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Small Mammals in portions of Great Basin National Park Susceptible to Groundwater Withdrawal: Diversity and Stable Isotope Perspectives

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Small Mammals in portions of Great Basin National Park Susceptible to

Groundwater Withdrawal: Diversity and Stable Isotope Perspectives

by

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As chair of the candidate's graduate committee, I have read the thesis of Bryan Hamilton in its final form and have found that (1) its format, citations, and bibliographical style are consistent and acceptable and fulfill university and department style requirements; (2) its illustrative materials including figures, tables, and charts are in place; and (3) the final manuscript is satisfactory to the graduate committee and is ready for submission to the university library.

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ABSTRACT

Small Mammals in portions of Great Basin National Park Susceptible to Groundwater

Withdrawal: Diversity and Stable Isotope Perspectives

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Master of Science

To support population growth in Las Vegas, Nevada, large scale increases in groundwater pumping are planned across the state. This pumping could affect riparian areas in Great Basin National Park by lowering groundwater levels, reducing stream flows, and xerifying riparian vegetation. Great Basin National Park (GBNP) is mandated to manage its resources unimpaired for future generations. Loss of biodiversity is unacceptable under this mandate. If groundwater levels are reduced beyond a threshold, aquatic and riparian diversity would be lost, but the effects on small mammal communities are less clear. To provide baseline information and to consider the effects of groundwater withdrawal a priori, we sampled and compared small mammal communities in two watersheds susceptible to groundwater withdrawal and one non-susceptible watershed. We also used to stable isotopes of nitrogen, carbon, deuterium and oxygen to characterize small mammal communities.

Evenness was higher in susceptible watersheds, which were distinct in species composition. Riparian and upland habitats in susceptible watersheds supported complementary small mammal communities, while communities in the non-susceptible watershed were more homogenous. Susceptible watersheds are located at the lowest elevations of GBNP where habitat heterogeneity due to the contrast between mesic riparian and xeric upland habitats is important in maintaining small mammal diversity.

Partitioning was primarily seen in nitrogen and carbon isotopes which reflect feeding ecology (trophic level and primary production source), but was also seen in oxygen isotopes. Major differences in nitrogen and carbon isotopes were between taxonomic groups, while similarity was highest within these groups. Shrews and ermine were highest in nitrogen reflecting their high trophic positions. Harvest and piñon mice were intermediate in nitrogen suggesting omnivory, while chipmunks, voles, woodrats and pocket mice were apparently herbivorous. Carbon ratios were consistent with C_3 based diets but were relatively enriched in Sigmodontinae species. Small mammal deuterium was similar to stream water suggesting that stream water is an important water source of water to small mammals. Oxygen enrichment relative to stream water and precipitation suggested that small mammals are sensitive to body water evaporation. Contrary to a previous study, oxygen isotopes were inversely related to water use efficiency.

Increases in the rate of groundwater pumping adjacent to Great Basin National Park could lower water tables, reduce stream flows, and xerify riparian vegetation. We suggest that groundwater levels, streams flow and riparian vegetation, in addition to small mammal species composition will be important response variables in monitoring the effects of groundwater withdrawal. If predictions of groundwater withdrawal are realized, groundwater levels, stream flows, vegetation, microclimate, and invertebrates riparian dependent as well as small mammals will be negatively affected resulting in a decrease in diversity and loss of riparian species from affected areas.

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ABSTRACT

To support population growth in Las Vegas, Nevada, large scale increases in groundwater pumping are planned across the state. This pumping could affect riparian areas in Great Basin National Park by lowering groundwater levels, reducing stream flows, and xerifying riparian vegetation. Great Basin National Park (GBNP) is mandated to manage its resources unimpaired for future generations. Loss of biodiversity is unacceptable under this mandate. If groundwater levels are reduced beyond a threshold, aquatic and riparian diversity would be lost, but the effects on small mammal communities are less clear. To provide baseline information and to consider the effects of groundwater withdrawal a priori, we sampled small mammal communities in two watersheds susceptible to groundwater withdrawal and one non-susceptible watershed. Evenness was higher in susceptible watersheds, which were distinct in species composition. Riparian and upland habitats in susceptible watersheds supported complementary small mammal communities, while communities in the non-susceptible watershed were more homogenous. Susceptible watersheds are located at the lowest elevations of GBNP where habitat heterogeneity due to the contrast between mesic riparian and xeric upland habitats is important in maintaining small mammal diversity. If groundwater withdrawal affects riparian areas, small mammal communities in GBNP would be negatively affected. We suggest that groundwater levels, streams flow and riparian vegetation, in addition to small mammal species composition will be important response variables in monitoring the effects of groundwater withdrawal.

Keywords: biodiversity, species composition, riparian, evenness, richness, abundance

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INTRODUCTION

In arid regions human population growth is increasingly limited by water availability (Postel et al. 1996, Vorosmarty et al. 2000). Increased use of groundwater can allow continued population growth but can also alter stream flow regimes and reduce regional biodiversity (Elliot et al. 2006, Deacon et al. 2007). Groundwater development has historically favored short term human population growth over longer term environmental stewardship (Glennon 2002). Understanding the potential consequences of groundwater development on biodiversity is an important objective for conservation biologists to address.

In the southwestern United States, human population growth is among the highest in the country. Much of this growth is driven by Las Vegas, Nevada, the fastest growing city in the region with a population of 1.8 million (Deacon et al. 2007). Located in the central Mohave Desert, the climate of Las Vegas is extremely arid, with a mean annual precipitation of 10 cm (Jones and Cahlan 1975). To support continued growth in the Las Vegas region, officials and municipalities have applied for permits to annually harvest and transport 1.3 billion m^3 (1.07 million acre feet) of groundwater from rural Nevada to Las Vegas (Deacon et al. 2007). The annual harvest of over 1.2 million m^3 (100,000 acre feet) of groundwater is currently planned from the valleys adjacent to Great Basin National Park (SNWA 2008).

Great Basin National Park (GBNP) was established to preserve a representative segment of the Great Basin, North America's largest desert. The park is mandated to protect its resources "unimpaired for both present and future generations" (NPS 1916). Under this law, loss of biological diversity is unacceptable (NPS 2001). Increases in groundwater pumping adjacent to GBNP could reduce biodiversity in riparian areas by altering groundwater levels and reducing stream flows. A priori

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consideration of the effects of groundwater withdrawal is important for park managers developing

monitoring programs and predicting the future effects of groundwater withdrawal on park resources.

Riparian areas in GBNP are narrow, linear corridors, characterized by high primary production,

abundant surface water, moderate microclimate, and a distinct physiognomy relative to the upland

matrix (Gregory et al. 1991). Maintenance of groundwater levels and natural flow regimes are

fundamental to maintaining riparian biodiversity and ecological function (Harris 1986, Auble et al. 1994,

Beever et al. 2005). Groundwater withdrawal disrupts natural flow regimes, lowers water tables, and

turns perennial streams intermittent; killing riparian vegetation (Glennon 2002).

Groundwater withdrawal results in a cone of depression around the area of pumping, usually a

pump or well, when more groundwater is removed from the aquifer than is replaced (Glennon 2002). If

this cone of depression extends into effluent streams, flows are reduced or eliminated (Glennon 2002).

Elliot et al. (2006) used syntopic discharge, specific conductance, and temperature measurements to

determine stream reaches in GBNP susceptible to groundwater withdrawal. Susceptible reaches are

effluent streams at the lowest elevations of the park, where streams are directly recharged by

groundwater through permeable geological strata (Elliot et al. 2006); Figure 1). If cones of depression

from groundwater withdrawal contact these reaches, stream flows will be reduced or eliminated.

Reductions in stream flow negatively affect aquatic species, such as trout and aquatic

invertebrates (Kraft 1972, Erman et al. 1973, Gore 1977, Solomon and Paterson 1980, Canton et al.

1984, McIntosh et al. 2002) and riparian vegetation (Harris 1986, Auble et al. 1994) but the effects on

small mammals are not well understood (Nilsson and Dynesius 1994).

Small mammals are important component of biodiversity and ecological function in GBNP. Seed

caching by small mammals enhances plant germination (McAdoo et al. 1983) and burrowing aerates

soils (Huntly and Inouye 1988), cycles nutrients (Sirotnak and Huntly 2000), and maintains early seral

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state plant communities (Kitchen and Jorgensen 1999) . As the prey base for many predators, small mammals are an important link in park food webs (Bekoff 1977, Glaudas et al. 2008).

There are 40 non-volant small mammal species in GBNP (Rickart et al. 2008). Habitat affinities range from xeric adapted species that do not require drinking water (Kenagy 1973, French 1993) to species strongly associated with streams and mesic riparian habitats (Hall 1946, Sera and Early 2003, Gillihan and Foresman 2004). Riparian associated small mammals in GBNP depend on riparian habitat for water, microclimate, cover, and food. If groundwater withdrawal reduces stream flows, riparian vegetation, invertebrate diversity, and microclimate will be altered, changes which would affect small mammals.

To provide information to park managers about the effects of groundwater withdrawal on small mammal communities in Great Basin National Park, we sampled reaches of two watersheds susceptible to groundwater withdrawal and reaches of a third watershed which is unlikely to be affected (Elliot et al. 2006). Our primary objectives were (1) to document and compare small mammal diversity between susceptible and non-susceptible watersheds, (2) to compare small mammal diversity between riparian and upland habitats, and (3) to discuss the conservation implications of groundwater withdrawal on small mammal communities.

METHODS

Study Area

Great Basin National Park (N – 38.98°, W - -114.30°; 31,201 hectares) is located in the South Snake Range of east central Nevada in the Great Basin desert (Figure 2). Elevations in the South Snake range vary from 1,621 m in the town of Baker to over 3,982 m at the summit of Wheeler Peak. The climate is cool and arid and varies dramatically with elevation. In Garrison Utah (elevation - 1609 m) mean annual precipitation is 19 cm and mean annual temperature is 10°C (Western Regional Climate Center, unpubl.

data). At the Lehman Caves Visitor Center (elevation – 2832 m) annual precipitation is 33 cm and the mean annual temperature is 9°C (Western Regional Climate Center, unpubl. data). Although there are no weather stations below Wheeler Peak, mean annual precipitation is estimated between76 and 89 cm (Western Regional Climate Center, unpubl. data).

Hydrology

There are 10 perennial streams in the park which originate at high elevations (Jacobs and Flora 1994). Snowmelt and groundwater are important sources of stream recharge (Elliot et al. 2006). Riparian corridors are well developed along streams and form narrow linear contrasts of dense, highly productive vegetation against the sparsely vegetated precipitation dependant upland matrix (Figure 3).

Field Methods

Susceptible reaches of two watersheds, Lehman and Snake, and non-susceptible reaches of one watershed, Strawberry, were sampled (Figure 1). Detailed descriptions of these watersheds can be found in Beever et al. (2005) and Elliot et al. (2006) .

Four transects per watershed were sampled. Transects were oriented perpendicular to streams and extended through the riparian corridor, across the stream, and into the uplands. Transect locations were chosen randomly from sites in sagebrush habitat where Great Basin pocket mice (*Perognathus parvus*) had previously been documented with museum specimens and directed trapping.

Each transect consisted of 31 traps and was divided into three habitats: riparian, near upland, and far upland (Figure 4). Riparian habitat included the entire riparian corridor, stream, and ecotone (i.e. precipitation dependent xeric vegetation communities immediately adjacent to the riparian corridor). Riparian habitat was characterized by dense, vegetation such as narrowleaf cottonwood (*Populus anguistifolia*), quaking aspen (*P. tremuloides*), willow (*Salix spp.*), sedges (*Carex ssp.*), Woods' rose (Rosa *woodsii)*, and rushes (*Juncus ssp.*). Ten traps per transect were located in the riparian corridor, spaced at

10 meter intervals. Riparian habitat extended 0 - 80 meters from the stream. Near upland habitat was located 90 - 250 meters from the stream and riparian corridor and was characterized by sparse, xeric vegetation such as basin big sagebrush (*Artemesia tridentata*), Mormon tea (*Ephedra viridis*), singleleaf piñon (*Pinus monophylla*), Utah juniper (*Juniperus osteosperma*), and various grass species. Ten traps per transect were located in the near upland spaced at 20 meter intervals. Far upland habitat was 270 – 440 meters from the stream and riparian corridor and vegetation was similar to near upland habitat. Eleven traps per transect were located in the upland spaced at 20 meter intervals. The primary difference between near and far upland habits was proximity to the stream and riparian corridor. Trapping was conducted from 23 July to 23 August 2007 and effort measured by trap nights.

Sherman live traps were set and baited with sunflower and milo seed between 17:00 - 20:00 and checked between 05:00 - 10:00. Captured small mammals were ear tagged, identified to species, visually assessed for sex, weighed, and released. Recaptured individuals were weighed and assessed for ear tag number, species, and sex.

Data Analysis

We used species richness, evenness, and abundance as response variables of alpha (α) diversity. We compared rarefied richness and evenness between watersheds (Lehman, Snake, and Strawberry) and habitats (riparian, ecotone, and upland) using the program Ecosim (Gotelli and Entsminger 2006). Our evenness metric was the inverse of Simpsons index (Magurran 2004). Samples were rarefied by the smallest number of individuals observed, resampled 1,000 times, and means and 95% confidence intervals for richness and evenness were generated. Statistical differences for richness and evenness are reported when there is no overlap between 95% confidence intervals, the equivalent of setting $\alpha = 0.05$ (Keller 2001). We compared abundance between watersheds and habitats using one-way ANOVA. Species differences and Bray Curtis similarity indices were used as response variables of beta (β)

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diversity. Pairwise species differences between watersheds and habitats were generated by transforming abundances to presence absence data, using the Resemblance function, Manhattan Distance in Program Primer to generate the number of species differences between sites (Clarke and Warwick 2001). We used Analysis of Similarity (ANOSIM), a non-parametric test conceptually similar to ANOVA, in the Program Primer, to compare Bray Curtis Similarity Indices between watersheds and habitats (Clarke and Warwick 2001). ANOSIM generates R and P values for the global dataset and for all pairwise comparisons. The SIMPER function was used to generate within watershed and habitat similarity, between watershed and habitat dissimilarity, and species contributions to similarity and dissimilarity. SIMPER evaluates each species contribution to Bray Curtis similarly and dissimilarly and for pairs of sites within and among watersheds and habitats. Data are graphically presented as Multi Dimensional Scaling (MDS) and Cluster graphs of Bray Curtis Similarity Indices.

At each trap location we used a Global Information System Digital Elevation Model to calculate elevation, slope, and aspect by watershed. One-way ANOVA was used to compare elevation and slope between watersheds. Mean aspect was calculated according to Fisher (1995) and 95% confidence interval were compared between watersheds (Fisher 1995). Statistical analyses were done with Minitab 14 (Minitab 2004) except analysis of circular data which used NCSS (Hintze 2007).

