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SMALL MAMMALS WITHIN RIPARIAN HABITATS OF A REGULATED AND UNREGULATED ARIDLAND RIVER

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ABSTRACT.—In northwestern Colorado, flow regulation on the Green River has created a transitional plant community that features encroachment by upland vegetation into cottonwood *(Populus fremontii)*-dominated, riparian forest on topographically high floodplain sites and reduced cottonwood regeneration on low floodplain sites. To assess how these changes might have affected small mammal distributions, in 1994 and 1995 we live-trapped during periods surrounding spring flooding at 3 sites: above and below the confluence of the regulated Green River and at the ecologically similar, but unregulated, Yampa River (reference site). More species were captured at the most regulated site along the Green River above its confluence with the Yampa River. Within sites, more species were captured in riparian habitats than adjacent upland habitats. Despite river regulation-induced habitat changes, we did not detect changes in species distributions within low and high floodplain habitat for *Peromyscus maniculatus* or *Microtus montanus,* but changes may have occurred for *Dipodomys ordii.* The total effect of regulation-induced habitat change on small mammal populations may not be fully revealed until current, mature cottonwood forests disappear and associated woody debris decomposes.

Key words: small mammals, riparian, river regulation, Peromyscus maniculatus, Dipodomys ordii, Microtus montanus, *Green River, Yampa River.*

In arid regions riparian zones are more productive than adjacent uplands due to relatively high soil moisture, greater nutrient content of alluvial soils, and higher rates of gaseous exchange facilitated by flowing water (Brinson et al. 1981). In addition, riparian corridors constitute an inherent edge in the landscape, thus contributing to between-habitat (beta) and regional (gamma) diversity (Logan et al. 1985, Naiman et al. 1993). Although the disproportionately high value of riparian habitat within the arid West has been documented for birds (Stevens et al. 1977, Knopf 1985) and reptiles and amphibians (Brode and Bury 1984, Warren and Schwalbe 1985), its value to small mammals is less clear. For example, Boeer and Schmidly (1977) found lower species richness for small mammals in riparian habitats than in upland habitats of south Texas, but Szaro and Belfit (1987) found the opposite in south central Arizona. In western Arizona along the lower Colorado River, Andersen (1994) found support for the hypothesis that riparian sites provide source habitat for most small mammal species, but Ellison and van Riper (1998) in central Arizona and Hanley and Barnard (1999) in Alaska found no such evidence.

Agricultural and municipal demands for water have led to dam and reservoir construction that has left few western watersheds unregulated. A recent consequence of water management has been an increase in research into the effects of altered hydrology on riparian ecosystems (Nilsson and Dynesius 1994, Jansson et al. 2000). However, little research has focused on linkages between hydrology and the structure or dynamics of small mammal assemblages (Andersen and Cooper 2000). Despite its potential importance in understanding effects of regulation, a basic understanding of the linkages between small mammals and the structure and functioning of aridland riparian ecosystems is lacking. Our objective was to assess changes in the distributions of small mammals, principally the most abundant species (deer mouse, *Peromyscus maniculatus;* Ord's kangaroo rat, *Dipodomys ordii;* and montane vole, *Microtus montanus*) within riparian habitats at 3 sites that differed primarily in the level of river regulation.

STUDY AREAS

Three alluvial valleys along the Green and Yampa Rivers in northwestern Colorado and

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northeastern Utah were chosen for study. Deerlodge Park (DL), 1634 m elevation, is located on the Yampa River, 75 river-km above its confluence with the Green River; Brown's Park (BP), 1707 m elevation, is located on the Green River, 68 river-km below Flaming Gorge Dam and 34 river-km above its confluence with the Yampa River; and Island Park (IP), 1510 m elevation, is located on the Green River, 21 river-km below the confluence (Fig. 1). The Yampa River is one of the last relatively free-flowing rivers in the Colorado River basin (Cooper et al. 1999), but since 1963 the creation of Flaming Gorge dam has regulated the Green River (Fig. 2). From 1922 to 1994, both rivers along these reaches averaged similar daily discharge rates, 59 and 56 $m^3 \cdot sec^{-1}$ for the Yampa River and Green River, respectively (Fig. 1). Domestic livestock grazing has occurred at all sites, but levels are unknown and we assume that they were comparable at all sites in the past. Currently, grazing is regulated at BP and has been prohibited at IP and DL since ~1980. Some trespass grazing occurs at DL.

