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Current and Potential Future Elevational Distributions of Birds Associated with Pinyon–Juniper Woodlands in the Central Great Basin, U.S.A.

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Abstract

We examined the relationship of breeding birds to elevation across and within four adjacent mountain ranges in the central Great Basin, a cold desert in western North America. Data came from 7 years of point counts at elevations from 1,915 to 3,145 m. We focused on eight passerine species that in this region are associated frequently with *Pinus monophylla–Juniperus* spp. (pinyon–juniper) woodland. Mean elevation of species' presence differed significantly among mountain ranges for all species except *Spizella passerina* (Chipping Sparrow); all species except *Spizella breweri* (Brewer's Sparrow) occurred at the highest mean elevation in the Toquima Range. Observed patterns were consistent with the elevational distribution of pinyon–juniper woodlands that provide nesting and foraging habitat for these species. Across the Great Basin, driven in part by climate change, pinyon–juniper woodland is increasing in density and expanding its distribution at lower elevations. However, breeding habitat for species dependent on mature trees may not be available in expansion woodlands for several decades, and increased tree densities may have negative effects on bird species that are dependent on shrubs within open pinyon–juniper woodlands. Responses of individual species to elevation differed from the response of assemblage-level patterns. Responses to biotic and abiotic variables within guilds of birds are sufficiently diverse, and responses of individual species sufficiently heterogeneous, that one management strategy is unlikely to meet the needs of all species in the group.

Key words: **arid woodlands, bird–habitat associations, breeding birds, climate change, Great Basin, guilds, Intermountain West, land-cover change, passerines, pinyon–juniper woodlands.**

Introduction

Elevation constrains the spatial and temporal distribution of virtually all groups of plants and animals (e.g., Merriam 1890; MacArthur & Wilson 1967; Patterson et al. 1998). Elevation often represents abiotic influences on species occurrence. For example, mean air temperature decreases 0.65°C with every 100 m increase in elevation. Likewise, precipitation tends to be correlated positively with elevation, especially in montane regions (Daly et al. 1994). Other directional environmental changes along elevational gradients include resource diversity, primary productivity, and climatic severity or variability (Lawton et al. 1987; Olson 1994). The direct and indirect effects of elevation may bound the response of some species of animals, including breeding birds, to elements of vegetation structure and composition (Mac Nally et al. 2008).

Understanding whether species' distributions are associated reliably with major environmental gradients, and whether those patterns generalize across space, is highly relevant to land-use planning and implementation in managed landscapes worldwide. For example, insight into species' responses to elevation may improve quantitative and qualitative projections of the ecological effects of climate change, land-use change, and associated changes in the area and configuration of different land-cover types. The Great Basin encompasses more than 425,000 km^2 of mountainous internal drainage in the western United States, extending from the east slope of the Sierra Nevada in California to the west slope of the Wasatch Range in Utah (Fig. 1). Approximately three quarters of the region is managed by federal agencies, including the U.S. Department of the Interior Bureau of Land Management and U.S. Department of Agriculture Forest Service. Issues germane to management of the Great Basin, such as interactions among marked topographic gradients, fire regimes, and fuels