RESULTS

Four transects were sampled per watershed. Each transect consisted of 31 traps, sampled for 12 nights resulting in a total effort of 4,127 trap nights, after accounting for sprung traps. The frequency of sprung traps did not differ between watersheds, transects, or habitats allowing use of raw capture data rather than capture rates. 326 individuals of 11 species were captured. The total recapture rate was 76% (326 individuals/1006 total captures) suggesting that the population was reasonable well censused. Recapture rates varied by watershed and were lowest in Lehman Creek.

Watersheds are summarized in Table 1 and differed in elevation (ANOVA; $F_{2,369}$=2469, P < 0.0001) and slope (ANOVA; $F_{2,369}$=14.89, P < 0.0001). Strawberry Creek was higher in elevation than Lehman and Snake by 488 m and 497 m respectively. Lehman was shallower in slope that Snake and Strawberry by 4° and 5°. Watersheds did not differ in mean aspect (95% CI). Eight species and 107 individuals were captured in Lehman Creek, seven species and 91 individuals in Snake Creek, and seven species and 128 individuals in Strawberry Creek (Table 2). There were no differences in species richness (95% CI, P < 0.05; Figure 5) or abundance (ANOVA; $F_{2,11}$=2.34, P = 0.152; Figure 5) between watersheds. Evenness was higher in Snake and Lehman Creeks than in Strawberry Creek (95% CI, P < 0.05; Figure 5).

Lehman and Snake Creek differed by a single species, Lehman and Strawberry by 7 species, and Snake and Strawberry by 8 species (Table 2). Montane vole *(Microtus montanus)*, Deer Mouse (*Peromyscus maniculatus)*, and Great Basin Pocket Mouse (*Perognathus parvus)* occurred in all watersheds (Table 2). A single Uinta chipmunk (*Tamias umbrinus)* was captured in Lehman Creek, six in Strawberry Creek, and none in Snake Creek. Single individuals of Ermine (*Mustela erminea)* and vagrant shrew (*Sorex vagrans)* were trapped in Strawberry Creek but were not observed in Snake or Lehman. Desert woodrat (*Neotoma lepida)*, Western Harvest Mouse (*Reithrodontomys megalotis)*, Cliff chipmunk (*Tamias dorsalis)*, and piñon mouse (*Peromyscus truei)* occurred in both Lehman and Snake Creeks but were not observed in Strawberry. Least chipmunks (*Tamias minimus)* occurred in Strawberry Creek but were not captured in Lehman or Snake.

Watersheds differed in Bray Curtis Similarity Index (ANOSIM, Global R = 0.711, P = 0.002; Figures 6 and 7). Pairwise tests showed that Lehman and Snake Creek did not differ (R = -0.01, P = 0.543), while Lehman and Strawberry (R = 1, P = 0.029) and Snake and Strawberry (R = 1, P = 0.029) differed significantly.

Similarly was highest within Strawberry Creek, followed by Snake and Lehman (Table 3). Deer mice contributed most to similarity across watersheds (Table 3). Similarity was higher between Lehman and Snake than Lehman and Strawberry of Snake and Strawberry (Table 4). Lehman and Snake dissimilarity was due to Western Harvest Mouse, piñon mouse, and cliff chipmunk (Table 4). Lehman and Strawberry dissimilarity was due to Western Harvest Mouse, Deer mouse, and piñon mouse. Snake and Strawberry dissimilarity was due to piñon mouse, deer mouse, Western Harvest Mouse, and cliff chipmunk. Deer mice were primarily responsible for within watershed similarity (Table 3), while Western Harvest mice and piñon mice were primarily responsible for between watershed dissimilarity (Table 4).

Habitats are summarized in Table 5 and did not differ in richness (95% CI, $P > 0.05$, Figure 8), abundance (ANOVA; $F_{2,8}=0.87$, $P = 0.467$; Figure 8) or evenness (95% CI, $P > 0.05$; Figure 8). Upland habitats differed by a single species, far upland and riparian by six species, and near upland and riparian by five species. Montane voles, Ermine, and vagrant shrew were trapped in riparian but not in ecotone or upland habitats (Table 5). Western Harvest Mice were not captured in upland habitat. Although they occurred in both riparian and near upland habitats, harvest mice were strongly associated with riparian habitat, where 87% were captured. Least chipmunks occurred in near and far upland but were not trapped in riparian habitats. Deer mice, Great Basin pocket mice, piñon mice, cliff chipmunk, and Uinta chipmunk occurred across habitats.

Habitats differed in Bray Curtis Similarity indices (ANOSIM, Global R=0.145, $P = 0.007$; Figures 6 & 9). Pairwise test showed that near and far upland habitats did not differ (R = -0.016, $P = 0.494$), while far upland (R = 0.342, $P = 0.002$) and near upland (R = 0.143, $P = 0.017$) differed from riparian.

Similarity was highest within riparian habitats, followed by far and near upland (Table 6). Deer mice contributed most to similarity across habitats. Dissimilarity was highest between riparian and far upland and riparian and near upland, and lowest between near and far upland (Table 7). Harvest mice,

deer mice, piñon mice, and montane voles contributed most to dissimilarity between riparian and near upland; piñon mice harvest mice, deer mice, and cliff chipmunk to dissimilarity between riparian and far upland; and piñon mice, deer mice and cliff chipmunk to dissimilarity between near and far upland habitats (Table 7).

DISCUSSION

Although groundwater withdrawal has not yet occurred, our study suggests that small mammal communities in Great Basin National Park could be adversely affected by increased groundwater pumping. Increased harvest of groundwater adjacent to GBNP may lower water tables, reduce perennial stream flows, decrease mesic riparian vegetation, alter the riparian microclimate, and decrease invertebrate diversity. These changes to riparian habitat would negatively affect small mammal diversity.

Small mammal communities in susceptible watersheds (Lehman and Snake) were similar to each other and distinct from non-susceptible communities (Strawberry). This was likely a function of habitat heterogeneity due to differences in climate between watersheds. Lehman and Snake Creeks were lower in elevation, warmer, and drier than Strawberry Creek. These climactic differences created a greater contrast between mesic riparian vegetation and precipitation dependent, xeric upland vegetation in susceptible watersheds. Habitat heterogeneity and plant diversity (richness, productivity, structure, and cover) are correlated with small mammal diversity (Rosenzweig and Winakur 1969, Hafner 1977, Manson et al. 1999) and these contrasts between habitats likely contributed to greater beta diversity and species specific habitat segregation in Lehman and Snake Creeks. For example, western harvest mice and piñon mice segregated habitats in Lehman and Snake Creeks, with harvest mice restricted to riparian habitat and piñon mice to upland habitats. In Strawberry Creek small mammal communities were more homogeneous across habitats and habitat segregation was less apparent (Figure 9).

Riparian habitats differed from upland habitats in species composition and these differences were most apparent in susceptible watersheds. Riparian small mammal communities in Lehman and Snake were more similar to Strawberry Creek communities than to their own upland communities (Figure 9). Riparian corridors are mesic, cold air drainages with a more moderate climate than the surrounding uplands (Gregory et al. 1991, Zimmerman et al. 1999), conditions which allow plant and animal communities to extend from high to low elevations. Small mammal communities in Lehman and Snake may have followed the riparian corridor down from higher elevations into xeric upland communities. As a mesic linear feature, the riparian corridor increases habitat heterogeneity, plant diversity and small mammal evenness and beta diversity in the otherwise dry and sparsely vegetated Snake and Lehman Creeks.

Small mammals segregated habitat by species and this segregation was most apparent in susceptible watersheds. Deer mice were generalists and occurred across habitats, Desert woodrats and least chipmunks were only captured in upland habitats as were 89% of pocket mice, 98% of piñon mice, and 79% of cliff chipmunks. Montane voles, ermine and vagrant shrews were found only in riparian habitat as were 87% of western harvest mice.

Although our recapture rate (>75%) suggests adequate sampling, some species may have been present and not captured. Desert woodrat, piñon mouse, western harvest mouse, and cliff chipmunk were captured in Lehman and Snake Creeks but not Strawberry Creek. Although harvest mice and piñon mice are both documented from Strawberry Creek (Rickart et al. 2008), these species are both commonly sampled with live traps and our findings were likely representative of their distribution along transects during our sampling period. Similarly, although Uinta chipmunks are documented from Snake Creek and least chipmunks from Snake and Lehman Creeks (Rickart et al. 2008), these records are from higher elevations and in different habitats than we sampled. Although ermine and vagrant shrew were

captured only in Strawberry Creek, neither species are regularly captured by live traps. Shrews are particularly underrepresented by live trap sampling methods (Kirkland and Sheppard 1994) and ermine are rare in the park (Hall 1946, Rickart et al. 2008). Consequently, our failure to capture them in Lehman and Snake Creeks is not strong evidence of absence.

Stream incision (stream bed lowering due to erosion; Shields et al. 1994) is a process analogous to groundwater withdrawal in its hydrologic and ecological effects. Stream incision lowers groundwater levels and reduces stream flows (Chambers et al. 2004). Such hydrologic alterations negatively affect aquatic diversity (Shields et al. 1994) and kill riparian vegetation (Bravard et al. 1997) leading to an increase in xeric upland vegetation and a decrease in mesic riparian vegetation in riparian areas (Wright and Chambers 2002). Beyond these immediate effects, there is little work on the trophic consequences of hydrologic changes, particularly in small mammal communities (Nilsson and Dynesius 1994). Thus while the major benefit of this study may be to provide a baseline of the small mammal communities in areas susceptible to groundwater withdrawal, it is important to consider the effects of groundwater on the small mammal community a priori.

If groundwater withdrawal alters stream flows in susceptible watersheds, it is reasonable to expect changes in small mammal diversity. Although the exact mechanisms of decline will be difficult to isolate, synergistic effects between stream flow, vegetation, microclimate, and invertebrates are all potential mechanisms which would likely contribute to declines of riparian dependent small mammals.

Perennial streams provide a reliable water source to small mammals. Reductions in flow would reduce the availability of surface water, particularly if perennial streams become intermittent. This may be particularly important for riparian species, such as voles which require more drinking water than xeric adapted upland species (Rose and Birney 1985).

Due to groundwater availability and elevated soil moisture, vegetation in riparian areas is characterized by higher primary production, higher moisture content, different species composition, and a distinct physiognomy relative to the upland matrix (Gregory et al. 1991). If groundwater levels are reduced beyond a threshold, riparian vegetation would die (Scott et al. 1999, Amlin and Rood 2002) and xeric vegetation would encroach into riparian areas, reducing plant cover, production and biomass. Small mammals utilize riparian areas due to the increased cover it provides relative to the uplands (Stamp and Ohmart 1979) and reductions in vegetation could increase vulnerability to predation. Riparian plants are characterized by greater production, higher palatability and water content, relative to upland vegetation (Parsons et al. 2003). As such they are an important source of forage and water to small mammals. As herbivores, voles feed primarily on riparian plants and are therefore quite vulnerable to loss of riparian vegetation (Rose and Birney 1985).

Decreases in vegetation cover would alter the riparian microclimate due to increased insolation and decreased transpiration (Chambers et al. 2004). Increased temperature and decreased relative humidity would increases water stress in small mammals. For riparian species which require cooler and more humid conditions than upland species these conditions would increase water stress (Rose and Birney 1985).

Changes in groundwater levels would also reduce invertebrate production and alter invertebrate species composition. Aquatic invertebrates would be affected by reduced stream flows and terrestrial invertebrates by changes in riparian vegetation. Vagrant shrews are insectivorous (Gillihan and Foresman 2004) and reductions in invertebrates, their sole food source, would be disastrous. As omnivores, harvest mice often feed on invertebrates (Johnson 1961, Webster and Jones 1982) and would similarly be negatively affected by reductions in invertebrates. Ermine are carnivores and would be affected indirectly by loss of small mammals, their primary prey (King 1983).

Conservation Implications

Susceptible small mammal communities were located at relatively low elevations of watersheds where habitat heterogeneity was highest. Within GBNP these habitats occur only in susceptible watersheds. Although susceptible areas are small portion of GBNP (Elliot et al. 2006), small mammal communities within these areas are a unique park resource, maintained by the contrast between mesic, riparian and xeric, upland habitats. If groundwater withdrawal reduces stream flows, riparian vegetation, invertebrate diversity, and microclimate will be altered, reducing both habitat heterogeneity and small mammal diversity.

Species composition in susceptible watersheds will be an important response variable to monitor groundwater induced changes in small mammal communities. Changes in small mammal communities due to alterations to the natural flow regime may be manifested as an increase in upland species, such as desert woodrats, piñon mice, and Great Basin Pocket mice in addition to a decrease in riparian species such as harvest mice, shrews and voles in riparian habitat. Initially, evenness of affected areas would decrease and will be a more sensitive response variable than richness and abundance.

By the time groundwater withdrawal affects small mammals, the riparian habitat will have been dramatically altered. Therefore we recommend monitoring stream flow, climate, and riparian vegetation together with small mammal communities.

Large scale increases in groundwater pumping are proposed across rural Nevada (Deacon et al. 2007). If these proposals are realized, very few areas in Nevada will be unaffected by groundwater withdrawal. Increases in pumping have great potential to affect regional biodiversity across Nevada (Deacon et al. 2007) as well as small mammal diversity in GBNP. If small mammals are affected, stream flows and riparian habitats in the park will be drastically altered, aquatic and riparian diversity devastated, and serious impairment of park resources will have occurred. Minimal pumping adjacent to

GBNP would allow the park to more fully meet its Congressional mandate to preserve its resources unimpaired and would provide a control area with which to compare the effects of groundwater withdrawal on montane riparian communities in Nevada.

