

Response of avian species richness to elevation in the central Great Basin

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INTRODUCTION

Elevation is known to constrain the spatial and temporal distributions of numerous taxonomic groups (e.g., Merriam 1890, Terborgh 1985, Fernández-Palacios and de Nicolás 1995). Species richness often decreases, either monotonically or with an intermediate-elevation peak, from the lowest to the highest end of an elevational gradient (Terborgh 1977, Brown 1988, Yu 1994, Lieberman et al. 1996, Fleishman et al. 1998). Nonetheless, positive correlations between species richness and elevation are not without precedent (Obseo 1992, Wettstein and Schmid 1999). Understanding whether species richness responds predictably to major environmental gradients, and whether those patterns generalize across space, is highly relevant to planning and decision-making in managed landscapes such as the Great Basin. Data on current elevational patterns of species richness also may improve predictions of how climate change will affect the region's fauna and flora.

Numerous ecological hypotheses have been proposed to explain why species richness tends to be correlated with elevation. Island biogeography, for instance, suggests that negative correlations between species richness and elevation are driven by decreasing area and increasing isolation at higher elevations (MacArthur and Wilson 1967). Other directional environmental changes along elevational gradients that may account for variation in species richness include resource diversity or primary productivity and climatic severity or unpredictability (Lawton et al. 1987, Olson 1994). For example, mean air temperature, which drops 0.65°C with every 100 m increase in elevation, is closely linked to the distribution and viability of many plants. Although some observed associations between species richness and elevation may reflect or be exacerbated by sampling design, ecological mechanisms generally play an important role (Wolda 1987, McCoy 1990, Colwell and Hurr 1994).

The response of biodiversity patterns to elevation may differ among

taxonomic groups (Patterson et al. 1998). Previous work in the Great Basin documented statistically significant relationships between species richness of montane butterflies and elevation. The functional form of the relationship, however, varied among mountain ranges. In the Toiyabe Range, species richness decreased unimodally as elevation increased (Fleishman et al. 1998), whereas in the Toquima Range, eastern Sierra Nevada, and Wassuk Range, species richness increased linearly as elevation increased (Fleishman et al. 2000, 2001). In other mountain ranges, including the Shoshone Mountains and Spring Mountains, the relationship between species richness and elevation was not statistically significant (Fleishman et al. 2001). Range-specific gradients in climatic severity appeared to influence these patterns (Fleishman et al. 2000). Here, we examine whether the species richness of breeding birds responds predictably to elevation in three mountain ranges of the central Great Basin. We also evaluate whether elevational patterns vary among subsets of bird species with different resource requirements.

METHODS

Data for our analyses were collected in three adjacent mountain ranges in the central Great Basin that have similar biogeographic and human land-use histories: the Shoshone Mountains (1850 km², approximate north-south boundaries 39°14' to 38°57'), Toiyabe Range (3100 km², 39°54' to 38°30') and Toquima Range (1750 km², 39°17' to 38°29') (Lander and Nye counties, Nevada). Numerous canyons incise the east and west slopes of the ranges. Resource agencies generally develop separate management plans for individual mountain ranges under their jurisdiction. Within mountain ranges, land uses commonly are delineated at the extent of individual or several adjacent canyons.

Our data collection incorporated established techniques that reliably detect species presence and permit assessment of distributional trends (Bibby et al. 2000). We provide an abbreviated description here; these methods have been described in considerable detail in previous publications, as well as tested for adequacy in sampling the species present at each location throughout the breeding season (e.g., Dobkin and Wilcox 1986, Dobkin and Rich 1998, Mac Nally et al. 2004).

We sampled birds during the breeding season (late May through June) using 75-m variable-radius point counts. Species that do not breed in mountains in the central Great Basin and species detected beyond 75 m were not included in our analyses. All detections within 75 m of the point center were treated equally. Most point centers were at least 350 m apart. Points were located along the full elevational gradient of every canyon we sampled, typically with two or three points per 100 m vertical elevation change. Points were located to sample, in approximate proportion to areal extent, the dominant vegetation types throughout the canyon as judged by researchers with considerable experience in the study system (e.g., aspen, willow, pinyon-juniper, wet meadow, sagebrush). Dominant vegetation was consistent within the point. We did not attempt to classify points according to land use because the spatial distribution and

intensity of livestock grazing and human recreation, the dominant land uses in the study area, are inconsistent over time.