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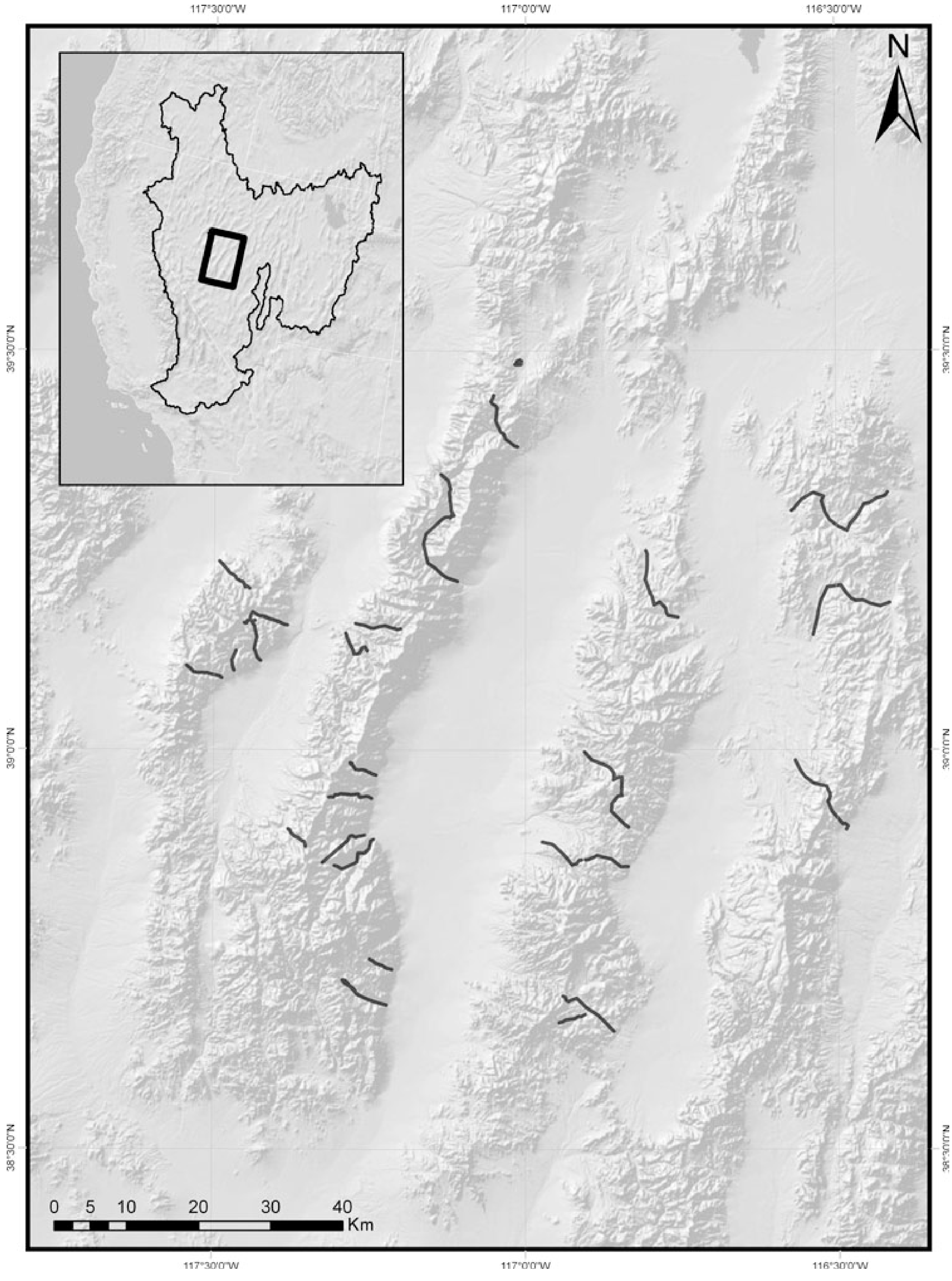

Figure 1. The Great Basin of western North America, with our study area outlined by the thick black rectangle (inset map). Canyons sampled in the four mountain ranges we examined (from west to east: Shoshone Mountains, Toiyabe Range, Toquima Range, and Monitor Range) are indicated by irregular black lines.

treatments, and expansion of non-native invasive grasses, are similar to those that confront natural-resource professionals in Australia, South Africa, and other arid landscapes (Spehn et al. 2006; Lindenmayer et al. 2008).

Across the Great Basin, and the even more-extensive Intermountain West of North America (which lies between the Sierra Nevada to the west, Cascade Range to the north, and Rocky Mountains to the east), pinyon–juniper woodland is among the land-cover types experiencing the most rapid change. Since the mid 1800s, the cover and density of two of the most characteristic trees in the Great Basin, *Pinus monophylla* (pinyon) and *Juniperus osteosperma* and *Juniperus occidentalis* (juniper), have increased across the region (Miller et al. 2008) at the expense of ecosystems dominated by *Artemisia tridentata* ssp. (sagebrush), other native shrubs, and *Populus tremuloides* (quaking aspen) (Bartos 2008). Higher woody fuel loads and changes in stand structure alter fire behavior; as the age and density of woodland increases, fire severity tends to increase. Some changes in land-cover across the Great Basin, as in any landscape, can be related to elevation and other topographic variables (e.g., Bradley & Mustard 2006; Johnson & Miller 2006; Weisberg et al. 2007). For example, analysis of a series of Landsat TM images suggested that across the central Great Basin, increases in conifer cover and density between 1986 and 2005 were most likely to occur at elevations below 2,000 m and on south facing slopes, whereas overall cover and density of woodlands tended to be the greatest at elevations between 2,200 and 2,600 m (Bradley & Fleishman 2008).