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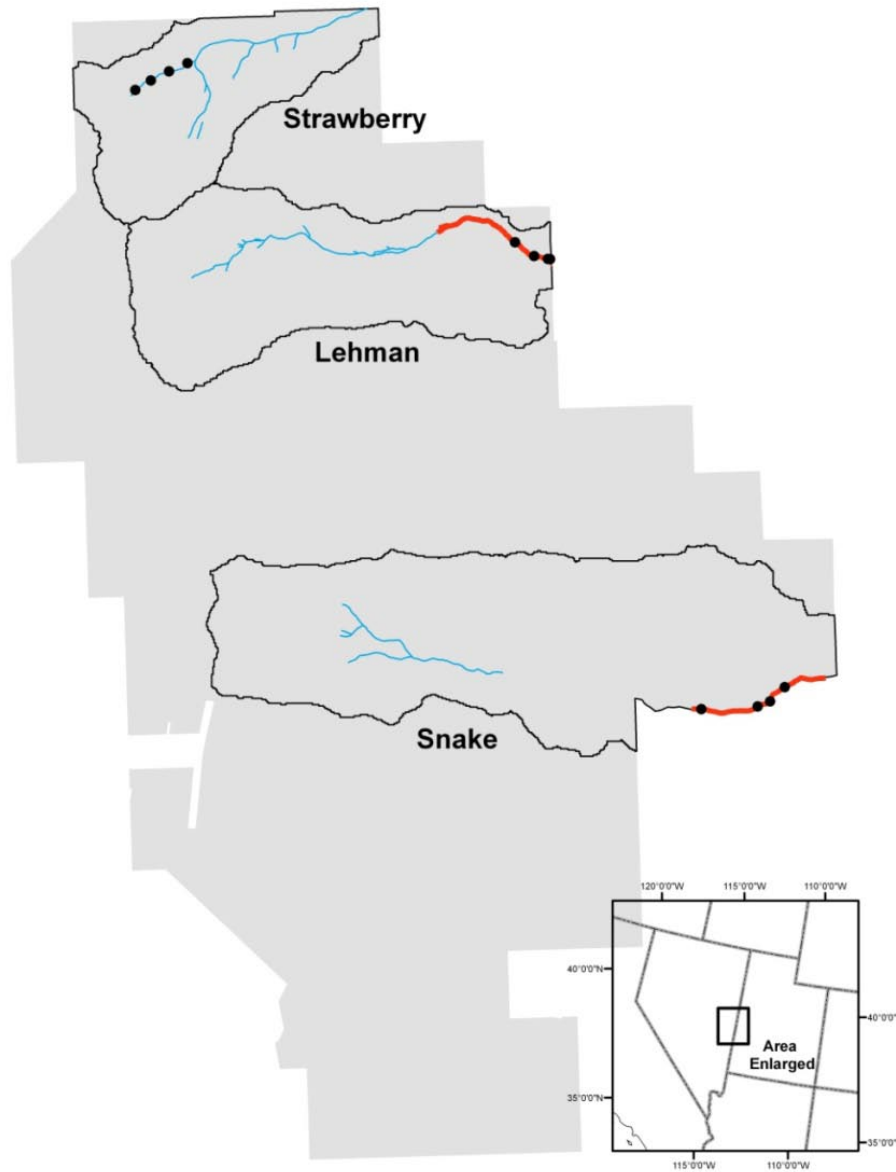
Figure 1. Stream reaches in Great Basin National Park susceptible to groundwater withdrawal and sampling locations for small mammal communities. Details about susceptible areas can be found in Elliot et al. (2006). Red indicates susceptible stream reaches and black dots represent sampling transects. Blue lines are stream reaches that are not susceptible to groundwater withdrawal. The gap between susceptible and non-susceptible reaches in Snake Creek is a six mile water diversion.

Figure 2. Location of Great Basin National Park, Las Vegas, and the Great Basin desert. The Great Basin

desert is defined biologically by contiguous sagebrush communities (Grayson 1993). A 250 mile pipeline

would transport groundwater from valleys adjacent to GBNP to Las Vegas.

Figure 3. Riparian and upland vegetation forms sharp contrasts in the lower elevations of Snake Creek,

Great Basin National Park, White Pine County, Nevada.
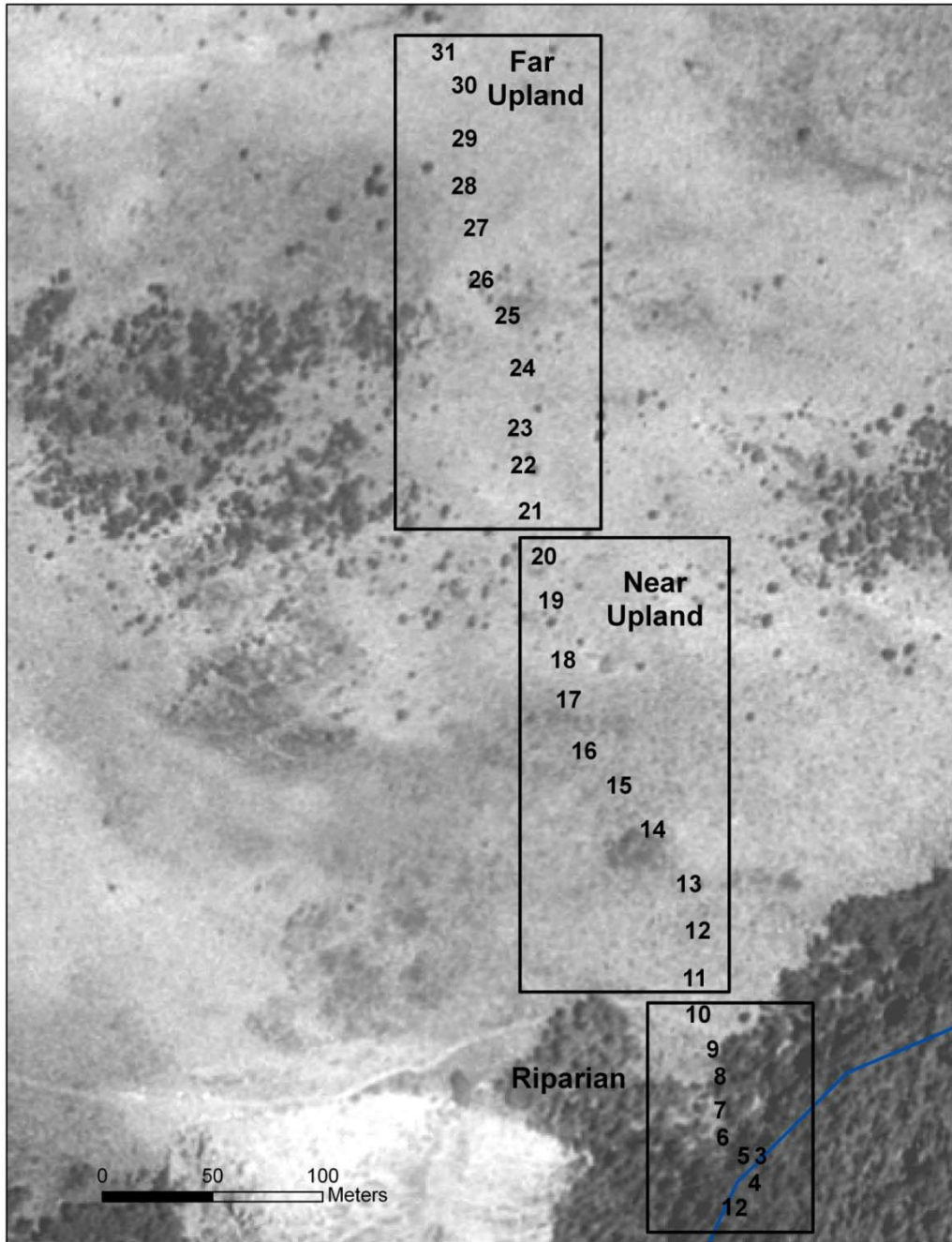
Figure 4. An example of a small mammal transect with riparian, near upland, and far upland habitats.

Numbers indicate trap location, boxes indicate habitat divisions, and blue indicates the stream.
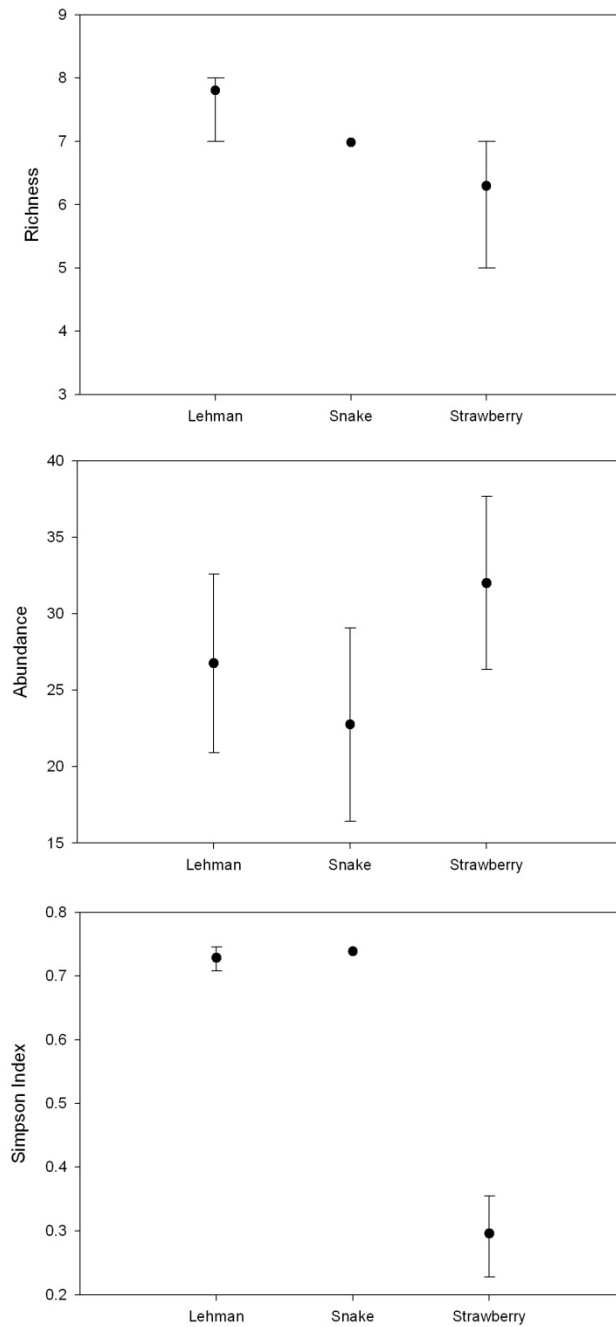
Figure 5. Mean small mammal species richness, abundance, and evenness for three watersheds in Great Basin National Park. Error bars indicate 95% CI. For richness and evenness watersheds were rarefied by 91 individuals.
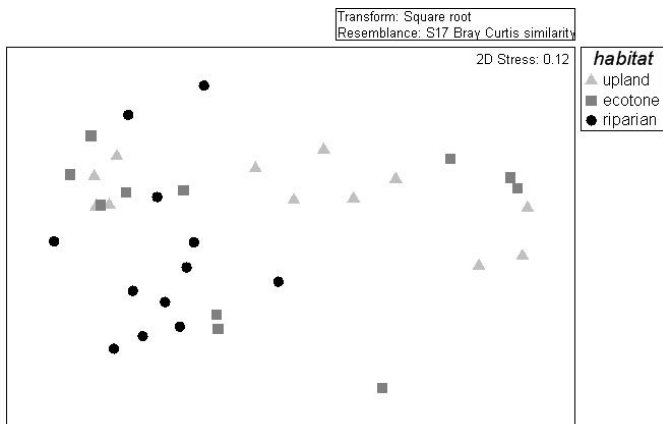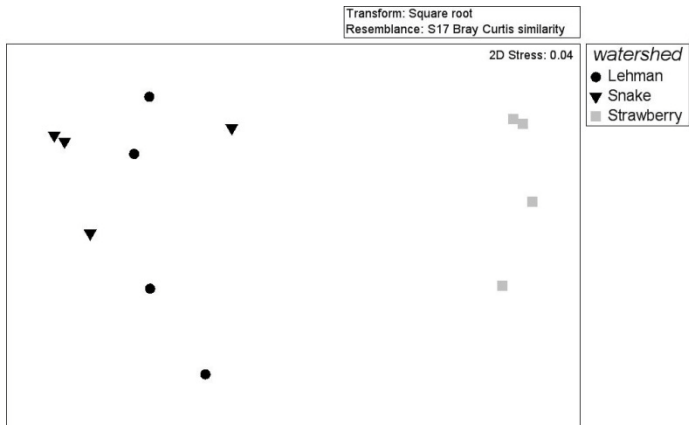
Figure 6. Non-parametric multidimensional scaling of Bray Curtis Similarity indices of small mammal communities by watershed and habitat in Great Basin National Park. Proximity of symbols is proportional to similarity (%).