During each visit, we recorded by sight or sound all birds using terrestrial habitat within the point. Point counts were conducted only in calm weather, and none were conducted > 3.5 hours after dawn. Each point was visited three times per year for five minutes per visit. Three surveys are considered sufficient to determine which species of birds are present at point count locations in a given year (Buckland et al. 2001, Siegel et al. 2001); in our work, species accumulation curves generally approached an asymptote before the third round of surveys (Betrus 2002).

From 2001 - 2005, we conducted point counts in 218 locations for two or more years. Our analyses included 53 points in the Shoshone Mountains, 55 points in the Toquima Range, and 110 points in the Toiyabe Range. Sampled elevations ranged from 1939 to 3038 m.

In addition to examining the relationship between species richness of all breeding birds and elevation, we investigated the response of number of species grouped by nest site and by dependence on riparian areas. Each of these traits had a moderate number of classes, and assignment of species to classes was relatively unambiguous based on extensive knowledge of the species (e.g., Ehrlich et al. 1988) and ecological system. Riparian dependence was of particular interest because water tends to be a limiting resource for many animals in the Great Basin and because much land management focuses on maintenance and restoration of riparian areas (e.g., Chambers and Miller 2004). Nest site categories were ground or low shrub cup, high shrub or canopy cup, and tree cavity. Species that build nests in other locations (e.g., cliffs, rocks, tunnels) and an obligate nest parasite were not included in our analyses because sample sizes were small (one to six species per mountain range).

We examined relationships between species richness and elevation with both linear regression (testing for monotonic responses) and quadratic regression (testing for unimodal responses). Across taxonomic groups, linear and unimodal responses to elevation are the most common functional relationships reported in the literature (e.g., Brown 1988, McCoy 1990, Stevens 1992). In addition, as noted above, both types of response have been observed for butterflies at different mountain ranges in the Great Basin.

RESULTS

Across the three mountain ranges, we recorded 79 breeding species of birds (Table 1). We recorded 65 species in the Shoshone Mountains, 73 species in the Toiyabe Range, and 48 species in the Toquima Range. Across all mountain ranges, the number of points in which each species was recorded ranged from 1 to 180 (38 ± 41 , mean \pm SD). Individual species were recorded in 1 to 48 points (13 ± 13) in the Shoshone Mountains, 1 to 83 points (20 ± 23) in the Toiyabe Range, and 1 to 49 points (12 ± 14) in the Toquima Range. The number of species in different nest site and riparian dependence categories in each mountain range ranged from 7 to 29 (Table 2).

Table 1. Species of breeding birds recorded from the Shoshone Mountains Toiyabe Range and Toquima Range and classification with respect to nesting type and degree of riparian dependence.