Potential responses of species to environmental variables and environmental change in any region can be examined at several levels, from species to assemblages (Lemoine et al. 2007). Models for individual species identify ecological variables with the greatest influence on occurrence of that species or explore relationships between the species and particular variables in some detail. Models at the level of guilds collectively investigate many species using a common set of key variables, sometimes retaining information about responses of individual species (Olden 2003; Leathwick et al. 2005). Models at the assemblage or community level examine environmental correlates of patterns of species richness or turnover (e.g., Downes et al. 1998), but rarely account explicitly for species identity.

Around the world, birds frequently are monitored because they have regulatory protection or to assess biological consequences of management of specific land-cover types and disturbances (George & Dobkin 2002; Knick et al. 2003; Radford & Bennett 2007). We recently examined whether the species richness of breeding birds was associated closely with elevation in three adjacent mountain ranges of the central Great Basin (Fleishman & Dobkin 2007). When data were pooled across the mountain ranges, only a small proportion of the variance in species richness was explained by elevation. Among mountain ranges, the direction and magnitude of correlations between species richness and elevation varied widely. In many cases, patterns at the mountain-range level were consistent for the entire assemblage of birds and for most subsets of species defined on the basis of nesting type or dependence on riparian habitats (Fleishman & Dobkin 2007). Related work demonstrated that elevation was a more consistent predictor of the distribution of ecological guilds of birds than elements of vegetation structure and composition (Mac Nally et al. 2008). However, models at the level of assemblages or guilds can mask differences in responses of individual species, especially those whose resources are most likely to respond to changes in climate and land use.

Here, we examine the relationship of individual species of breeding birds to elevation across mountain ranges and within mountain ranges in the central Great Basin. We focus on eight species that in this region are associated strongly with pinyon–juniper woodland. In addition, we explore how the distribution of breeding birds may respond to potential changes in the extent and attributes of pinyon–juniper woodland by 2100. Our approach is applicable to diverse assemblages and ecosystems: we link data on relationships between species and major environmental gradients with projected responses of land cover to environmental change, and then examine how species may respond to environmental change.

Methods

Field Methods

We collected data in four adjacent mountain ranges with similar biogeographic and human land-use histories. From west to east, these are the Shoshone Mountains, Toiyabe Range, Toquima Range, and Monitor Range (Lander, Eureka, and Nye counties, Nevada, U.S.A.) (Fig. 1). Canyons, many of which have perennial or ephemeral streams, drain the east and west slopes of the ranges.

We surveyed birds during the breeding seasons (late May through June) of 2001–2007 using 75-m fixed-radius point counts. Most point centers were >350 m apart. Points were located along the full elevational gradient of each canyon we sampled, typically with two or three points per 100 m vertical elevation change. We estimated the geographic coordinates of each point using a global positioning system and differential correction. We estimated the elevation at each point by intersecting its centroid with a 30-m (1:24,000) U.S. Geological Survey digital elevation model. Mountain-range topography and inaccessibility prevented us from distributing points evenly on the east and west slopes of each mountain range. At the level of mountain ranges, however, we have not observed a consistent relationship between aspect and the elevational distribution of land-cover types across the central Great Basin. Points were positioned to sample, in approximate proportion to areal extent, the dominant land-cover types throughout the canyons: aspen, pinyon–juniper woodland, *Salix* spp. (willow), sagebrush, and other montane shrubs (e.g., *Symphoricarpos albus* [snowberry], *Cercocarpus ledifolius* [mountain mahogany]), and mixed vegetation (combination of coniferous and deciduous trees, with variable understory). We did not attempt to classify land use because livestock grazing and human recreation, the ubiquitous dominant uses in this region, vary considerably through time.

We established 179 survey points in 2001 and added additional points annually during 2004–2007. In all, 356 permanent survey points were established: 60 in the Shoshone Mountains, 168 in the Toiyabe Range, 75 in the Toquima Range, and 53 in the Monitor Range. During each visit, we recorded by sound or sight 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 surveyed three times per year for 5 minutes per visit. We considered a species to be present at a point in a given year when it was detected during one or more of the three visits. We were unable to visit all points in all years due to logistical constraints (e.g., severe weather, impassable roads). Eighty-nine percent of the 356 established points were surveyed in two or more years. The number of points surveyed annually ranged from 112 points (2007) to 250 points (2004). In all, we conducted surveys (i.e., three point counts per point) at a sum total of 1,230 survey points.