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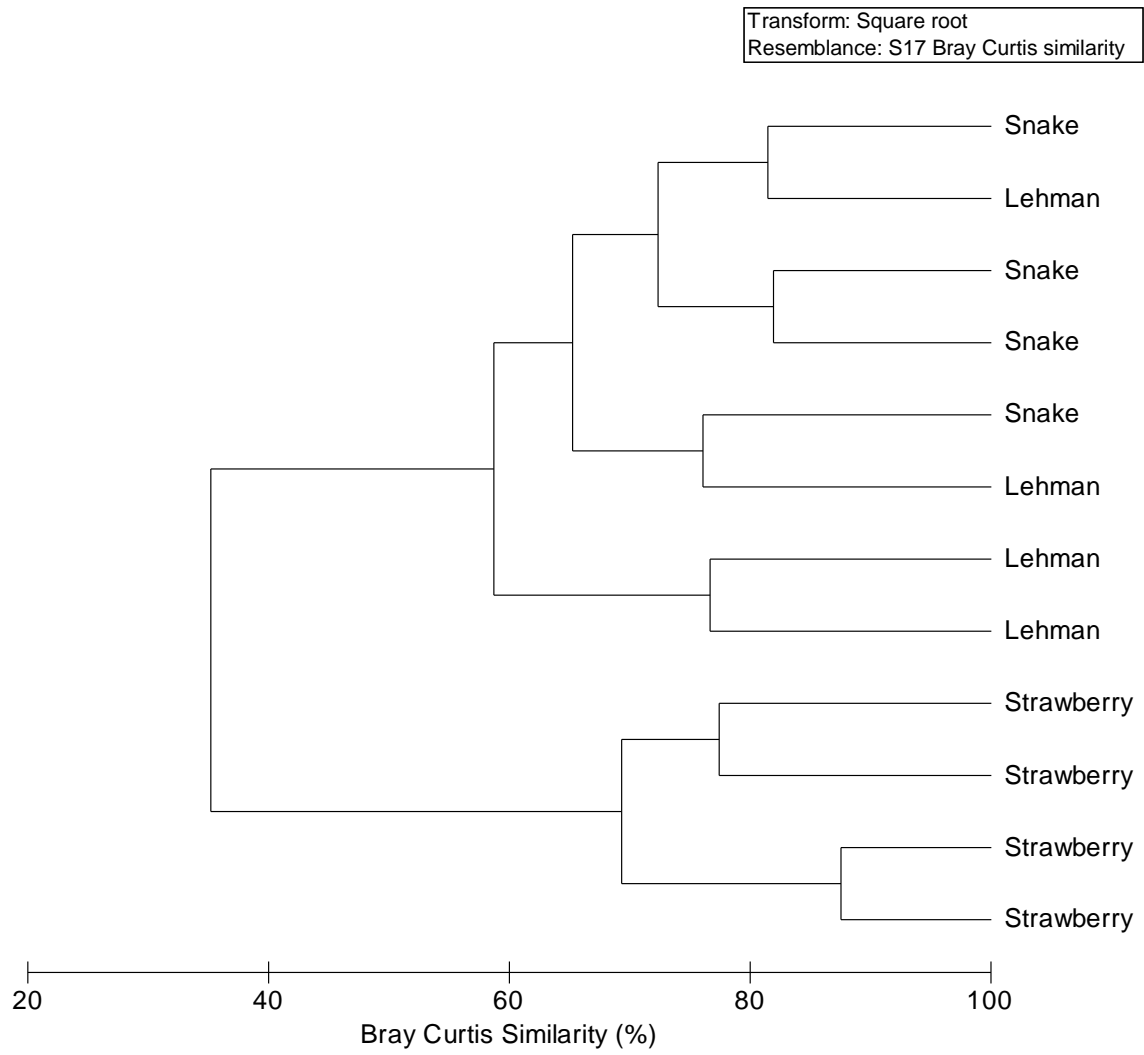
Figure 7. Cluster diagram of Bray Curtis Similarity indices (%) for three watersheds in Great Basin National Park.
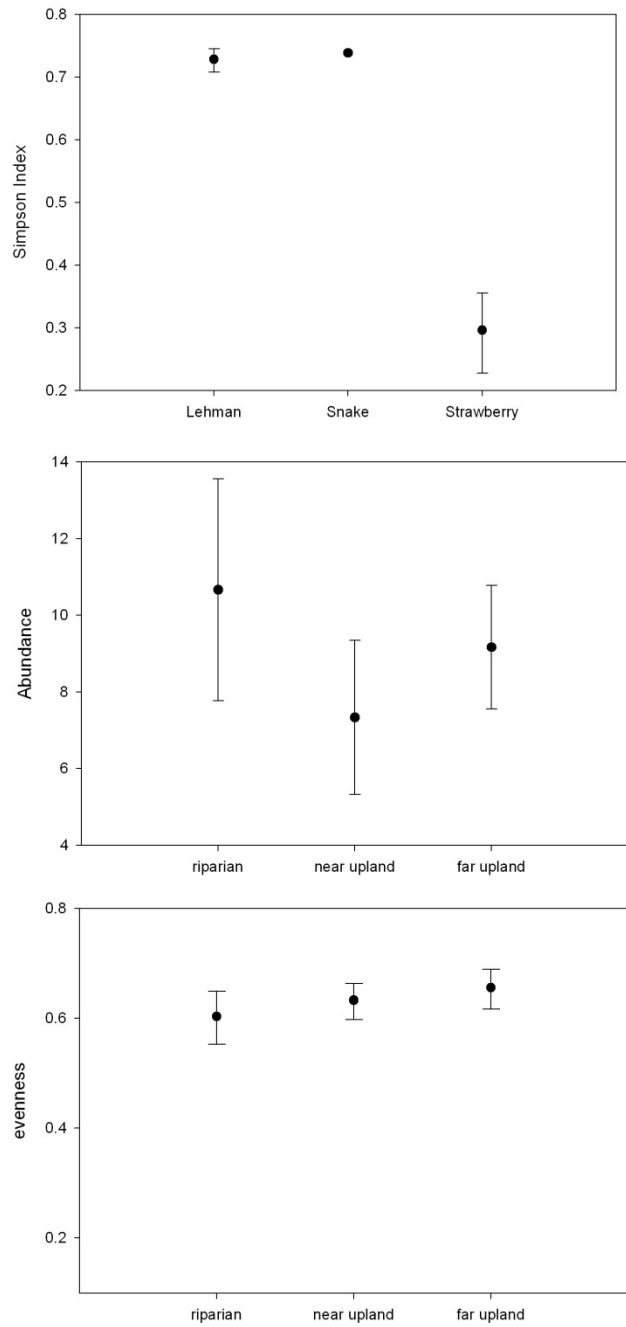
Figure 8. Mean small mammal richness, abundance, and evenness for three habitats in Great Basin National Park. Error bars indicate 95% CI. For richness and evenness, habitats were rarefied by 80 individuals.
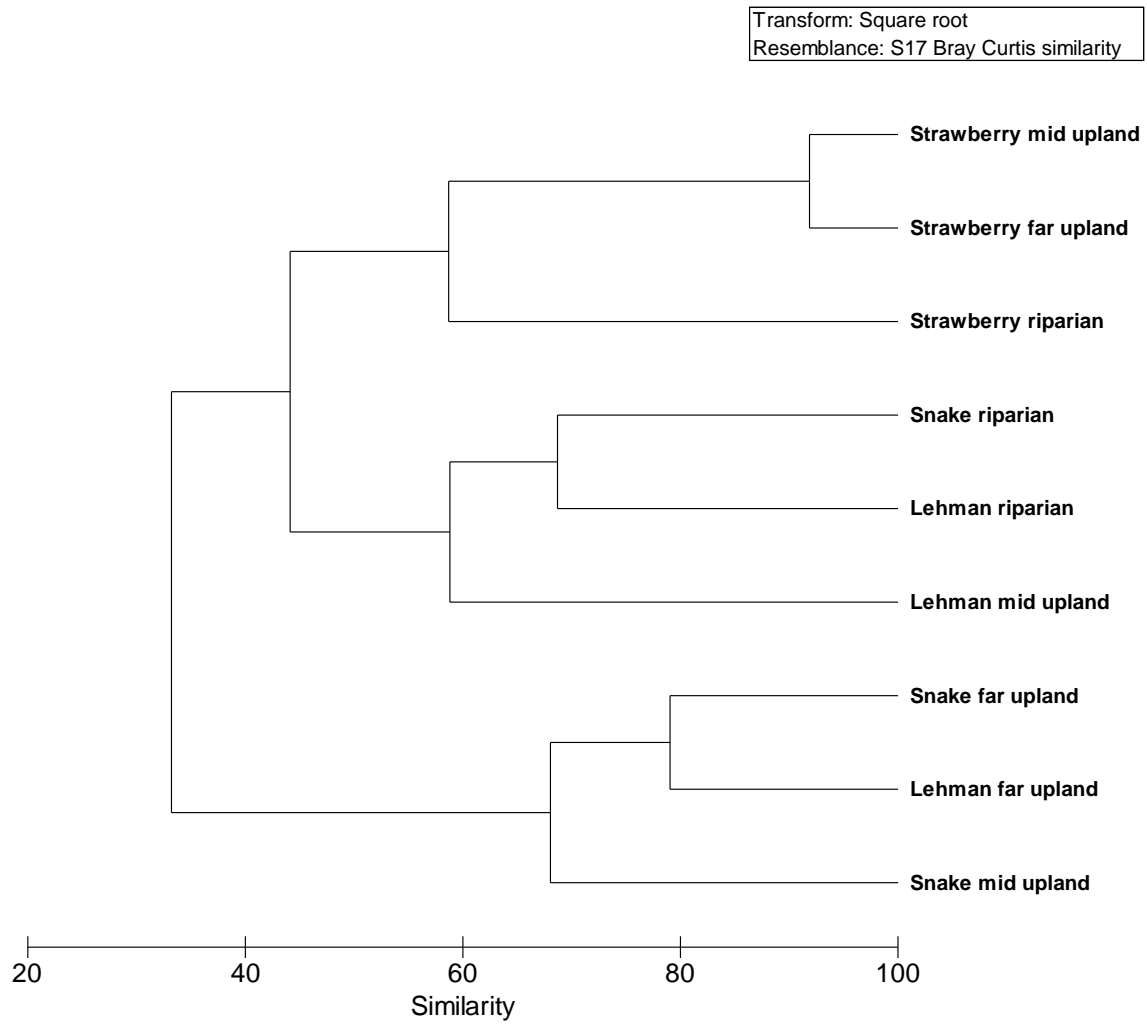
Figure 9. Cluster diagram of Bray Curtis similarity indices by watershed for three habitats in Great Basin National Park. Graph was generated using the CLUSTER function in Program Primer.

TABLES

Table 1. Summary of watersheds sampled for small mammal diversity in Great Basin National Park in 2007. Values for elevation, slope, and aspect were obtained from a Global Information System and are means ± SE, ranges in parentheses.

Watershed	drainage area (ha)[1]	susceptible to groundwater withdrawal[2]	February stream flow (ft^2/sec)[2]	June stream flow (ft^2/sec)[2]	Elevation (m)	Slope (°)	Aspect (°)
Lehman	3939	yes	26.81	524	2053 ± 3.7 (2004 - 2144)	11 ± 1 (1 - 33)	106.8 ± 9.2 (7-330)
Snake	6099	yes	0.9	14.8	2044 ± 4.4 (1981 - 2137)	15 ± 1 (1 - 33)	125.3 ± 7.8 (2 - 287)
Strawberry	2713	no	1.5	15.8	2541 ± 8.1 (2426 - 2715)	16 ± 1 (3 - 33)	90.5 ± 3.8 (18 - 175)

[1] Beever et al 2005

[2] Elliot et al 2006

Table 2. Small mammal richness and abundance for three watersheds in Great Basin National Park. Trapping was conducted along 12 transects, four per watershed in 2007. Each transect was comprised of 31 traps.

	Lehman	Snake	Strawberry
Montane Vole	3	1	2
Ermine	0	0	1
Desert Woodrat	3	3	0
Deer Mouse	38	28	107
Great Basin Pocket Mouse	2	2	5
Piñon Mouse	18	34	0
Western Harvest Mouse	37	9	0
Vagrant shrew	0	0	1
Cliff chipmunk	5	14	0
Least Chipmunk	0	0	6
Uinta chipmunk	1	0	6

Table 3. Average Bray Curtis similarity indexes (%) and species contributions (%) to similarity of small mammal communities for three watersheds in Great Basin National Park. Values are from the SIMPER function in Program Primer (Clarke and Warwick 2001). Percent species contribution is given in parenthesis.

	Lehman	Snake	Strawberry
average similarity	63.12	67.9	73.69
species contributions	Deer Mouse (44.12)	Deer Mouse (35.22)	Deer Mouse (71.92)
	Western Harvest Mouse (34.45)	Piñon Mouse (32.75)	Great Basin Pocket Mouse (15.14)
	Piñon Mouse (14.97)	Western Harvest Mouse (19.70)	Uinta Chipmunk (8.19)
		Cliff Chipmunk (9.87)	

Table 4. Pairwise comparisons of small mammal community dissimilarity and species contributions to dissimilarity between three watersheds in Great Basin National Park. ± indicates the direction of the species contribution. Species dissimilarity indices are given in parenthesis. For example, Lehman and Snake Creek were 34.67% dissimilar, Western harvest mice were more abundant in Lehman than Snake Creek and contributed 21.57% to dissimilarity between watersheds. Data were generated by the SIMPER function in the program Primer.

	Lehman	Snake
Snake	34.67	
	Western harvest mouse + (21.57)	
	Piñon mouse - (20.62)	
	Cliff chipmunk - (18.24)	
	Desert woodrat - (10.53)	
	Montane vole + (9.15)	
	Deer mouse + (8.26)	
Strawberry	61.85	67.79
	Western harvest mouse + (24.20)	Piñon mouse + (21.89)
	Deer mouse - (17.71)	Deer mouse - (20.33)
	Piñon mouse + (15.23)	Western harvest mouse + (11.83)
	Great Basin pocket mouse - (7.81)	Cliff chipmunk + (11.40)
	Uinta chipmunk - (7.69)	Uinta chipmunk + (8.14)
	Least chipmunk - (7.68)	Least chipmunk - (7.25)

Table 5. Richness and abundance data by habitat for three watersheds in Great Basin National Park. Trapping was conducted along 12 transects, four per watershed in 2007. Each transect was comprised of 31 traps, divided into three habitats. Habitats definitions are given in the text.

	Riparian	Near Upland	Far Upland
Montane Vole	6	0	0
Ermine	1	0	0
Desert Woodrat	0	3	3
Deer Mouse	70	51	52
Great Basin Pocket Mouse	1	5	3
Piñon Mouse	1	14	37
Western Harvest Mouse	40	6	0
Vagrant shrew	1	0	0
Cliff chipmunk	4	3	12
Least Chipmunk	0	5	1
Uinta chipmunk	4	1	2

Table 6. Average Bray Curtis similarity and species contributions to similarity of small mammal communities for two susceptible (Lehman and Snake) and one non-susceptible watershed in Great Basin National Park. Magnitude of species contribution is given in parenthesis.

	Riparian	Near Upland	Far Upland
average similarity	56.99	40.38	44.81
species contributions	Deer Mouse (69.41)	Deer Mouse (49.84)	Deer Mouse (48.05)
	Montane Vole (17.08)	Great Basin Pocket Mouse (28.69)	Piñon Mouse (28.55)
	Western Harvest Mouse (13.51)	Piñon Mouse (12.57)	Cliff Chipmunk (15.96)
		Western Harvest Mouse (8.89)	Uinta Chipmunk (7.43)

Table 7. Pairwise comparisons of small mammal community dissimilarity and species contributions to dissimilarity between three habitats in Great Basin National Park. ± indicates the direction of the species contribution. Species dissimilarity indices are given in parenthesis. For example, riparian and near upland habitats were 56.58% dissimilar, Western harvest mouse was more abundant in riparian than near upland and contributed 19.75% to dissimilarity between those habitats. Data were generated by the SIMPER function in the program Primer (Clarke and Warwick 2008).

	Riparian	Near Upland
Near Upland	56.58	
	Western harvest mouse + (19.75)	
	Deer mouse + (18.08)	
	Piñon mouse - (12.79)	
	Montane vole + (11.33)	
	Great basin pocket mouse - (7.91)	
	Cliff chipmunk - (7.15)	
Far Upland	61.93	50.54
	Piñon mouse - (20.09)	Piñon mouse - (22.57)
	Western harvest mouse + (20.05)	Deer mouse - (21.50)
	Deer mouse + (16.09)	Cliff chipmunk - (13.97)
	Cliff chipmunk - (10.27)	Western harvest mouse + (10.84)
	Montane vole + (10.11)	Great basin pocket mouse + (9.84)
	Uinta chipmunk = (6.63)	Least chipmunk + (8.17)

CHAPTER 2 - Small mammal Communities within areas of Great Basin National Park Susceptible to Groundwater Withdrawal: A Stable Isotope Perspective

ABSTRACT

Increases in the rate of groundwater pumping adjacent to Great Basin National Park could lower water tables, reduce stream flows, and xerify riparian vegetation. These alterations to the riparian habitat template could affect small mammal communities. We used to stable isotopes of nitrogen, carbon, deuterium and oxygen to characterize small mammal communities and we use this information to discuss the potential effects of groundwater withdrawal on small mammal communities. Partitioning was primarily seen in nitrogen and carbon isotopes which reflect feeding ecology (trophic level and primary production source), but was also seen in δ^{18}O. Major differences in δ^{15}N and δ^{13}C isotopes were between taxonomic groups, while similarity was highest within these groups. Shrews and ermine were highest in nitrogen reflecting their high trophic positions. Harvest and piñon mice were intermediate in nitrogen suggesting omnivory, while chipmunks, voles, woodrats and pocket mice were apparently herbivorous. Carbon ratios were consistent with C_3 based diets but were relatively enriched in Sigmodontinae species. Small mammal deuterium was similar to stream water suggesting that stream water is an important water source of deuterium to small mammals. Differences in oxygen were enriched relative to stream water and precipitation indicating that small mammals are sensitive to body water evaporation. Contrary to a previous study, oxygen isotopes were inversely related to water use efficiency. If groundwater withdrawal alters groundwater levels, stream flows, vegetation, microclimate, and invertebrates riparian dependent small mammals will be negatively affected resulting in a decrease in diversity and loss of riparian species from affected areas.