Species		Nest Site ^a	Riparian Dependence ^b
Black-crowned Night-Heron	<i>Nycticorax nycticorax</i>	2	1
Turkey Vulture	<i>Cathartes aura</i>	4	3
Northern Harrier	<i>Circus cyaneus</i>	1	1
Cooper's Hawk	<i>Accipiter cooperii</i>	2	2
Northern Goshawk	<i>Accipiter gentilis</i>	2	2
Red-tailed Hawk	<i>Buteo jamaicensis</i>	2	3
American Kestrel	<i>Falco sparverius</i>	3	3
Prairie Falcon	<i>Falco mexicanus</i>	4	3
Chukar	<i>Alectoris chukar</i>	1	2
Mourning Dove	<i>Zenaidura macroura</i>	2	2
White-throated Swift	<i>Aeronautes saxatalis</i>	4	3
Broad-tailed Hummingbird	<i>Selasphorus platycercus</i>	2	1
Northern Flicker	<i>Colaptes auratus</i>	3	2
Red-naped Sapsucker	<i>Sphyrapicus nuchalis</i>	3	1
Downy Woodpecker	<i>Picoides pubescens</i>	3	1
Hairy Woodpecker	<i>Picoides villosus</i>	3	1
Western Wood-Pewee	<i>Contopus sordidulus</i>	2	1
Gray Flycatcher	<i>Tyrannus dominicensis</i>	2	3
Dusky Flycatcher	<i>Empidonax oberholseri</i>	2	2
Cordilleran Flycatcher	<i>Empidonax occidentalis</i>	3	1
Plumbeous Vireo	<i>Vireo plumbeus</i>	2	3
Warbling Vireo	<i>Vireo gilvus</i>	2	1
Clark's Nutcracker	<i>Nucifraga columbiana</i>	2	3
Western Scrub-Jay	<i>Aphelocoma californica</i>	2	3
Pinyon Jay	<i>Gymnorhinus cyanocephalus</i>	2	3
Black-billed Magpie	<i>Picus hudsonia</i>	2	2
American Crow	<i>Corvus brachyrhynchos</i>	2	2
Common Raven	<i>Corvus corax</i>	4	3
Horned Lark	<i>Eremophila alpestris</i>	1	3
Violet-green Swallow	<i>Tachycineta thalassina</i>	3	2
Juniper Titmouse	<i>Baeolophus ridgwayi</i>	2	3
Mountain Chickadee	<i>Poecile gambeli</i>	3	2
Bushtit	<i>Psaltiriparus minimus</i>	2	2
Brown Creeper	<i>Certhia americana</i>	3	2
White-breasted Nuthatch	<i>Sitta carolinensis</i>	3	1
Red-breasted Nuthatch	<i>Sitta canadensis</i>	3	2
House Wren	<i>Troglodytes aedon</i>	3	1
Rock Wren	<i>Salpinctes obsoletus</i>	4	3
Canyon Wren	<i>Catherpes mexicanus</i>	4	3
American Dipper	<i>Cinclus mexicanus</i>	4	1
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	1	3
Mountain Bluebird	<i>Sialia mexicanus</i>	3	2
Townsend's Solitaire	<i>Myadestes townsendi</i>	2	2
Swainson's Thrush	<i>Catharus ustulatus</i>	1	1
Hermit Thrush	<i>Catharus guttatus</i>	1	2
American Robin	<i>Turdus migratorius</i>	2	2

Table 1. (continued)

Species		Nest Site ^a	Riparian Dependence ^b
Sage Thrasher	<i>Oreoscoptes montanus</i>	1	3
Cedar Waxwing	<i>Bombycilla cedrorum</i>	2	1
Orange-crowned Warbler	<i>Vermivora celata</i>	1	1
Virginia's Warbler	<i>Vermivora virginiae</i>	1	2
Yellow-rumped Warbler	<i>Dendroica coronata</i>	2	2
Black-throated Gray Warbler	<i>Dendroica nigrescens</i>	2	3
Yellow Warbler	<i>Dendroica petechia</i>	1	1
MacGillivray's Warbler	<i>Oporornis tolmiei</i>	1	1
Common Yellowthroat	<i>Geothlypis trichas</i>	1	1
Yellow-breasted Chat	<i>Icteria virens</i>	1	1
Western Tanager	<i>Piranga ludoviciana</i>	2	2
Green-tailed Towhee	<i>Pipilo chlorurus</i>	1	3
Spotted Towhee	<i>Pipilo maculatus</i>	1	2
Chipping Sparrow	<i>Spizella passerina</i>	2	3
Brewer's Sparrow	<i>Spizella breweri</i>	1	3
Lark Sparrow	<i>Chondestes grammacus</i>	1	3
Black-throated Sparrow	<i>Amphispiza bilineata</i>	1	3
Sage Sparrow	<i>Amphispiza belli</i>	1	3
Fox Sparrow	<i>Passerella iliaca</i>	1	1
Song Sparrow	<i>Melospiza melodia</i>	1	1
Vesper Sparrow	<i>Pooecetes gramineus</i>	1	3
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	1	2
Dark-eyed Junco	<i>Junco hyemalis</i>	1	3
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	2	2
Lazuli Bunting	<i>Passerina amoena</i>	1	1
Western Meadowlark	<i>Sturnella neglecta</i>	1	3
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	1	1
Brewer's Blackbird	<i>Euphagus cyanocephalus</i>	2	2
Brown-headed Cowbird	<i>Molothrus ater</i>	5	2
Cassin's Finch	<i>Carpodacus cassinii</i>	2	2
House Finch	<i>Carpodacus mexicanus</i>	2	3
Pine Siskin	<i>Carduelis pinus</i>	2	2
American Goldfinch	<i>Carduelis tristis</i>	2	2