The elevation of our survey points ranged from 1,915 to 3,145 m. Because selection of survey locations partially was a function of accessibility, which varied in space and time, we checked whether the mean elevation of survey locations differed by mountain range or by year. The mean elevation of bird-survey points did not vary significantly among mountain ranges (analysis of variance, $F_{[3,352]} = 0.2$, $p = 0.23$). However, the mean elevation of points surveyed differed among years ($F_{[6,1223]} = 3.0$, $p < 0.01$). The mean elevation of points surveyed in 2004 was significantly higher (Fisher's PLSD) than the mean elevation of points surveyed in 2001, 2002, and 2007, and the mean elevation of points surveyed in 2007 was significantly lower than those in 2003, 2005, and 2006.

Analyses

We examined whether mean elevation of survey locations varied as a function of land-cover type (as categorized qualitatively and measured in the field, see Dickson et al. 2009) among or within mountain ranges or whether the point was "riparian"—i.e., within approximately 100 meters of running or standing water.

We included eight passerine species of birds in our analyses: *Empidonax wrightii* (Gray Flycatcher), *Poecile gambeli* (Mountain Chickadee), *Polioptila caerulea* (Blue-gray Gnatcatcher), *Dendroica nigrescens* (Black-throated Gray Warbler), *Pipilo chlorurus* (Green-tailed Towhee), *Pipilo maculatus* (Spotted Towhee), *Spizella passerina* (Chipping Sparrow), and *Spizella breweri* (Brewer's Sparrow). We selected these eight species based on their frequent association with pinyon–juniper woodlands, as indicated by the results of our point-count surveys across the 7 years of our study, and based on extensive research experience with these species in the Intermountain West (e.g., Dobkin & Wilcox 1986; Thomson et al. 2005; Fleishman & Dobkin 2007). In the Great Basin, six of the eight species on which we focus occur only as summer residents (Mountain Chickadee and Spotted Towhee are year-round residents, although the latter moves to lower elevations for winter and many likely migrate out of the Great Basin entirely). All eight species nest and forage extensively in pinyon–juniper woodlands (Linsdale 1936, 1938). We recorded additional species of birds that frequently were associated with pinyon–juniper woodland (e.g., *Baeolophus ridgwayi* [Juniper Titmouse]), but sample sizes were too small for robust analysis.

For each of the eight bird species, we used log-likelihood G-tests to assess their association with land-cover types. For each species and for the eight species as a group, we used analysis of variance to examine whether mean elevation of species presence varied as a function of mountain range, year, and the interaction between range and year.

Results

On the basis of field measurements of vegetation (see Dickson et al. 2009), we characterized the dominant land cover of 20 survey points as aspen, 96 as pinyon–juniper woodland, 18 as willow, 146 as sagebrush, 2 as mountain mahogany, and 74 as mixed vegetation. Because the sample size of points dominated by mountain mahogany was so small, we eliminated those two points from our analysis of elevational distributions among land-cover types. Across the four mountain ranges, mean elevation differed significantly among survey points as a function of land-cover type ($F_{[4,349]} = 3.6$, $p < 0.01$). This difference was driven by the low mean elevation of points dominated by pinyon–juniper woodland relative to those dominated by sagebrush or mixed vegetation (Fig. 2).

Although the mean elevation of survey points did not vary among mountain ranges, the mean elevation of points dominated by pinyon–juniper woodland was significantly different among mountain ranges ($F_{[3,92]} = 7.1$, $p < 0.001$). Points with pinyon–juniper woodland were significantly higher in the Toquima Range and in the Monitor Range than in the Shoshone Mountains or Toiyabe Range. There were no other significant differences in mean elevation of points with a given type of land cover as a function of mountain range. The mean elevation of riparian points ($n = 159$) and non-riparian points ($n = 197$, including the two points dominated by mountain mahogany) was not significantly different either among or within mountain ranges.