Riparian vegetation was probably quite similar in composition and structure within their alluvial reaches (Hayward et al. 1958, Cooper et al. 1999, Merritt and Cooper 2000). Because of reductions in both flood flows and river sediment load, most of the Green River floodplain is no longer subject to extreme disturbance events. Thus, vegetation patterns above their confluence differ today and habitats previously maintained via flooding potentially no longer exist; e.g., higher floodplain soils are never inundated, and plant communities are becoming more upland-like (Merritt and Cooper 2000).

We divided riparian areas at each study site into 2 topographic zones reflecting the frequency of flooding. "Low floodplain" consisted of the lowest areas, where substrate condition and vegetation indicated flooding was essentially occurring every other spring. "High floodplain" consisted of adjacent, higher areas that were flooded to a varying extent at intervals longer than experienced on the low floodplain, with the lower boundary clearly delimited by a steep gradient in vegetation density and/or topography. High floodplain was bounded from above by upland habitat, areas that were never inundated. For Green River sites, we delineated historic low and high floodplains on the basis of substrate combined with current topographic features and, for BP sites, vegetation conditions in 1938 aerial photographs. IP is affected by flows on the Yampa and Green Rivers, and thus the influence due to regulation is intermediate between that at DL and BP.

Vegetation types on the low and high floodplains of IP and DL reaches were more similar to each other than to the vegetation of similar reaches at BP. Low floodplain at DL included areas of bare sand, areas containing smaller size-classes of cottonwood (*Populus fremontii*) and willow (*Salix* spp.), and a large variety of annual forbs, whereas IP had less bare sand, fewer willows, and some tamarisk (*Tamarix ramosissima*). Consistent, year-round flows at BP (Fig. 2) have resulted in an artificially high water table in the low floodplain at BP and thus a more hydrophytic plant community of grasses, sedges (*Carex* spp.), and rushes (*Juncus* spp.). Cottonwood gallery forest with an understory of grasses dominated the high flooplain at all sites. At BP tamarisk grew along the lower edge of the historic, high floodplain while desert shrubs such as rabbitbrush (*Chrysothamnus viscidiflorus*), greasewood (*Sarcobatus vermiculatus*), and sage (*Artemisia tridentata*) were evident. Sage, greasewood, and saltbush (*Atriplex* spp.) shrubs dominated all upland sites.

MATERIALS AND METHODS

Capture-recapture trapping occurred at all sites in 1994 and 1995 (Falck 1996). Trapping occurred only after spring runoff in 1994. In 1995 trapping occurred prior to, during, and after spring runoff and was used to determine species distribution.

In 1994 we established 2 trapping grids at BP and DL. Sherman live-traps (3 × 3.5 × 9 inches) were placed adjacent to the river at BP and DL sites in 14 × 14 grids with 7-m spacing. At the IP site a single 13 × 15 grid configuration was used with 15-m spacing. Longer traps (3 × 3.5 × 12 inches) were used in portions of the grid where *D. ordii* were likely present. We trapped each site once for a period of 4 days between 6 July and 9 August. Traps were baited in the evening with rolled oats and peanut butter and checked the following morning. Polystyrene fiberfill provided insulation for captured animals. Species, sex, age, reproductive condition, mass, physical condition, and trap location were recorded