^a 1: ground / low shrub cup 2: high shrub / canopy cup 3: tree cavity 4: other (e.g. cliff rocks tunnel) 5: obligate nest parasite

^b 1: obligate 2: intermediate 3: non-riparian

Table 2. Species richness of breeding birds and of birds in different functional groups in the Shoshone Mountains, Toiyabe Range, and Toquima Range.

	Shoshone	Toiyabe	Toquima
Breeding species	65	73	48
Nest site			
Ground / low shrub cup	19	26	15
High shrub / canopy cup	27	29	23
Tree cavity	12	11	7
Riparian dependence			
Obligate	14	21	8
Intermediate	25	24	17
Non-riparian	26	28	23

The mean elevation of riparian points ($n = 103$) versus non-riparian points ($n = 115$) was not significantly different across the three mountain ranges or within any mountain range (analysis of variance, $P > 0.05$; Table 3). The proportion of riparian versus non-riparian points, however, differed considerably among the three mountain ranges. In the Toiyabe Range, 75% of points were riparian, as compared with 34% in the Shoshone Mountains and just 5% in the Toquima Range.

The mean elevation of points dominated by different types of vegetation (aspen, mixed tree, pinyon-juniper, non-riparian shrub, and willow) was not significantly different across the three mountain ranges or within any mountain range (analysis of variance, $P > 0.05$; Table 3). The proportion of points dominated by trees versus shrubs differed somewhat among the three ranges (40% in the Shoshone Mountains, 69% in the Toquima Range, and 52% in the Toiyabe Range), but not as markedly as the proportion of riparian to non-riparian points.

Table 3. Elevation in meters of sampling points representing different types of habitat for birds in the Shoshone Mountains, Toiyabe Range, and Toquima Range. Values are mean \pm standard deviation. All $P > 0.05$. Neither the mean elevation of riparian versus non-riparian points nor the mean elevation of points dominated by different types of vegetation was significantly different across the three mountain ranges or within any mountain range ($P > 0.05$).

	Shoshone	Toiyabe	Toquima	All
Riparian ($n = 103$)	2250 \pm 144	2369 \pm 182	2254 \pm 90	2345 \pm 179
Aspen	2468	2252 \pm 147	2394 \pm 136	2301 \pm 155
Mixed tree	2266 \pm 183	2418 \pm 261	2373 \pm 141	2383 \pm 218
Willow	2205 \pm 150	2305 \pm 180	2387 \pm 238	2294 \pm 175
Non-riparian ($n = 115$)	2369 \pm 195	2343 \pm 281	2351 \pm 175	2355 \pm 210
Pinyon-juniper	2233 \pm 130	2322 \pm 148	2355 \pm 176	2309 \pm 159
Non-riparian shrub	2381 \pm 193	2379 \pm 206	2293 \pm 205	2365 \pm 203

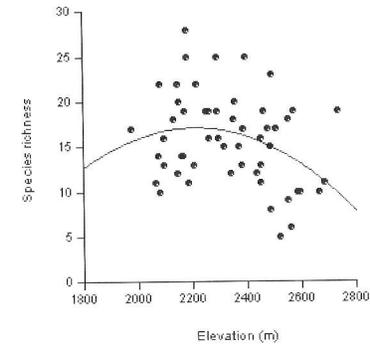
In all cases, quadratic regression yielded better fits to the observed data, in terms of both statistical significance and proportion of variance explained, than linear regression; whether the association between species richness and elevation was positive or negative, species richness peaked at an intermediate elevation. Therefore, all results reported here refer to quadratic regression.