Across mountain ranges, pinyon–juniper woodland tended to occur at lower elevation than sagebrush and other montane shrubs or mixed vegetation ($F_{[4,349]} = 3.6$, $p < 0.01$). We detected the same pattern within two of the four mountain ranges. In the Shoshone Mountains, the mean elevation of points dominated by pinyon–juniper woodland was significantly lower than those dominated by shrubs ($F_{[4,55]} = 3.5$, $p < 0.05$). In the Toiyabe Range, the mean elevation of points dominated by pinyon–juniper woodland was significantly lower than those dominated by shrubs, mixed vegetation, or willow ($F_{[4,163]} = 3.0$, $p < 0.05$).

Gray Flycatcher and Chipping Sparrow were primarily associated with pinyon–juniper woodland (both $G \geq 21.9$, $p < 0.001$). Blue-gray Gnatcatcher ($G = 10.2$, $p < 0.025$) and Black-throated Gray Warbler (post hoc partition test,

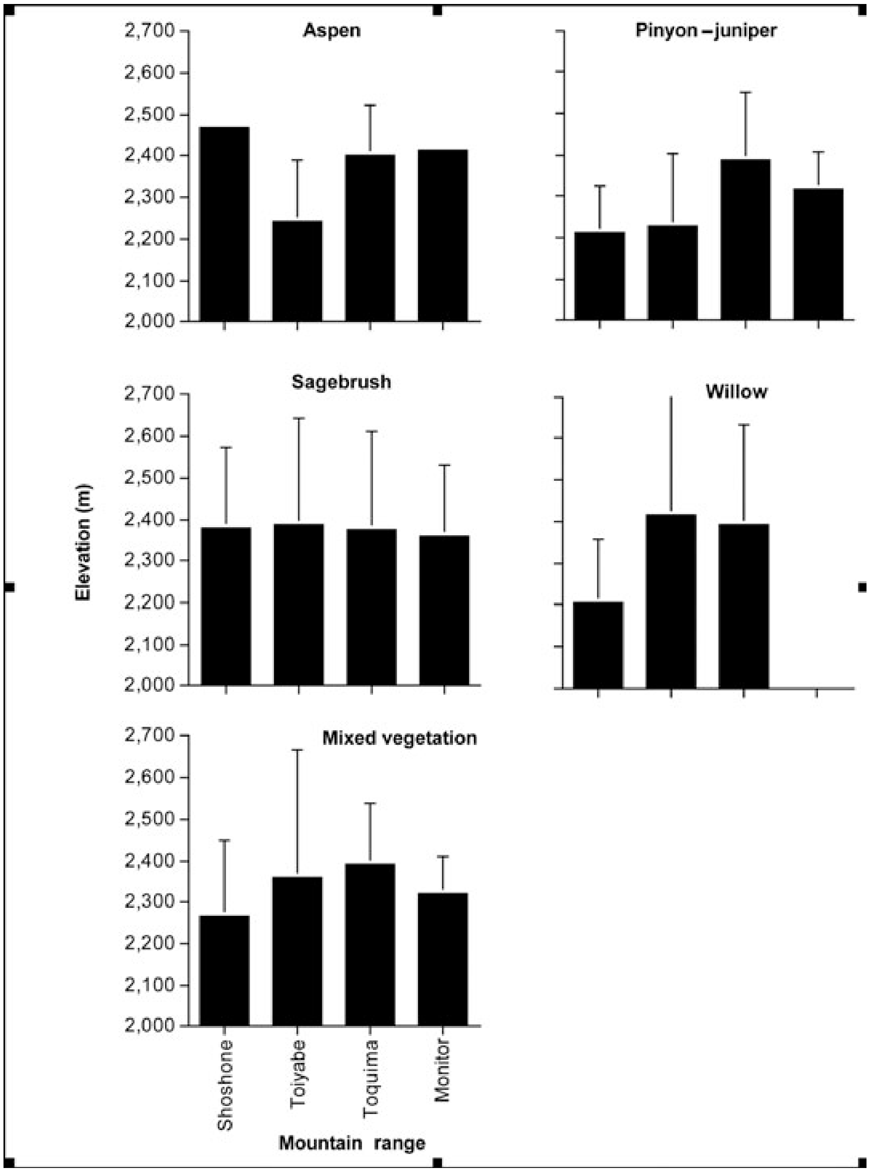

Figure 2. Mean elevation (± SD) of principal land-cover types in four adjacent mountain ranges in the central Great Basin of the western United States. No points dominated by willow were sampled in the Monitor Range.