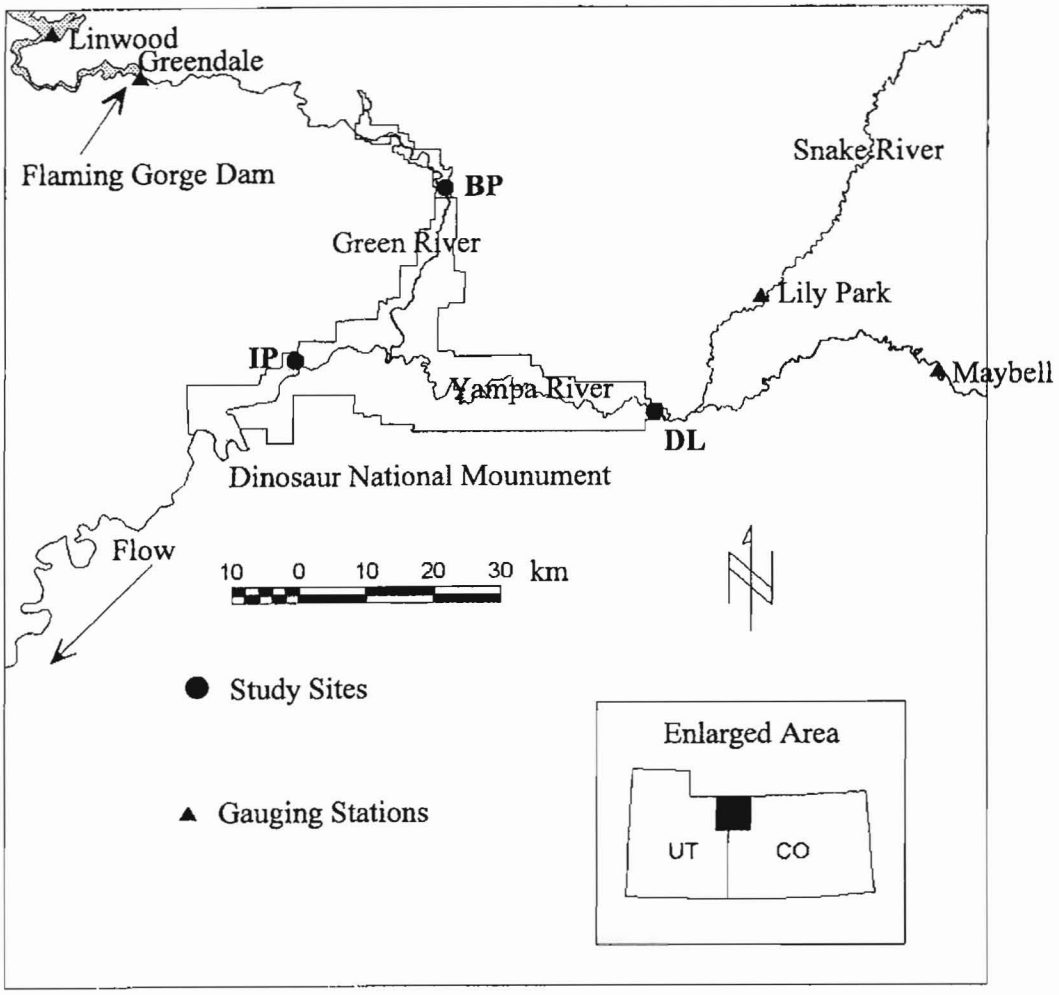

Fig. 1. Study sites along the Green and Yampa Rivers in Colorado and Utah.

upon capture. Captured animals were uniquely numbered with ear tags and released at the capture location. The Colorado State University Animal Care and Use Committee approved the trapping protocol (#94-084A-01).

In 1995 we expanded the 4 grids at BP and DL to 15-m spacing to encompass a larger portion of the riparian zone and to include adjacent upland habitat. In addition, we shifted 1 grid at DL downstream to increase coverage of the low floodplain and adjusted the configuration to 12 × 17. Traps were also added to the IP grid, bringing its configuration to 13 × 17. Due to the configurations of the riparian zones at each site, we felt it was more important to maximize inclusion of riparian habitat than to conform to a standard grid size. Within all configurations, we maintained a similar number of traps per grid.

Four trapping sessions were conducted prior to, during, and after the 1995 spring runoff with the exception of IP, which was inaccessible during the pre-flood session. The number of trapping occasions per session varied from 2 to 6 trap-nights depending on weather conditions. During sessions 2 and 3 (spring runoff), DL grids were adjusted with changing water levels to maintain consistent trapping effort and to increase the probability of capturing animals that had moved as a result of flooding. As traps within the low floodplain were inundated during the spring runoff, they were relocated to the sides of the grid. These grids were adjusted from 12 × 17 to 9 × 23 and from

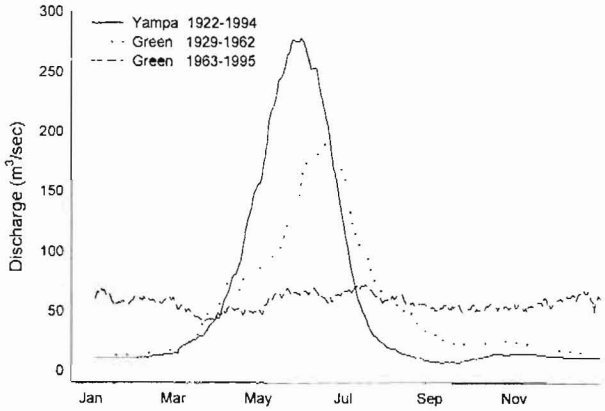

Fig. 2. Historic flow discharges on the Green and Yampa Rivers near Brown's Park National Wildlife Refuge, Colorado, and Deerlodge Park, Colorado.