When data for the three mountain ranges were pooled, several of the tested relationships between species richness and elevation were statistically significant, but only a small proportion of the variance in species richness was explained by elevation (Table 4). All statistically significant correlations in the Shoshone Mountains, Toiyabe Range, and across the three mountain ranges were negative (i.e., species richness decreased unimodally as elevation increased), whereas all statistically significant correlations in the Toquima Range were positive (species richness increased unimodally as elevation increased) (Fig. 1). Although there is considerable scatter in these plots, the "factor-ceiling," or upper limit of the point cloud, suggests that elevation places a ceiling on species richness (Thomson et al. 1996). The response of species richness to elevation in the Toiyabe Range generally was not statistically significant. Regardless of whether the data were examined at the mountain range level or across mountain ranges, the response of species richness of ground and low shrub cup nesters to elevation also was not statistically significant.

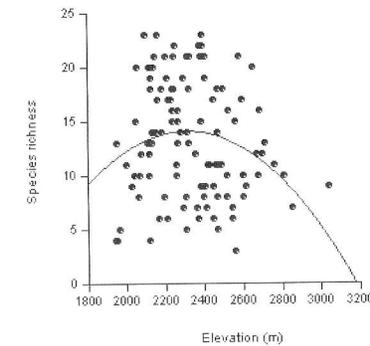
Table 4. Associations between species richness and elevation in the Shoshone Mountains, Toiyabe Range, and Toquima Range, and for data pooled across mountain ranges. Values are R^2 . *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$. All statistically significant associations in the Shoshone Mountains, Toiyabe Range, and across the three mountain ranges were negative, whereas all associations in the Toquima Range were positive.

	Shoshone	Toiyabe	Toquima	All
All breeding species	0.19**	0.03	0.19**	0.04*
Nest site				
Ground / low shrub cup	0.03	0.02	0.06	0.00
High shrub / canopy cup	0.18**	0.03	0.18**	0.03*
Tree cavity	0.24***	0.04	0.21**	0.05**
Riparian dependence				
Obligate	0.16**	0.06*	0.03	0.02
Intermediate	0.26***	0.03	0.13*	0.03*
Non-riparian	0.02	0.02	0.13*	0.01

a. Shoshone Mountains



b. Toiyabe Range



c. Toquima Range

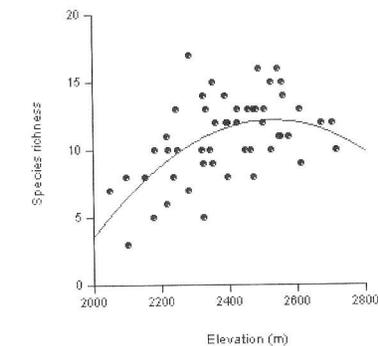


Figure 1. Relationship between elevation and species richness of breeding birds for sampling points in three mountain ranges in the central Great Basin. Note that axis values differ among ranges.

DISCUSSION

Although climate, land cover, land use, and faunal assemblages are broadly similar across the central Great Basin, our work demonstrates that fundamental ecological patterns may not be generalizable among mountain ranges. Species richness of birds was negatively correlated with elevation in the Shoshone Mountains, positively correlated with elevation in the Toquima Range, and uncorrelated with elevation in the Toiyabe Range. In virtually all cases, these patterns were consistent for the entire assemblage of birds and for subsets of species defined on the basis of nest site or dependence on riparian areas. The three mountain ranges described here are adjacent, with similar types of land cover and land use and pools of species, but there are dramatic differences in proportion of land-cover types and availability of surface water among ranges. These differences may drive the establishment of distinct avian assemblages with different numbers and proportions of riparian obligates and different distributional patterns.

Our work echoes previous research on relationships between species richness of butterflies and elevation in the same region in two ways. First, the functional relationship between species richness of birds and elevation, as with butterflies, varied among mountain ranges. Second, in both taxonomic groups, and contrary to general biogeographic expectations, species richness was positively correlated with elevation in the Toquima Range.