Keywords: nitrogen, carbon, oxygen, hydrogen, deuterium, riparian

INTRODUCTION

In arid regions, perennial streams and their associated riparian areas are critical sources of biodiversity. Groundwater availability, flood regimes, stream channel geomorphology, microclimate, and upland inputs (Naiman and Decamps 1997) strongly influence riparian biota, which form narrow, linear corridors, characterized by high primary production, abundant surface water, and a distinct physiognomy relative to the upland matrix (Gregory et al. 1991, Chambers and Miller 2004). Maintenance of groundwater levels and surface flow regimes are fundamental to maintaining properly functioning riparian areas (Harris 1986, Auble et al. 1994, Chambers et al. 2004, Beever et al. 2005). In the western United States, population growth is placing increasing demands on groundwater resources. Increased groundwater utilization has high potential to degrade riparian areas, reducing regional biodiversity (Elliot et al. 2006, Deacon et al. 2007).

Great Basin National Park (GBNP) was established as a representative portion of the Great Basin, North America's largest desert. The park's primary purpose is to preserve its resources "unimpaired for future generations" (NPS 1916). Proposed increases in groundwater pumping adjacent to GBNP threaten riparian biodiversity in the park.

Officials and municipalities in southern Nevada have applied for permits to annually harvest and transport 1.3 billion m^3 (1.07 million acre feet) of groundwater from rural Nevada to the Las Vegas metropolitan area (Deacon et al. 2007). The annual harvest of over 120 million m^3 (100,000 acre feet) is currently planned from the valley aquifers adjacent to GBNP (SNWA 2008). Snowmelt from Great Basin National Park is a major source of recharge to these aquifers. In turn valley aquifers support effluent park streams during periods of low flow. Groundwater pumping will reduce or eliminate stream flows if the influence of the pumping (cone of depression) extends into the park (Elliot et al. 2006). Alterations to groundwater levels and surface flow regimes directly reduce aquatic diversity (Kraft 1972, Erman et

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al. 1973, Gore 1977, Solomon and Paterson 1980, Canton et al. 1984, McIntosh et al. 2002) and mesic

riparian vegetation (Harris 1986, Auble et al. 1994) but the trophic effects on small mammals are not

well understood (Nilsson and Dynesius 1994).

Although there are 40 non-volant small mammal species in Great Basin National Park (Rickart et

al. 2008), only the water shrew (*Sorex palustris*) is aquatic (Beneski and Stinson 1987). Other species

range from xeric adapted species in the Family Heteromyidae that do not require drinking water (Kenagy

1973, French 1993) to riparian obligates such as vagrant shrews (*Sorex vagrans*) and long-tailed voles

(*Microtus longicaudus*) that have high water requirements and are strongly associated with riparian

habitats (Hall 1946, Sera and Early 2003, Gillihan and Foresman 2004).

Stable isotope are important tools in understanding animal diversity and community

interactions (West et al. 2006). Stable nitrogen ($^{15}N/^{14}N$), carbon ($^{13}C/^{12}C$), hydrogen ($^{2}H/^{1}H$), and oxygen

($^{18}O/^{16}O$) isotope ratios reflect feeding ecology, water utilization, and physiology (Fry 2006, Karasov and

Martinez del Rio 2007). Nitrogen isotopes indicate trophic level (Deniro and Epstein 1981). Fractionation

during urea formation causes $^{15}N/^{14}N$ to increase approximately 3‰ with trophic level. Carbon isotopes

reflect the photosynthetic pathway of plants forming the base of the food web (Kelly 2000). C_3 plants

are depleted relative to C_4 and crassulacean acid metabolism (CAM) plants in $^{13}C/^{12}C$ and form distinct

signatures in animal tissue (Tieszen et al. 1983). Hydrogen isotopes (D/H) integrate drinking water, free

water from food, and exchangeable hydrogen and are often used to determine the source water utilized

during tissue formation (Hobson et al. 1999). Oxygen isotopes integrate drinking water, atmospheric

oxygen, and food (Podlesak et al. 2008) and generally increases with aridity and water stress (Levin et al.

2006). Ecological inferences based on stable isotope ratios vary with climate, geography, taxonomic

group, and physiological condition (Gannes et al. 1997, Post 2002, McCutchan et al. 2003, Vanderklift

and Ponsard 2003, Hwang et al. 2007, Podlesak et al. 2008). In spite of such variability, the utility of stable isotopes in ecological investigations is unquestionable (West et al. 2006).

Given proposals to dramatically increase groundwater pumping near GBNP, the potential of groundwater pumping to negatively affect park riparian areas, and the park's mandate to preserve biodiversity, we examined the stable isotope ecology of small mammal communities in Great Basin National Park. Our objectives were to use stable isotopes to characterize the feeding ecology, water utilization, and interactions of the small mammal community and we use this information to discuss the future effects of groundwater withdrawal on small mammal communities.

METHODS

Study Area

Great Basin National Park (N – 38.98°, W - -114.30°; 31,201 hectares) is located in the South Snake Range, east central Nevada, in the Central Basin and Range ecoregion (Figure 1). Elevations range from 1,621m in the town of Baker to over 3,982m at the summit of Wheeler Peak. The climate is cool and arid. Although most precipitation falls as snow, summer convection generates thunderstorms which also contributes to local precipitation (Acheampong 1992).Climate varies dramatically with elevation. In Garrison Utah (elevation - 1609 m) mean annual precipitation is 19 cm and mean annual temperature is 10°C (Western Regional Climate Center, unpubl. data). At the Lehman Caves Visitor Center (elevation – 2832 m) annual precipitation is 33 cm and the mean annual temperature is 9°C (Western Regional Climate Center, unpubl. data). Although there are no weather stations below Wheeler Peak, mean annual precipitation is estimated between 76 and 89 cm (Western Regional Climate Center, unpubl. data).

There are twelve perennial streams in the park which originate at high elevations (Jacobs and Flora 1994) from snowmelt and become increasingly influenced by groundwater as they descend (Elliot

et al. 2006). Riparian plant communities are well developed along streams and include plant species

such as narrowleaf cottonwood (*Populus anguistifolia*), redosier dogwood (*Cornus sericea)*, quaking

aspen (*P. tremuloides*), willow (*Salix spp.*), Woods' rose (Rosa *woodsii)*, sedges (*Carex ssp.*) and rushes

(*Juncus ssp.*) (Beever et al. 2005). Riparian trees are primarily deciduous at lower and intermediate

elevations and become coniferous at higher elevations (Beever et al. 2005).

Field Methods

*Small Mammal*s - Small mammals were trapped with Sherman live traps (sizes; SFAL;5 X 6 X 23 cm; LFA –

8 X 9 X 23 cm; XLF15 – 10 X 11 X 38 cm) in Lehman, Snake and Strawberry Creek watersheds. Trapping

methods consisted of randomly selected transects oriented perpendicular to streams (four transects per

watershed; Chapter 1) and directed transects which focused on underrepresented habitats preferred by

rarer species, such as shrews and voles. Trapping was conducted from 23 July to 27 September 2007.

Traps were set and baited with sunflower and milo seeds between 17:00-20:00 and checked

between 05:00 - 10:00. Small mammals were ear tagged, identified to species, visually assessed for sex,

hair samples collected, weighed with a Pesola spring scale, and released. Recaptured individuals were

weighed and assessed for ear tag number, species, and sex.

Water – Stream water was sampled at the intersection of each trapping transect with the stream, four

samples per watershed in August of 2007. Precipitation samples were collected at the Resource

Management Office near Lehman Creek (2081 meters) and the Great Basin Visitors Center in Baker

(1620 meters) in August and September 2007.

Isotope Analysis

Hair samples, approximately 3 cm^2 in area, were collected dorsally, immediately anterior to the

base of the tail. To supplement samples sizes of rare species, data from 14 study skins collected in 2006

are included. Hair was sonicated with deionized water for 30 minutes, lipid extracted with petroleum

ether for 30 minutes, and subsamples of approximately 0.75 mg measured in tin cups (Costech - 5 X 9 mm). Deuterium and oxygen samples were prepared similarly except that subsamples of approximately 0.5 mg were measured in silver cups (Costech – 5 X 9 mm).

Nitrogen and carbon stable isotopes were analyzed on Brigham Young University's Elemental Analyzer (EA) interfaced to a Delta V Advantage Isotope Ratio Mass Spectrometer (IRMS). Hydrogen and oxygen stable isotopes were analyzed by Cornell University's Stable Isotope Laboratory on a Temperature Conversion Elemental Analyzer (TC/EA) interfaced to a Thermo Delta V IRMS. Water samples were analyzed on Brigham Young University's Finnigan Delta Plus (Bremen, Germany) IRMS interfaced to Gasbench (Finnigan, Bremen, Germany) for oxygen and deuterium.

Isotope results are presented relative to international standards in conventional delta (δ) notation as ‰: $\delta_{sample} = R_{sample} - R_{standard}/R_{standard}$ X 1000, where R is the ratio of the heavy isotope to the light isotope.

Data are reported as the ratio of heavy to light isotope relative to atmospheric nitrogen for nitrogen, Vienna Peedee belemnite marine limestone (VPDB) for carbon, and Vienna Standard Mean Ocean Water (VSMOW) for deuterium and oxygen (Fry 2006). Data were normalized against standards for accuracy using linear regression and checked for precision against duplicate samples. When duplicate samples were ran we report their mean value. Mean reproducibility for duplicate hair samples was: 0.69‰ ± 0.61 (n=53) for $\delta^{15}N$ and 0.31‰ ± 0.29 (n=51) for $\delta^{13}C$. Standards, measured values, precision and true values for $\delta^{15}N$, $\delta^{13}C$, δD and $\delta^{18}O$ are summarized in table 1.

Data Analysis

Small Mammal Isotopes - I used one-way ANOVA and post hoc Tukey tests to compare $\delta^{15}N$, $\delta^{13}C$, δD, and $\delta^{18}O$ between species with sample sizes greater than ten. Although no statistical analyses were performed for species with sample sizes less than ten, data for all species are presented for preliminary

comparison and discussion. When statistical differences are reported, they are the difference in mean isotope ratios between species. For discussion purposes, small mammals were broken into the following taxonomic groups: Order Carnivora, Insectivora, and Rodentia. Rodentia was further divided into families: Sciuridae, Heteromyidae, and Muriade. Muridae was broken into subfamilies: Sigmodontinae, Arvicolinae, and Sigmodontinae (Vaughan 1986).

Water Isotopes - I compared stream water and precipitation using a t-test with unequal variances. Statistical differences are reported as differences in means. I used simple linear regression to correlate δD and δ^{18}O of stream and precipitation samples and present the regression equation as local meteoric water line for the Snake Range. I compare this equation with the global meteoric water line.

Correlation of mammal hair isotopes with plants and water - I used one-way ANOVA and post hoc Tukey tests to compare δD and δ^{18}O between mammal hair, stream water, and precipitation.

All statistical analyses were done with Minitab 14 (Minitab 2004).

<div align="center">RESULTS</div>

Small Mammal Isotopes

A total of total of 901 isotope results, excluding duplicates, were obtained from 13 species and 254 individuals (Table 2). Small mammals differed in δ^{15}N ($F_{4,214}$ = 15.7, $P <$ 0.0001; Table 2; Figures 3 and 4). Piñon mice were higher in δ^{15}N than Great Basin pocket mice by 3.34‰, deer mice by 1.88‰, and cliff chipmunks by 2.60‰. Western harvest mice were higher in δ^{15}N than pocket mice by 3.71‰, deer mice by 2.23‰, and cliff chipmunks by 2.95‰. Pocket mice, deer mice and cliff chipmunks did not differ in δ^{15}N. Piñon and harvest mice did not differ in δ^{15}N.

Species differed in δ^{13}C ($F_{4,212}$ = 2.90, P = 0.023; Table 2; Figures 3 and 4). Mean pocket mouse δ^{13}C was less than piñon mice by 1.58‰. No other species differences were found.

There were no interspecific differences in δD ($F_{4,176}$ = 1.49, P = 0.206; Table 2; Figures 5 and 6).

Species differed in δ^{18}O ($F_{4,176}$ = 7.34, P < 0.0001; Table 2; Figures 5 and 6). Mean pocket mouse δ^{18}O

was less than deer mice by 5.8 ‰, piñon mice by 6.5‰, harvest mice by 6.9‰, and cliff chipmunk by

5.0‰. No other differences in δ^{18}O were found between species.

Water Isotopes

One stream sample from Snake Creek showed an evaporative signature and was dropped from analysis

(Table 3). Stream water δD differed by watershed ($F_{2,10}$ = 117.28, P < 0.0001; Figure 7). Lehman was

7.5‰ higher than Snake and 7.0‰ higher than Strawberry in δD (Post Hoc-Tukey test). Stream water

δ^{18}O also differed by watershed ($F_{2,10}$ = 13.02, P = 0.003; Figure 8). Lehman was 0.9‰ higher than Snake

and 0.8‰ higher than Strawberry. These differences likely reflect differences in source water or

underlying geology.

Mean precipitation δD was 40.97‰ greater than stream water but this difference was not

significant (t = 1.51, df = 3, P = 0.229; Figure 9). Mean precipitation δ^{18}O was 6.7‰ greater than stream

water but this difference was also not significant (t = 1.61, df = 3, P = 0.206; Figure 9).

The local mean water line for the South Snake Range was δD = - 14.02 + 6.324 δ^{18}O (R^2 = 0.991; P

< 0.001; Figure 10) differing slightly from the global mean water line of δD = -10 + 8 δ^{18}O (Craig 1961).

Correlation of mammal hair and water isotopes

Although no differences were found between mammal hair, precipitation, and stream water δD ($F_{2,214}$ =

2.70, P = 0.069), hair more closely reflected stream water than precipitation (Figures 9 and 10) .

Mammal hair was higher than water samples in δ^{18}O ($F_{2,214}$ = 232.99, P < 0.0001). Hair was 23.5‰ higher

than precipitation and 30.3‰ higher than stream water.

DISSCUSSION

Stable isotope data suggest resource partitioning by the small mammal community. Partitioning was primarily seen in $\delta^{15}N$ and $\delta^{13}C$ which reflect feeding ecology (trophic level and primary production source), but was also seen in $\delta^{18}O$. Major differences in $\delta^{15}N$ and $\delta^{13}C$ isotopes were between taxonomic groups, while similarity was highest within these groups.

The Sigmodontinae (excluding woodrats) were similar in $\delta^{15}N$ and $\delta^{13}C$ indicating similar food habits of deer, piñon, and harvest mice. Piñon and harvest mice did not differ in $\delta^{15}N$, suggesting potential competition between these species due to utilization of similar food resources. However, harvest mice in our study were generally restricted to riparian habitat, while piñon mice were found in xeric uplands (Chapter 1). Habitat segregation is an important mechanism that minimizes interspecific competition in small mammal communities (Findley 1954, Rosenzweig and Winakur 1969, Sheppard 1971). Sigmodontinae are opportunistic omnivores and feed on both insects and vertebrates (Johnson 1961, Douglas 1969, Hoffmeister 1981, Webster and Jones 1982). Harvest and piñon mouse $\delta^{15}N$ was significantly higher than deer mice, suggesting that these species fed on a higher proportion of insects and animal material than deer mice.

