; Baker, B.W.; Coughenour, M.B. 2009. Simulation modeling to understand how selective foraging by beaver can drive the structure and function of a willow community. Ecological Modelling. 220: 998–1012.

Pelster, A.J.; Evans, S.; Leininger, W.C.; [et al.]. 2004. Steer diets in a montane riparian community. Journal of Range Management. 57: 546–552.

Pollock, M.M.; Lewallen, G.; Woodruff, K.; [et al.], eds. 2015. The beaver restoration guidebook: Working with beaver to restore streams, wetlands, and floodplains. Version 1.0. Portland, OR: United States Fish and Wildlife Service. 199 p. http://www.fws.gov/oregonfwo/ToolsForLandowners/RiverScience/Beaver.asp

Polvi, L.E.; Wohl, E. 2013. Biotic drivers of stream planform: Implications for understanding the past and restoring the future. BioScience. 63: 439–452.

Powell, R.A.; Zielinski, W.J. 1983. Competition and coexistence in mustelid communities. Acta Zoologica Fennica. 174: 223–227.

Queheillalt, D.M.; Morrison, M.L. 2006. Vertebrate use of a restored riparian site: A case study on the Central Coast of California. Journal of Wildlife Management. 70: 859–866.

Rich, T.D. 2002. Using breeding land birds in the assessment of western riparian systems. Wildlife Society Bulletin. 30: 1128–1139.

Rickel, B. 2005a. Wildlife. In: Finch, D.M., ed. Assessment of grassland ecosystem conditions in the Southwestern United States: Wildlife and fish, volume 2. Gen. Tech. Rep. RMRS-GTR-135-vol. 2. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 1–12.

Rickel, B. 2005b. Small mammals, reptiles, and amphibians. In: Finch, D.M., ed. Assessment of grassland ecosystem conditions in the Southwestern United States: Wildlife and fish, volume 2. Gen. Tech. Rep. RMRS-GTR-135-vol. 2. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 35–70.

Ripple, W.J.; Beschta, R.L. 2012. Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. Biological Conservation. 145: 205–213.

Rosell, F.; Bozser, O.; Collen, P.; Parker, H. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. Mammal Review. 35: 248–276.

Sarr, D.A. 2002. Riparian livestock exclosure research in the western United States: A critique and some recommendations. Environmental Management. 30: 516–526.

Scheffer, T.H. 1945. Burrow associations of small mammals. The Murrelet. 26: 24–26.

Schultz, T.T.; Leininger, W.C. 1991. Nongame wildlife communities in grazed and ungrazed montane riparian sites. Great Basin Naturalist. 51: 286–292.

Shafroth, P.B.; Cleverly, J.R.; Dudley, T.L.; [et al.]. 2005. Control of *Tamarix* in the western United States: Implications for water salvage, wildlife use, and riparian restoration. Environmental Management. 35: 231–246.

Small, B.A.; Frey, J.K.; Gard, C.C. 2016. Livestock grazing limits beaver restoration in northern New Mexico. Restoration Ecology. 24: 646–655.

Spencer, D.A. 1958. Biological aspects of the 1957-58 meadow vole irruption in the Pacific Northwest. Special Report. Denver, CO: U.S. Fish and Wildlife Service, Denver Wildlife Research Laboratory. 9 p.

Sullivan, T.P.; Sullivan, D.S. 2013. Fertilisation, cattle grazing and voles: Collapse of meadow vole populations in young forests? Wildlife Research. 41: 367–378.

Suzuki, N. 1992. Habitat classification and characteristics of small mammals and amphibian communities in beaver-pond habitats of the Oregon Coast Range. Thesis. Corvallis, OR: Oregon State University. 91 p.

Taitt, M.J.; Krebs, C.J. 1985. Population dynamics and cycles. In: Tamarin, R.H., ed. Biology of New World Microtus. American Society of Mammalogists Special Publication. 8: 567–620.

Terwilliger, J.; Pastor, J. 1999. Small mammals, ectomycorrhizae, and conifer succession in beaver meadows. Oikos. 85: 83–94.

Trimble, S.W.; Mendel, A.C. 1995. The cow as a geomorphic agent—A critical review. Geomorphology. 13: 233–253.

Turner, F.B.; Chew, R.M. 1981. Production by desert animals. In: Goodall, D.W.; Perry, R.A., eds. Arid-land ecosystems: Volume 2, structure, functioning and management. New York, NY: Cambridge University Press: 199–260.

Van Vleck, D.B. 1969. Standardization of *Microtus* home range calculation. Journal of Mammalogy. 50: 69–80.

Weber, D.J. 1971. The Taos trappers: The fur trade in the far Southwest, 1540–1846. Norman, OK: University of Oklahoma Press. 228 p.

Whelan, C.J.; Şekercoiğulu, Ç; Wenny, D.G. 2015. Why birds matter: From economic ornithology to ecosystem services. Journal of Ornithology. 156(1): 227–238. doi: 10.1007/s10336-015-1229-y.

Whitford, W.G. 2002. Ecology of desert systems. San Diego, CA: Academic Press. 343 p.

Witmer, G.; Proulx, G. 2010. Rodent outbreaks in North America. In: Singleton, G.R; Belmain, R., Brown, P.R.; [et al.], eds. Rodent outbreaks: Ecology and impacts. Los Banos, Philippines: International Ride Research Institute: 253–267.

Wright, G.D.; Frey, J.K. 2014. Herbeal feeding behavior of the New Mexico meadow jumping mouse (*Zapus hudsonius luteus*). Western North American Naturalist. 74: 231–235.

Young, J.S.; Ammon, E.M.; Weisberg, P.J.; [et al.]. 2013. Comparison of bird community indices for riparian restoration planning and monitoring. Ecological Indicators. 34: 159–167.