Distinct gradients of resource availability and climatic severity in different mountain ranges may be driving species richness patterns of both birds and butterflies. Among the common land cover types in the central Great Basin, riparian areas generally have the greatest diversity of nesting sites and food resources for birds (as well as for butterflies). Accordingly, habitat quality of riparian areas is relatively high. In the Toiyabe Range, riparian habitat is relatively abundant and distributed fairly evenly along the elevational gradient. This distribution may account for the lack of correlation between birds and elevation in the Toiyabe Range. In addition, our data suggest that riparian-obligate birds will establish breeding territories along the full elevational gradient in a canyon with some riparian habitat. In other words, if one or more patches of riparian habitat are present in a given canyon, riparian-obligate birds may nest anywhere within the canyon. The distribution of species richness of butterflies in the Toiyabe Range (which declines as elevation increases), by contrast, may be constrained at high elevations by cold temperatures, strong winds, and low availability of host plants and nectar sources (Hidy and Klieforth 1990, McCoy 1990).

In the Toquima Range, riparian habitat and, more generally, availability of water may be limiting for both birds and butterflies. Decreases in temperature and increases in precipitation along an increasing elevational gradient in the Toquima Range may translate into greater abundance of resources and prolonged availability of resources at higher elevations.

Regardless of the functional form of the relationship between species richness of birds and elevation, the proportion of variance in species richness explained by elevation was relatively low (maximum 0.26, Table 4). The direct and indirect effects of elevation may contribute to, but certainly do not explain fully, patterns of species richness within or among mountain ranges. As a result, simple models of climate change that assume vegetation communities (when used as a surrogate measure of habitat) and associated wildlife in the Great Basin will move upward at a uniform rate as temperatures increase (McDonald and Brown 1992, Murphy and Weiss 1992) are unlikely to predict accurately the future distribution of birds. In addition, differences in the response of birds and butterflies to elevational gradients highlight the difficulty of generalizing how natural or anthropogenic environmental change will affect native species.

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Springs and sky islands: influence of springs and elevation on breeding bird communities in the Spring Mountains of southern Nevada

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INTRODUCTION

A dominant climatic feature of the Great Basin and Mojave Desert region is aridity. The lack of moisture, coupled with high temperatures and intense solar radiation, imposes severe limitations on vegetation communities, and the animals that depend upon them, throughout the region. Mountains supply most of the water the region receives: crossing air masses cool through orographic uplift, and moisture precipitates out at the higher elevations. This precipitation can generate surface streams and springs that carry the water to the lower elevations. In the arid and semi-arid western United States, these springs and spring-fed aquatic systems support a substantial proportion of aquatic and riparian species, and may provide resources for as many of 80% of terrestrial species in some systems (Thomas et al. 1979, Williams and Koenig 1980, Gubanich and Panik 1986, Hershler et al. 2002).

The moister, cooler climates found at the higher elevations of Great Basin and Mojave mountain ranges also provide refuge for unique assemblages of plants and animals. "Sky islands" such mountain ranges are frequently called, each isolated from one another by a vast sea of desert valley bottoms. Nevada's most classic sky island is the Spring Mountain range, on the northern edge of the Mojave Desert. The Spring Mountains are home to a rich collection of species, a large number of which appear to be sustained by one or more of the nearly 300 namesake springs that dot the mountains from their arid foothills to their alpine summits.

The challenge of conserving the unique and isolated biota of the Spring Mountains has become immediate and pressing as expanding Las Vegas, at the very foot of the range, increasingly exerts urban impacts upon what until recently was largely wilderness. Both springs and their distinctive ecological communities have suffered significantly from the effects of water impoundment, invasion of aggressive weeds, and trampling and grazing by feral horses and burros and transplanted elk. Increased recreation in the Spring Mountains has added new disturbances, concentrated at springs and their associated ecological communities. Few baseline data exist, but disturbances to the springs and their communities can have severe consequences for the species that depend on them. A tiny species of springsnail (*Pyrgulopsis* sp.) that was unique to the range was lost in the 1990s (Sada and Vinyard 2002), and the Mount Charleston blue butterfly (*Icaricia shasta charlestonensis*), last seen in 2005, may have recently joined the ranks of the extinct. These continuing, and often increasing, disturbances put many other Spring Mountains species at similar risk of disappearing.