14 × 14 to 10 × 20 at high water for DL grids 1 and 2, respectively. The process was reversed as floodwaters receded. Portions of the IP grid that were located on the channel floor (22 traps) were not trapped during the flood period.

We used the 1995 capture-recapture data to compare species distributions as a function of site (DL, BP, IP), period (pre-flood, during-flood, post-flood), and habitat (low floodplain, high floodplain, upland). Trapping in 1994 occurred only after spring runoff and was used as a reference to the 1995 data. *Peromyscus maniculatus, D. ordii,* and *M. microtus* provided sufficient captures among sites for comparison. Partitioning of the data sets by habitat resulted in small sample sizes that were inappropriate for population estimation (Otis et al. 1978), and so we report the number of individuals captured per 100 trap-nights for each species.

RESULTS

We trapped a greater number of species at Brown's Park (11) than at either Deerlodge Park (7) or Island Park (7; Table 1). Further, more species were captured within riparian habitats (low + high floodplain) of BP sites (9) than within riparian habitats of DL (7) and IP (6) sites. Differences were primarily due to captures of *Onychomys leucogaster, Tamias dorsalis, Spermophilus lateralis,* and *Sorex monticolus* in high floodplain habitats of BP sites.

Reithrodontomys megalotis was captured solely in riparian habitats at all 3 sites with the exception of 2 captures in upland habitat at DL (within 1 trap station of riparian habitat). With the exception of some captures in BP where downed trees protruded into upland habitat, captures of *Neotoma cinerea* and *Tamias minimus* were restricted to high floodplain habitats where the majority of mature cottonwood trees and woody debris were found.

Dipodomys ordii was captured primarily within open areas of high floodplain habitats at BP sites with only a few captures in the historic, low floodplain. In contrast, *D. ordii* was captured primarily in upland and low floodplain habitats at DL sites with few captures in high floodplain habitats. At IP, *D. ordii* was captured in all habitats in 1994 but not at all in 1995.

There was more variation in 1995 captures of *P. maniculatus* by site than between trapping periods or habitats (Table 2). Relatively fewer deer mice tended to be captured at IP. Captures of individuals varied more between periods for the low and high floodplains and were fairly consistent by periods in the upland.

Captures of *D. ordii* in 1995 varied by site, period, and habitat (Table 2). Compared to other sites, captures at DL were consistently greater in all periods, while at IP no kangaroo rats were captured in 1995. Few captures of *D. ordii* occurred after the post-spring runoff period at DL, and captures at BP during the same period declined to zero.

For *M. montanus,* captures varied little by site, period, or habitat (Table 2). Few montane

TABLE 1. Species captured (X) by habitat during 1994 and 1995 along the Green River at Brown's Park (BP) and Island Park (IP), and along the Yampa River at Deerlodge Park (DL).

	Low floodplain						High floodplain						Upland					
	BP		DL		IP		BP		DL		IP		BP		DL		IP	
Species	94	95	94	95	94	95	94	95	94	95	94	95	94	95	94	95	94	95
Dipodomys ordii	X	X	X	X	X		X	X	X	X	X		–[a]		–	X	X	
Microtus montanus	X	X	X		X	X	X	X	X	X	X	X	–	X	–	X		X
Neotoma cinerea										X			–	X	–		X	
Onychomys leucogaster								X					–	X	–			
Perognathus parvus					X						X	X					X	X
Peromyscus maniculatus	X	X	X	X	X	X	X	X	X	X	X	X	–	X	–	X	X	X
Peromyscus trueii				X			X		X	X		X	–		–	X		
Reithrodontomys megalotis	X	X	X		X		X	X	X	X	X		–		–	X		
Spermophilus lateralis							X	X					–		–			
Sorex monticolus		X						X					–	X	–			
Tamias dorsalis													–	X	–			
Tamias minimus							X	X		X			–	X	–			
TOTAL SPECIES	4	5	4	3	5	2	7	8	5	7	5	4	–	7	–	5	4	3

[a]Habitat was not sampled.