Sigmodontinae were relatively enriched in $\delta^{13}C$. Plants exhibiting C_4 and CAM photosynthetic pathways are relatively uncommon in GBNP (Clifton 2008), but may have been fed upon preferentially by Sigmodontinae species. Johnson (1961) found that deer and harvest mice fed on a large proportion of prickly pear cactus (*Opuntia ssp.*), a CAM plant. C_4 and CAM plants retain moisture and continue to photosynthesize later in the growing season relative to C_3 plants (Kemp and Williams 1980) and may provide an important source of water and nutrients to small mammals. For example scattered prickly pear cactus was present across our study site. Alternatively, fractionation of $\delta^{13}C$ may have occurred between ingestion of C_3 plants and assimilation into Sigmodontinae hair. While trophic enrichment of

$\delta^{13}C$ is generally considered less important than $\delta^{15}N$ (Kelly 2000), its occurrence is widespread (Tieszen et al. 1983) with a fractionation of 3‰ frequently reported in hair (Roth and Hobson 2000, Sponheimer et al. 2003, Dalerum and Angerbjorn 2005, Hwang et al. 2007).

$\delta^{15}N$ and $\delta^{13}C$ of Arvicolinae was consistent with the herbivorous trophic level and preference for C_3 plants of voles (Dubay et al. 2008). This similarity in $\delta^{15}N$ and $\delta^{13}C$ between the three vole species was somewhat unexpected, as habitat preferences vary dramatically between species. Long-tailed and montane voles prefer mesic, riparian habitats (Hall 1946, Getz 1985) while sagebrush voles are found in xeric uplands (Carroll and Genoways 1980). Long-tailed and montane voles are locally sympatric in riparian habitats and probably feed on similar plant species (Smolen and Keller 1987, Sera and Early 2003), while sagebrush voles occur in upland sagebrush habitat and feed on a different complement of plants (Carroll and Genoways 1980). These observations suggest that sagebrush voles minimize competition with montane and long-tailed voles by utilizing a different habitat. Competition has been suggested as a mechanism for explaining *Microtus* distribution (Findley 1954, Rose and Birney 1985) and is supported by our observations that long-tailed and montane voles utilize similar food resources within riparian habitats.

Chipmunks (Family Sciuridae) were similar in $\delta^{15}N$ and $\delta^{13}C$. Interference competition, aggressive interactions, habitat segregation, utilization of similar food sources, and altitudinal zonation are well documented in *Tamias* species (Brown 1971, Heller 1971, Sheppard 1971, Lawlor 1998, Rickart 2001). Similarity in stable isotope ratios corroborates findings that chipmunks compete for similar food resources, minimizing competition through habitat separation (Rickart et al. 2008).

Pocket mice (Heteromyidae) were lowest in $\delta^{15}N$. Although generally omnivorous (Verts and Kirkland 1988), similarity of pocket mouse $\delta^{15}N$ to herbivorous voles and desert woodrats, is evidence of

a plant based diet (Carroll and Genoways 1980, Verts and Carraway 2002). Competition with the more abundant, omnivorous Sigmodontinae may push pocket mice more strongly towards herbivory in GBNP.

Although our woodrat sample was small (n=5), it was most similar to pocket mouse δ^{15}N and δ^{13}C, reflecting a herbivorous diet facilitated by microbial fermentation (Smith 1997, Verts and Carraway 2002). Sample sizes were small for Carnivora (ermine, n = 1) and Insectivora (vagrant shrew, n = 3), but were highest in δ^{15}N, reflecting the high trophic positions of these species (King 1983, Gillihan and Foresman 2004).

Small mammal species were similar in δD which closely resembled stream water. Stream water in turn was consistent with deuterium isoclines in the western United States (Hobson and Wassenaar 1997). For the majority of the year stream water is the only surface water available GBNP and this similarity suggests that stream water is an important source of water to the small mammal community. However stream water δD closely reflects snow, the primary source recharge source to streams through direct snowmelt and groundwater (Steve Nelson, personal communication). Both snowmelt and groundwater are also sources of water for vegetation. Vegetation is important source of δD and water for small mammals. This similarity between water sources to the small mammal community confounds our ability to demonstrate a direct relationship between stream water and small mammal δD. Additionally small mammals living far from perennial streams are unlikely to move large distances (O'Farrell 1974) to regularly drink stream water and likely obtain most of their water and δD from free water in their food (Birchall et al. 2005, Podlesak et al. 2008). For riparian species and upland species which include riparian habitat in their home ranges, stream water is likely an important water source. Additional sampling of precipitation, stream water, cave water and small mammal body water should clarify the relative contributions of streams, precipitation and vegetation to small mammal δD.

Atmospheric oxygen and water are primary sources to body water $\delta^{18}O$ (Kohn 1996). To examine the contributions of atmospheric oxygen and stream water oxygen to small mammal hair $\delta^{18}O$, I used the following mixing model modified from Wheeler et al. (2007):

$F_{water} = (\delta^{18}O_{hair} - \delta^{18}O_{air})/ (\delta^{18}O_{water} - \delta^{18}O_{air})$. Where F_{water} is the fraction of air contributing to the hair $\delta^{18}O$, $\delta^{18}O_{hair}$ is the mean value for hair (16‰), $\delta^{18}O_{air}$ is the mean $\delta^{18}O$ value for atmospheric oxygen (23.5‰), and $\delta^{18}O_{water}$ is the mean $\delta^{18}O$ value for stream water (-16‰). The model estimates that 19% of hair $\delta^{18}O$ is from surface water while 81% is from atmospheric oxygen. While unlikely that atmospheric oxygen and stream water are the sole sources of $\delta^{18}O$ to the small mammal community (ie food also contributes) this model suggests that the contributions of atmospheric oxygen to small mammal $\delta^{18}O$ may be greater than those of drinking water. This may be due to generation of metabolic water.

Mammals lose significant volumes of body water through evaporation and breathing. Therefore body water (the source water for hair formation) does not reflect surface water in $\delta^{18}O$ (Kohn 1996). Fractionation associated with breathing during water vapor formation leads to substantially depleted $\delta^{18}O$ in exhaled vapor and higher $\delta^{18}O$ in body water than in drinking water (Kohn 1996). This is consistent with our results of higher $\delta^{18}O$ in hair than stream water. Species living in burrows inhabit a more humid environment than surface species which could affect their $\delta^{18}O$. However differences in $\delta^{18}O$ were not consistent between fossorial species, such as pocket mice and woodrats, and the effects of burrows on $\delta^{18}O$ seem relatively unimportant. The higher surface area to volume ratios of small mammals would be expected to lead to additional evaporative water losses in addition to those associated with breathing.

$\delta^{18}O$ generally increases with aridity (water deficit) in species sensitive to evaporative water loss (Levin et al. 2006). Pocket mice were lowest in $\delta^{18}O$, Sigmodontinae intermediate, and woodrats and

voles most enriched. Woodrats and voles have low water use efficiency (ie; high water flux; Schmidt-Nielsen 1979, Rose and Birney 1985) while Great Basin pocket mice have high water use efficiency (low water flux; Schmidt-Nielsen 1979). Thus in our small mammal community, water use efficiency (sensitivity to aridity) was inversely proportional to δ^{18}O. These results are directly opposite of Smith et al. (2002) who found that small mammal species with higher water requirements (grasshopper mice) were lowest in δ^{18}O while species with the lowest requirements (Heteromyidae) were highest. Smith et al. (2002) did not propose a mechanism for their observations but used carbonate apatite (bone) rather than hair as their tissue source. Bone is metabolically active and reflects the integration of δ^{18}O over the life of the animal, while hair is metabolically inactive after formation and reflects δ^{18}O at the time of its formation. However as Podelsak et al. (2008) found hair and bone δ^{18}O in close agreement, our conflicting results seem to reflect something other than turnover.

δ^{18}O integrates food, surface water, physiology, water flux, climate, and metabolism. Due to its complexity in interpretation δ^{18}O is seldom used in ecological investigations. While our data suggest that water flux is an important in interpreting δ^{18}O in small mammals, further lab work and field work are needed to elucidate its meaning.

Future Effects of Groundwater Withdrawal on Small Mammal Communities

Stream incision (stream bed lowering due to erosion; Shields et al. 1994) is a process analogous to groundwater withdrawal in its hydrologic and ecological effects. Stream incision lowers groundwater levels and reduces stream flows (Chambers et al. 2004). Such hydrologic alterations negatively affect aquatic diversity (Shields et al. 1994) and kill riparian vegetation (Bravard et al. 1997) leading to an increase in xeric upland vegetation and a decrease in mesic riparian vegetation in riparian areas (Wright and Chambers 2002). Beyond these immediate effects, there is little work on the trophic consequences of hydrologic changes, particularly in small mammal communities (Nilsson and Dynesius 1994). Thus

while the major benefit of this study may be to provide a baseline of the small mammal communities in areas susceptible to groundwater withdrawal, it is important to consider the effects of groundwater on the small mammal community a priori.

Similarity of small mammal δD to stream water suggests that perennial streams are an important source of drinking water to small mammals. Reductions in flow would reduce the availability of surface water, particularly where perennial streams become intermittent. Riparian species, such as voles require more drinking water than xeric adapted upland species (Rose and Birney 1985) and would most immediately be impacted by changes in stream flow. Additionally our $\delta^{18}O$ suggest that small mammals are very sensitive to evaporation and are already experiencing high water stress. For species relying on stream water, reductions in stream flows and conversion of perennial stream reaches into intermittent would increase water stress in already stressed animals.

If groundwater levels are reduced beyond a threshold, riparian vegetation would die (Scott et al. 1999, Amlin and Rood 2002) and xeric vegetation would encroach into riparian areas, reducing cover, production and biomass. Small mammals utilize riparian areas partially due to the increased cover it provides relative to the uplands (Stamp and Ohmart 1979) and reductions in vegetation would increase vulnerability to predation. Plant production in riparian areas is higher, of higher quality, has more free water, is more palatable than the uplands (Parsons et al. 2003) and is an important source of forage and water to small mammals. Reductions in mesic vegetation would also reduce the availability of free water in food also increasing water stress.

Decreases in vegetation cover alter riparian microclimates as insolation increases and transpiration decreases (Chambers et al. 2004). Increased temperature and decreased relative humidity would increase water stress in small mammals. This may be particularly important for riparian species

which require cooler and more humid conditions than upland species and would experience increased

water stress (Rose and Birney 1985).

Changes in groundwater levels would also reduce invertebrate production and alter

invertebrate species composition. Aquatic invertebrates would be affected by reduced stream flows and

terrestrial invertebrates by changes in riparian vegetation. Vagrant shrews are insectivorous (Gillihan

and Foresman 2004) and reductions in invertebrates, their sole food source, would be disastrous. As

omnivores, harvest mice often feed on invertebrates (Johnson 1961, Webster and Jones 1982) and

would similarly be negatively affected by reductions in invertebrates. Ermine are carnivores and would

be affected by loss of small mammals, their primary prey (King 1983).

Small mammals in GBNP are an important component of biodiversity and biodiversity processes.

These communities have recently shifted due to habitat changes caused by fire suppression (Rickart et

al. 2008) and are expected to be negatively impacted by climate change (McDonald and Brown 1992).

Increases in the rate of groundwater pumping adjacent to Great Basin National Park has high potential

to further alter small mammal communities by lowering water tables and converting riparian habitat to

habitat more closely resembling xeric upland habitat. Changes in groundwater levels, stream flows,

vegetation, microclimate, and invertebrates will provide the mechanisms affecting riparian dependent

small mammals and will likely result in a decrease in diversity and a loss of riparian species from affected

areas.

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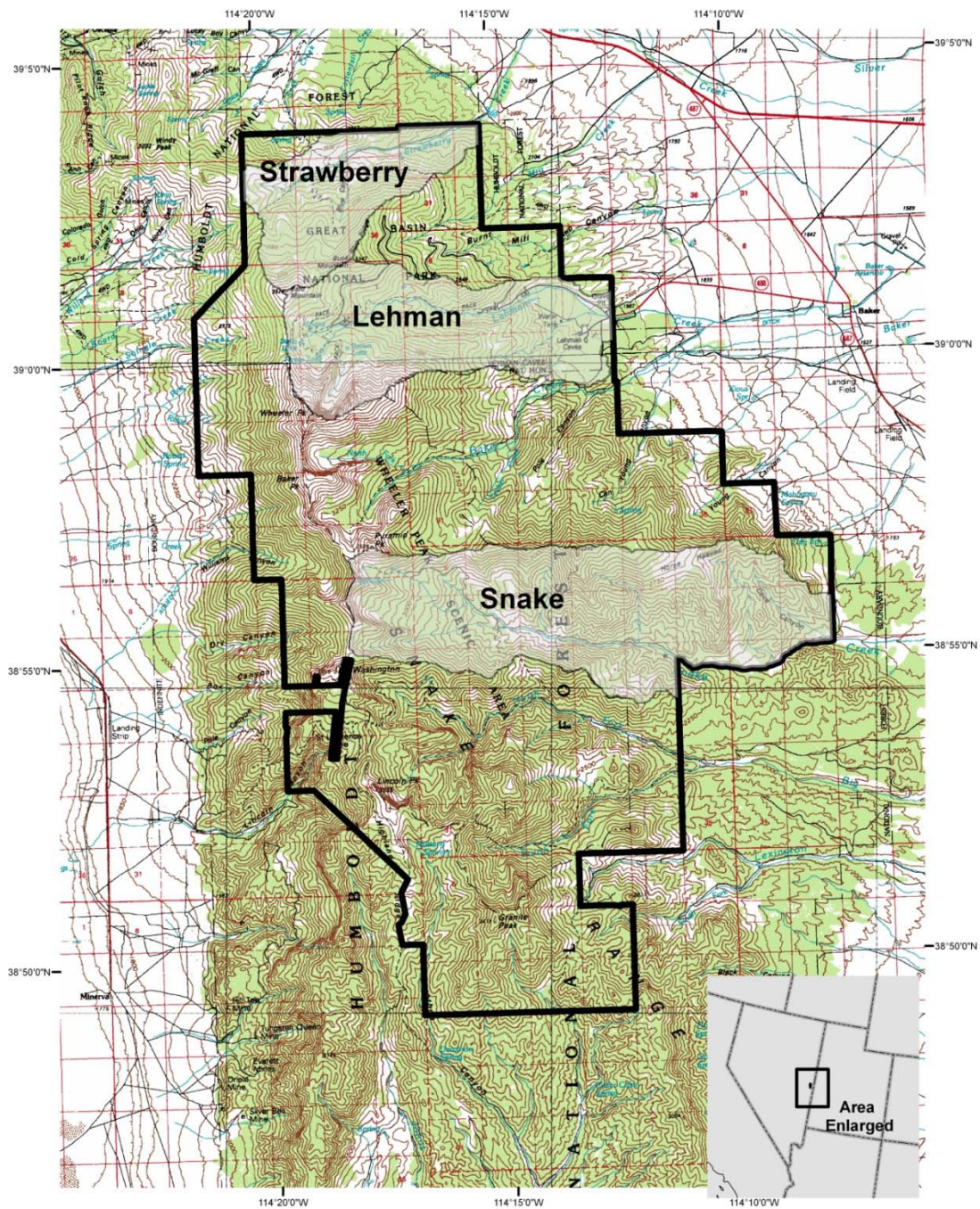Figure 1. Great Basin National Park and the Great Basin desert.

Figure 2. Watersheds sampled in Great Basin National Park. The mean elevations sampled by watershed were: Strawberry (2541 m), Lehman (2053 m), and Snake (2044 m).
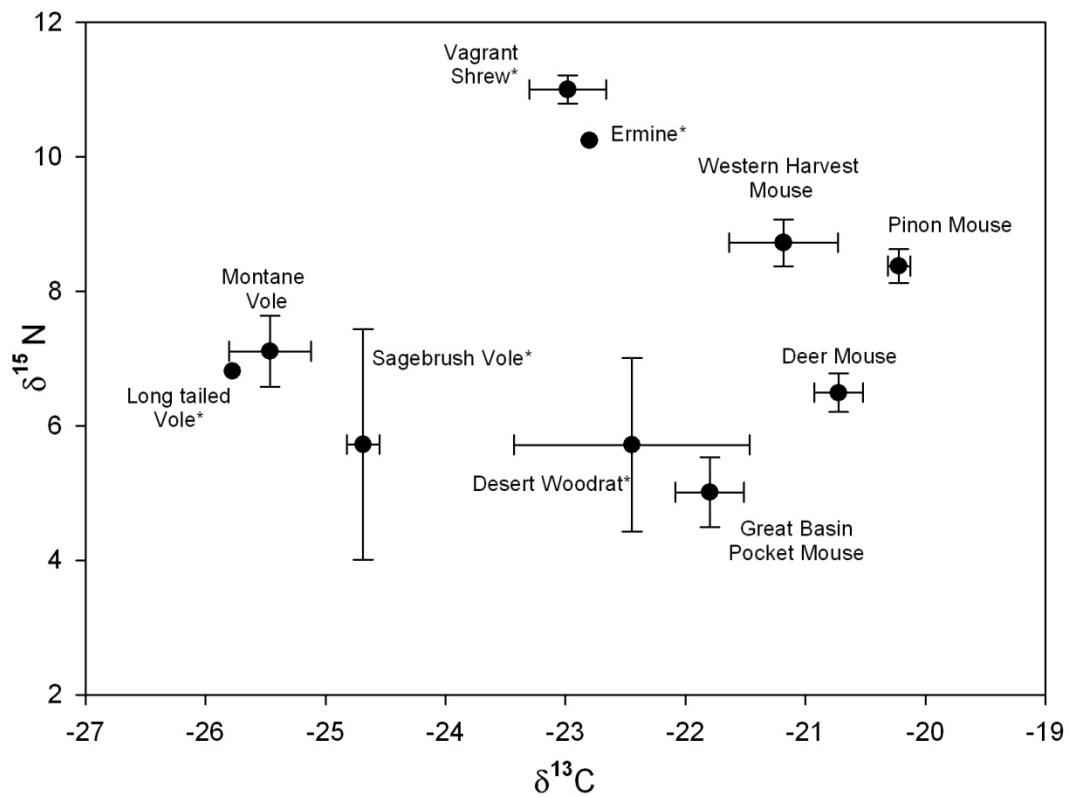
Figure 3. Mean δ^{15}N and δ^{13}C stable isotope ratios ± SE for 10 small mammal species from Great Basin National Park. Units for stable isotope ratios are per mil. Sample sizes for species with * were less than 10 and statistical analyses were not performed.

Figure 4. Mean δ^{15}N and δ^{13}C stable isotope ratios ± SE for three chipmunk species from Great Basin

National Park. Units for stable isotope ratios are per mil. Sample sizes for species with * was less than 10
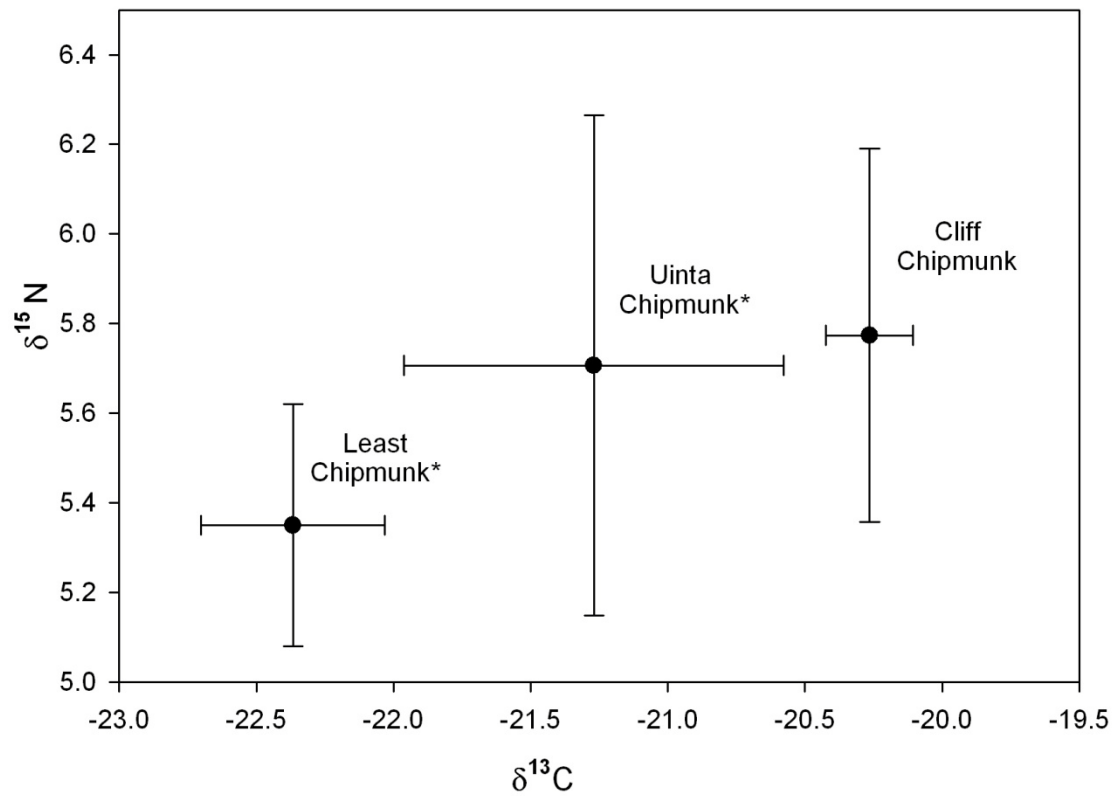
and statistical analyses were not performed.

Figure 5. Mean δD and δ^{18}O stable isotope ratios ± SE for six small mammal species from Great Basin National Park. Units for stable isotope ratios are per mil.

Figure 6. Mean δD and δ^{18}O stable isotope ratios ± SE for three chipmunk species from Great Basin

National Park. Units for stable isotope ratios are per mil. Sample sizes for species with * was less than 10
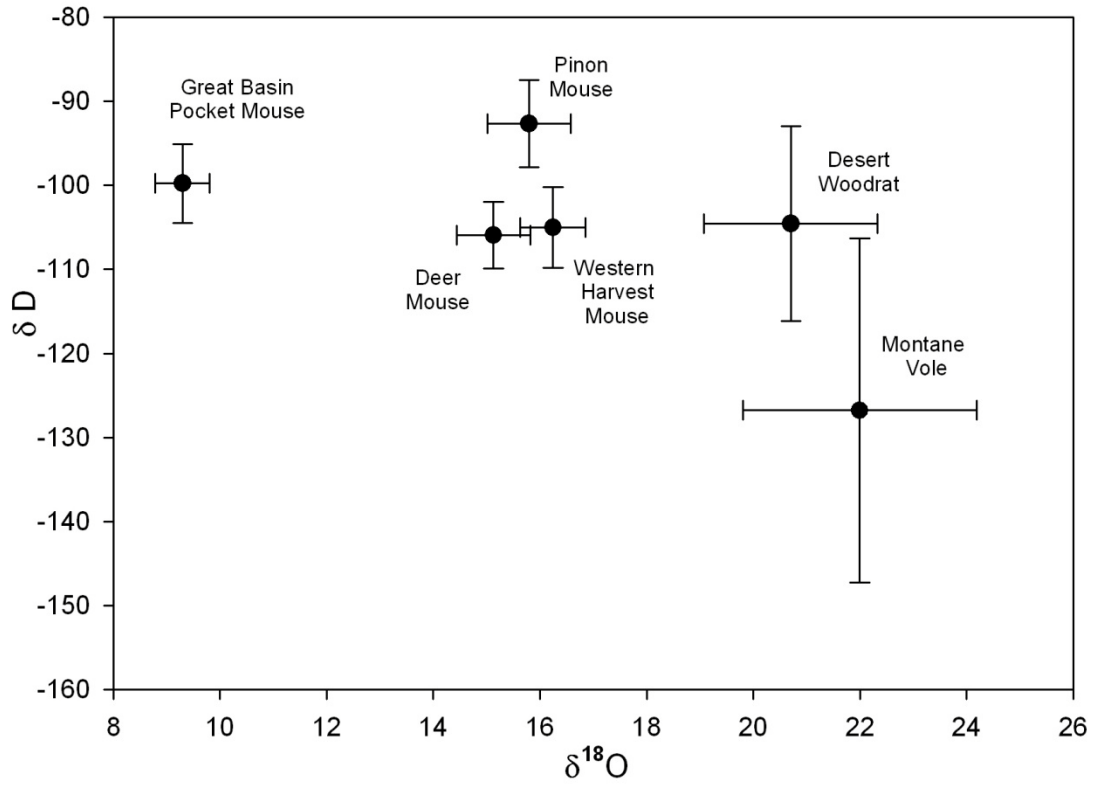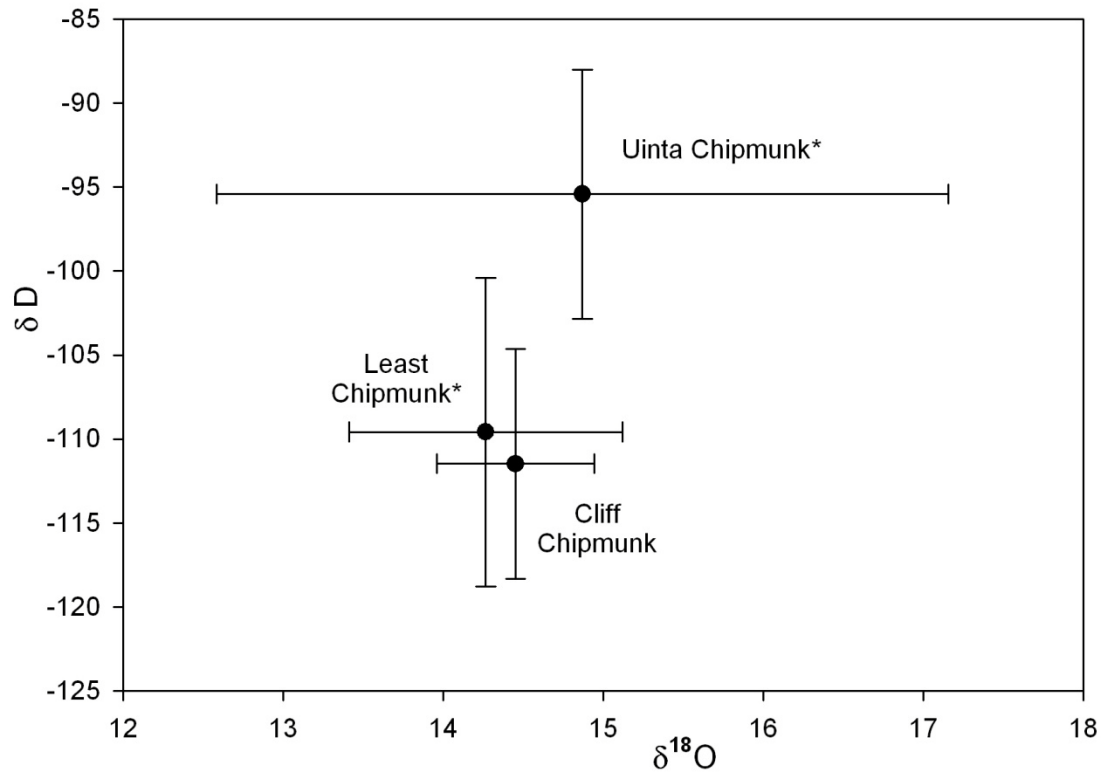
and statistical analyses were not performed.

Figure 7. Mean stream water δD ± SE with individual values for three watersheds in Great Basin National
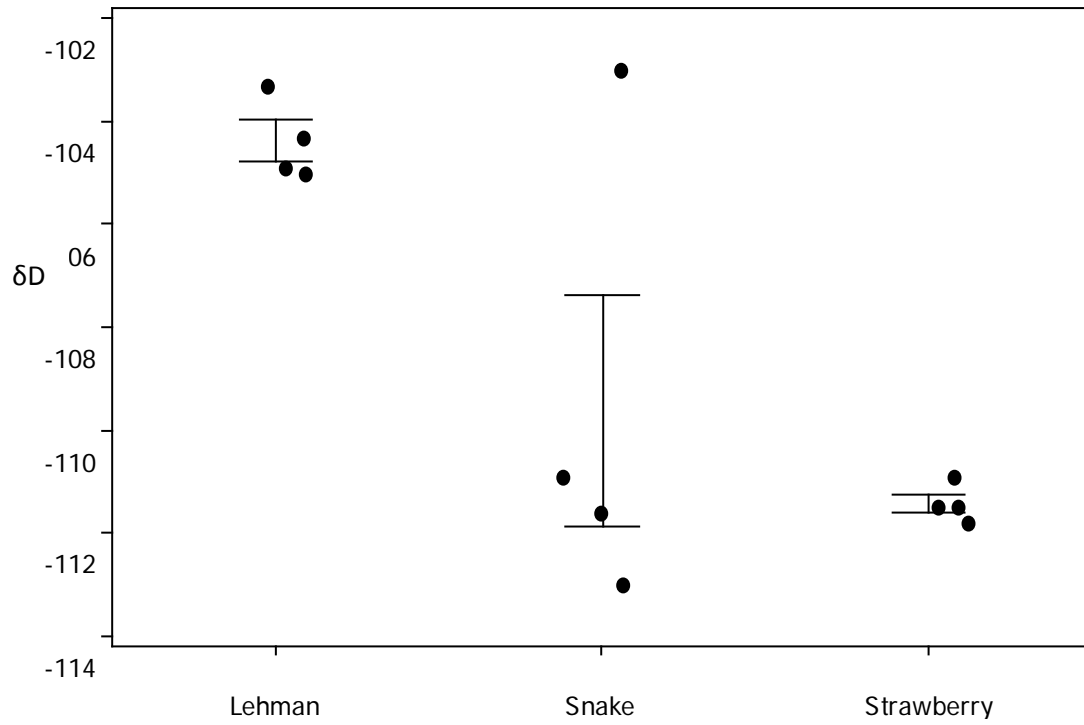
Park. Units are per mil.