TABLE 2. Individuals captured per 100 trap-nights (and trap-nights in parentheses for *Peromyscus maniculatus*, which are identical for other species) for *P. maniculatus*, *Dipodomys ordii*, and *Microtus montanus* along Green (Brown's Park, BP; Island Park, IP) and Yampa River sites (Deerlodge Park, DL) in 1995 in northwestern Colorado and northeastern Utah. Captures at each site are categorized by habitat (low floodplain, high floodplain, and upland) and by capture period (1, pre-spring flooding; 2, during spring flood; 3, post-spring flood).

Species	Low floodplain			High floodplain			Upland site		
Site	1	2	3	1	2	3	1	2	3
P. maniculatus									
DL	5.3 (582)	15.2 (46)	12.5 (520)	6.2 (1231)	7.3 (100)	14.2 (110)	6.1 (527)	12.2 (541)	8.9 (304)
BP	17.9 (223)	14.2 (204)	20.0 (180)	0.7 (1402)	1.5 (1139)	2.5 (1052)	7.9 (504)	7.6 (419)	7.7 (336)
IP	1.5 (134)	5.3 (19)	4.0 (50)	1.3 (896)	1.9 (739)	1.9 (750)	2.8 (288)	3.3 (240)	2.9 (240)
D. ordii									
DL	11.0	2.2	1.2	1.1	0.9	0.3	1.5	0.9	1.3
BP	3.1	0.0	0.0	0.2	0.3	0.0	0.0	0.0	0.0
IP	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
M. montanus									
DL	0.0	0.0	0.0	0.1	0.5	0.6	0.2	0.4	0.0
BP	4.0	12.7	8.3	0.5	0.5	1.6	0.2	1.9	1.2
IP	0.0	0.0	6.0	0.9	4.9	5.6	0.3	0.4	0.4

voles were captured at DL, with slightly more captures occurring at BP than IP. In general, more captures occurred during and after spring flooding. BP had greater numbers of captures in the low and high floodplain versus the upland, whereas IP had most captures in the high floodplain with relatively few in other habitats. There were no captures at DL in the low floodplain; most captures occurred in the high floodplain.

DISCUSSION

Researchers have examined small mammal communities in existing riparian habitats along regulated rivers (Szaro and Belfit 1987, Ellis et al. 1997) and in partially restored habitats (Andersen 1994, Andersen and Nelson 1999). Unfortunately, comparative studies of small mammal communities in regulated versus unregulated river systems of the south-

western U.S. have been limited. One reason is the lack of unregulated reference sites. Jansson et al. (2000) compared the vegetation of regulated and unregulated rivers, but our literature search found no study directly comparing small mammal communities of regulated and unregulated rivers (see Nilsson and Dynesius 1994 for a review of vertebrate studies associated with river regulation). We did have spatial replication within 2 of our sites, DL and BP, but our study lacks true replication; i.e., only 1 regulated river and 1 unregulated river were sampled. Consequently, our inferences are limited to sites studied. Unfortunately, there is no other large, unregulated river within the Colorado River basin; thus, inferences will always be limited.

More species were captured at our most regulated site, BP, than at the unregulated and intermediate sites, DL and IP, respectively. More species were captured in riparian habitats (low + high floodplain) than in upland habitat at all sites. Our finding agrees with studies in Oregon (Anthony et al. 1987, Doyle 1990, McComb et al. 1993), Wyoming (Jenniges 1991), and Arizona (Szaro and Belfit 1987), but disagrees with a study in south Texas (Boeer and Schmidly 1977). No species was captured exclusively in riparian habitats, although 3 species (*R. megalotis*, *N. cinerea*, and *T. minimus*) were caught primarily in riparian habitats.