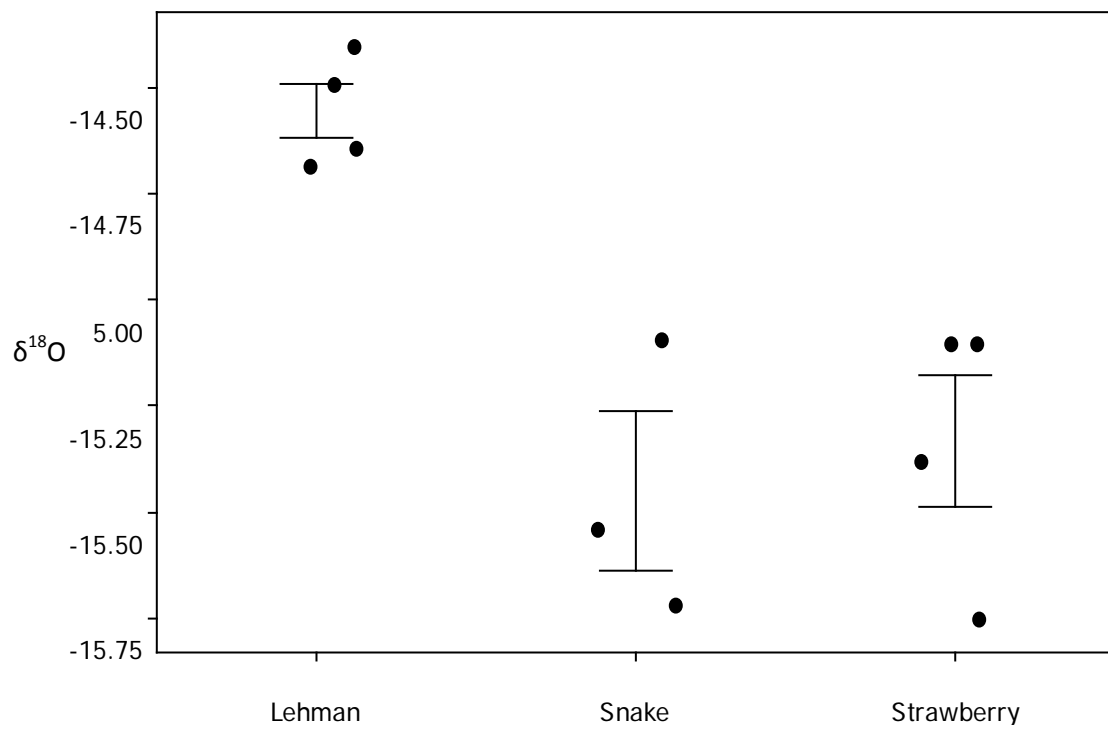Figure 8. Mean stream water $\delta^{18}O \pm SE$ of with individual values for three watersheds in Great Basin National Park. Units are per mil.

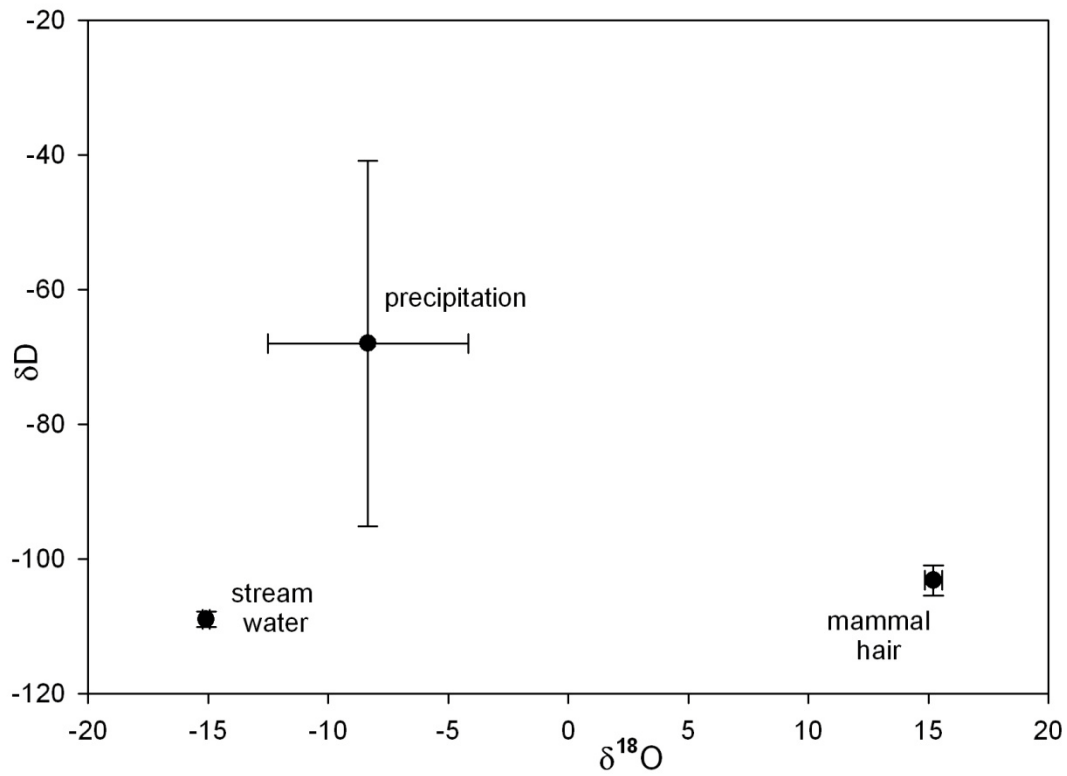Figure 9. δD and δ^{18}O mean ± SE for stream water, precipitation, and small mammal hair from Great
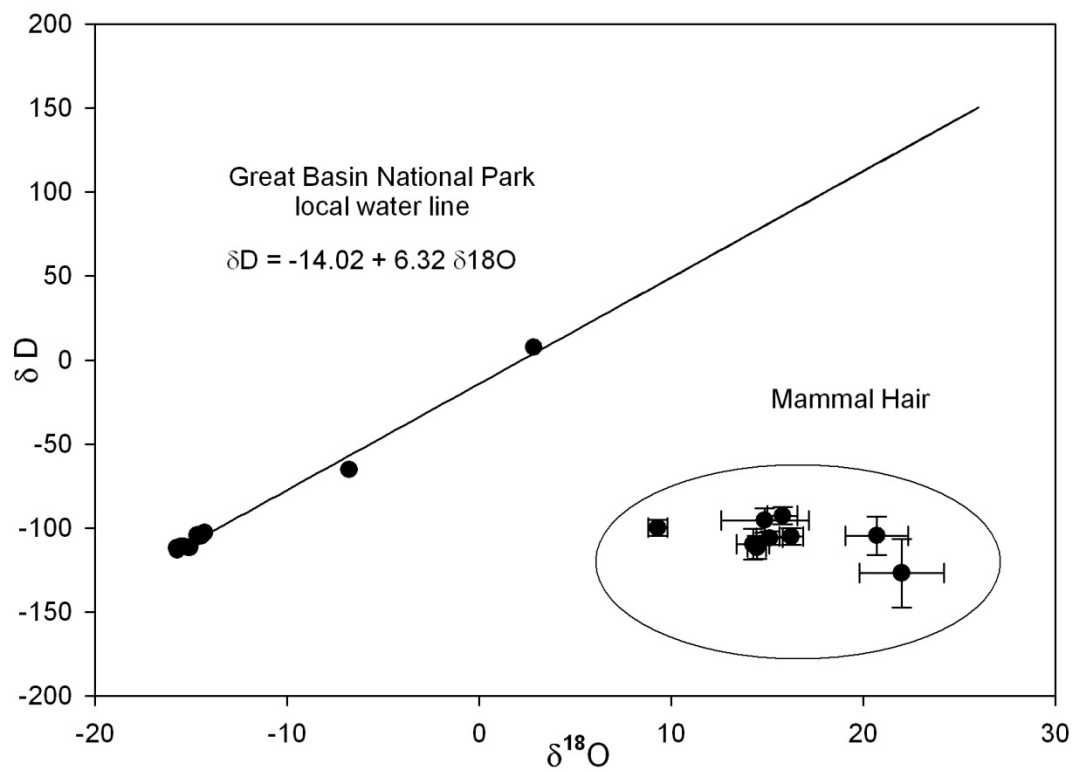
Basin National Park. Units are per mil.

Figure 10. Local meteoric water line and small mammal mean ± SE by species for δD and δ^{18}O. Units are per mil.

TABLES

Table 1. Mean measured values for isotopic standards ± 1SD with sample size in parenthesis and true values for isotopic standards. Units are per mil. Standards with an asterisk are internal laboratory standards. True values for other standards are from Coplen et al (2006).

Standard	Measured $\delta^{15}N$	True $\delta^{15}N$	Measured $\delta^{13}C$	True $\delta^{13}C$	measured δD	true δD	measured $\delta^{18}O$	true $\delta^{18}O$
Albacore Tuna*	11.2 ± 0.25 (42)	11.13	-19.6 ± 0.24 (38)	-19.62				
ASP1*	- 5.2 ± 0.27 (43)	-5.27	-27.8 ± 0.22 (39)	-28.05				
ASP2*	2.4 ± 0.32 (25)	2.38						
Bovine Liver*	7.4 ± 0.37 (45)	7.5	-21.9 ± 0.24 (41)	-21.5				
L-SVEC			-46.5 ± 0.40 (38)	-46.5				
UCLA*			2.519 ± 1.0 (34)	2.5				
USGS 25	-30.4 ± 0.16 (42)	-30.3						
USGS 26	53.6 ± 0.30 (4)	53.6						
benzoic acid*					-105.1 ± 1.4 (15)	-105	23.4 ± 0.18 (15)	23.4
deer hair*					-99.8 ± 1.8 (18)	-99.49	12.6 ± 0.30 (18)	12.38
Goose feather*					-144.3 ± 1.8 (5)	-144.62	7.7 ± 0.28 (5)	7.53
IAEA CH-7					-100.0 ±1.05 (9)	-100.33		
NBS 22*					-120.7 ± 2.0 (8)	-120		
IAEA CO-1							28.4 ± 0.06 (5)	28.4
IAEA CO-8							7.7 ± 0.14 (5)	7.5

Table 2. Mean isotope ratios ± SE for 13 small mammal species from Great Basin National Park. Units are per mil. Sample sizes are in parenthesis.

Taxon	Common name	Scientific Name	$\delta^{15}N$	$\delta^{13}C$	δD	$\delta^{18}O$
Arvicolinae	Sagebrush Vole	*Lemmiscus curtatus*	5.72 ± 1.72 (2)	-24.69 ± 0.14 (2)		
	Long-tailed Vole	*Microtus longicaudus*	6.81 ± (1)	-25.77 ± (1)		
	Montane Vole	*Microtus montanus*	7.11 ± 0.53 (12)	-25.46 ± 0.34 (11)	-126.77 ± 20.49 (5)	22 ± 2.19 (5)
Carnivora	Ermine	*Mustela erminea*	10.24 ± (1)	-22.8 ± (1)		
Insectivora	Vagrant Shrew	*Sorex vagrans*	11 ± 0.21 (3)	-22.98 ± 0.32 (3)		
	Desert Woodrat	*Neotoma lepida*	5.71 ± 1.29 (5)	-22.45 ± 0.98 (5)	-104.57 ± 11.61 (5)	20.7 ± 1.63 (5)
Sigmodontinae	Deer Mouse	*Peromyscus maniculatus*	6.49 ± 0.29 (84)	-20.72 ± 0.2 (82)	-105.94 ± 4 (61)	15.13 ± 0.69 (61)
	Piñon Mouse	*Peromyscus truei*	8.37 ± 0.25 (47)	-20.22 ± 0.09 (47)	-92.68 ± 5.18 (41)	15.79 ± 0.78 (41)
	Western Harvest Mouse	*Reithrodontomys megalotis*	8.72 ± 0.35 (48)	-21.18 ± 0.45 (48)	-105.01 ± 4.81 (39)	16.24 ± 0.61 (39)
Heteromyidae	Great Basin Pocket Mouse	*Perognathus parvus*	5.01 ± 0.52 (15)	-21.8 ± 0.28 (15)	-99.79 ± 4.65 (16)	9.3 ± 0.51 (16)
Sciuridae	Cliff Chipmunk	*Tamias dorsalis*	5.77 ± 0.42 (21)	-20.26 ± 0.16 (21)	-109.59 ± 9.19 (20)	14.27 ± 0.85 (20)
	Least Chipmunk	*Tamias minimus*	5.35 ± 0.27 (6)	-22.37 ± 0.33 (6)	-111.48 ± 6.85 (6)	14.45 ± 0.49 (6)
	Uinta Chipmunk	*Tamias umbrinus*	5.71 ± 0.56 (7)	-21.27 ± 0.69 (7)	-95.42 ± 7.41 (7)	14.87 ± 2.29 (7)

Table 3. Precipitation and stream data from Great Basin National Park. Snake # 4 showed an evaporative signature and was dropped from analysis.

Location	type	$\delta^{18}O$	SD	δD	SD	ID	Date	elevation (m)
Straw #1	stream	-15.10	0.2	-111.5	1.0	Straw1	August	2428
Straw #2	stream	-15.75	0.2	-111.8	1.0	straw2	August	2472
Straw #3	stream	-15.10	0.2	-111.5	1.0	straw3	August	2532
Straw #4	stream	-15.38	0.2	-110.9	1.0	straw4	August	2628
Lehman #1	stream	-14.40	0.2	-103.3	1.0	lehman1	August	2037
Lehman #2	stream	-14.68	0.2	-104.3	1.0	lehman2	August	2083
Lehman #3	stream	-14.49	0.2	-104.9	1.0	lehman3	August	2020
Lehman #4	stream	-14.64	0.2	-105.0	1.0	lehman4	August	2015
Snake #1	stream	-15.54	0.2	-110.9	1.0	snake1	August	1993
Snake #2	stream	-15.72	0.2	-113.0	1.0	snake2	August	1994
Snake #3	stream	-15.09	0.2	-111.6	1.0	snake3	August	2005
Snake #4	stream	-11.67	0.2	-103.0	1.0	snake4	August	2104
RM Office	precipitation	-15.15	0.2	-111.6	1.0	precip1	9/22/2007	2081
Baker	precipitation	-6.79	0.2	-65.2	1.0	precip2	August	1620
RM Office	precipitation	2.84	0.2	7.6	1.0	precip3	8/31/2007	2081
Baker	precipitation	-14.30	0.2	-102.8	1.0	precip4	9/24/2007	1620