No changes in species distributions in response to regulation-induced vegetation changes were detected for *P. maniculatus* and *M. microtus*, but changes may have occurred for *D. ordii*. In 1994 greater numbers of *D. ordii* were captured at BP in the high floodplain (5.74 captures · 100 trap-nights^{-1}) than at DL and IP (0.97 and 1.28, respectively). Tall, dense grasses characterized high floodplain habitats at DL and IP sites in 1994 and 1995. Conversely, the upper floodplain at BP in 1994 was more open, a condition that favors the saltatorial locomotion of kangaroo rats. Merritt and Cooper (2000) suggest that a reduction in flood frequency due to regulation contributes to this condition. In 1995 a region-wide decline in *D. ordii* occurred and although slightly greater numbers of *D. ordii* were captured in the upper floodplain at DL compared to BP (Table 2), we attribute some of the smaller numbers in the BP upper floodplain to habitat changes caused by increased grasses and less open habitat due to much greater spring precipitation in 1995 (26 and 17 cm at DL and BP, respectively, from February to April) than in 1994 (6 and 7 cm). The uplands sampled at DL were relatively open, younger stands created by a fire in 1977 (S. Petersburg, National Park Service, unpublished data) whereas uplands at BP were characterized by dense stands of mature sage and greasewood, and these differences may have contributed to the lack of *D. ordii* captures at BP.

Five *Sorex monticolus* were captured in livetraps at BP. Other shrew species may have been present but not detected, but a complete assessment of small mammal species would require pitfall traps, especially for species such as *Notiosorex*, *Sorex*, and *Thomomys* (Williams and Braun 1983). A pilot study using pitfall sampling in an approximately 50 trap-day effort at 3 DL locations in the high floodplain failed to detect any shrews (D. Andersen unpublished data). Certainly, our inference is limited to small mammals susceptible to our trapping methods. At BP we did see evidence of *T. talpoides* and caught one in the historic low floodplain, but at IP and DL we saw no physical evidence (i.e., soil mounds or collapsed tunnels) of *Thomomys*.

Olson and Knopf (1988), comparing small mammal species between riparian and upland habitats as a function of elevation along the South Platte watershed in northern Colorado, found as we did that *P. maniculatus*, an ecological generalist, dominated their lowest elevation riparian site (1200 m compared to our ~1600 m). Andersen et al. (2000) studied flood-induced movement of small mammals at our sites and considered most riparian species at these sites to be facultative rather than obligate riparian species. They noted that only the smaller-sized, obligate riparian species present elsewhere in the Green River basin, e.g., *Microtus richardsoni* and *Sorex palustris*, were absent. All species that we captured can also be found away from streams. Andersen et al. (2000) suggest that whereas obligate riparian small mammals may be associated with headwater streams, none in the western U.S. can cope with the large environmental gradients and expanses of vegetation-free channel margin produced by aridland rivers that are subject to large spring floods.

Large flood events are necessary to maintain plant community composition and structure (particularly the presence of mature cottonwood) of high floodplain habitats (Fenner

et al. 1985, Auble et al. 1994, Cooper et al. 1999, Merritt and Cooper 2000). Conversely, flow regulation may potentially affect small mammal communities by altering habitat (Andersen 1994, Andersen and Nelson 1999) and by changing species movement and survival patterns (Andersen et al. 2000). Regulation has not dramatically changed small mammal species assemblages on the Green River, but increases in downed, woody debris due to stress on large gallery cottonwoods seem to have augmented habitats for species such as *T. minimus* and *N. cinerea*. Although neither species is a riparian obligate, the functional role of each in this floodplain community may be important, e.g., through seed dispersal (Vander Wall 1993).

The current riparian vegetation at BP is transitional in the sense that, in the absence of periodic inundation or even a relatively shallow water table, high floodplains will eventually lack trees and convert to something close to upland (Merritt and Cooper 2000). Loss of cottonwood gallery forests may have significant impacts because live and dead cottonwoods provide foraging cover, den sites, and food resources. Cottonwood saplings in the low floodplain at DL provide an intermediate habitat that is now rare at BP. Lack of cottonwood could potentially favor *R. megalotis* and *M. montanus*, which were predominantly captured in dense grassland habitats. With reduced cottonwood regeneration and recruitment at regulated sites, the full effect of regulation on small mammal assemblages may not be completely revealed until current mature cottonwoods are dead and their woody debris lost from the system. In fact, abundance of some small mammals species may increase as mature trees die and woody debris is temporarily increased.

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