$p < 0.05$) were strongly associated with pinyon–juniper woodland. Green-tailed Towhee and Brewer's Sparrow were associated only with pinyon–juniper woodlands that were relatively open and had well-developed, shrub-dominated understories (primarily sagebrush) (both $G \geqslant 28.1$, $p < 0.001$). Mountain Chickadee and Spotted Towhee, although frequently recorded in pinyon–juniper woodland, showed no significant statistical relationship with any single land-cover type (both $G \leq 9.2$, $p > 0.05$).

Collectively, the eight species we examined were present in 339 survey points: 60 in the Shoshone Mountains, 152 in the Toiyabe Range, 75 in the Toquima Range, and 52 in the Monitor Range. The total number of presence records for each species ranged from a high of 736 for Green-tailed Towhee to a low of 124 for Blue-gray Gnatcatcher. (The total number of presence records for each species, and the number for each mountain range and year, is available from the senior author on request.) Mountain range, year, and the interaction between year and range all showed highly significant relationships with mean elevation of species presence (Table 1). Birds were recorded at higher mean elevations in the Toquima Range than in the other three ranges (Fig. 3). Birds were recorded at the highest mean elevation in 2004 and the lowest mean elevation in 2007.

Mean elevation of species presence differed significantly among mountain ranges for all species except Chipping Sparrow (Table 1), and all species except Brewer's Sparrow occurred at the highest mean elevation in the Toquima Range

Table 1. Effects of mountain range, year, and the interaction between range and year on the mean elevation of eight bird species associated with pinyon–juniper woodlands in the central Great Basin.

	Range	*Year*	*Interaction*
Eight species combined	30.0***	9.1***	5.9***
Gray Flycatcher	5.5**	2.9*	3.8***
Mountain Chickadee	6.2***	2.6*	1.0
Blue-gray Gnatcatcher	10.6***	0.5	1.2
Black-throated Gray Warbler	21.5***	0.8	0.8
Green-tailed Towhee	3.6*	2.1*	2.1*
Spotted Towhee	8.3***	0.7	0.5
Chipping Sparrow	2.0	3.9**	1.4
Brewer's Sparrow	12.8***	4.7***	2.6**

F-statistics and levels of significance are shown (*$p \leqslant 0.05$; **$p < 0.01$; ***$p < 0.001$).

(Fig. 3). Year had a significant effect on mean elevation of occurrence of five species: Gray Flycatcher, Mountain Chickadee, Green-tailed Towhee, Chipping Sparrow, and Brewer's Sparrow. Four of the latter species (all but Gray Flycatcher) were recorded at the highest elevation in 2004 and four species (all but Chipping Sparrow) were recorded at the lowest elevation in 2007. The interaction between mountain range and year had a statistically significant effect on occurrence of all species combined, Gray Flycatcher, Green-tailed Towhee, and Brewer's Sparrow.

Discussion

Our data illustrated considerable differences among mountain ranges in the elevational distributions of individual bird species that are associated with pinyon–juniper woodlands. These patterns cannot be explained by differences in the elevation of survey locations per se and are consistent with the elevational distribution of woodlands that provide key resources for these bird species. Our results at the level of individual species contrasted with models at the level of ecological guilds, in which elevation was a more consistent predictor of geographic distribution than measures of vegetation structure and composition in this system (Mac Nally et al. 2008).

Effects on occurrence of year and interactions between mountain range and year most likely are sampling artifacts rather than ecologically meaningful. The mean elevation of survey points differed among years. Furthermore, the pattern of annual variation in temperature and precipitation that appears to influence detection probability and occupancy of some species in the region (Dickson et al. 2009) was not consistent with our observed elevational differences among years.

The distribution of woodlands in the Great Basin, similar to the distribution of major categories of land cover in any ecosystem, reflects elevational differences in climate and deterministic changes in land cover (e.g., changes in fire dynamics); the latter often depend in part on the former. We also found substantial differences in the elevational distributions of species among years, but these patterns more likely result from temporal stochasticity in the distribution of survey locations than from short-term, deterministic shifts in bird distributions. Natural and anthropogenic changes in the elevational range of pinyon–juniper woodlands may affect the occurrence of bird species that are closely linked with this land-cover type, but the strength of these effects may vary among mountain ranges.

Land cover across the Great Basin is heterogeneous, and our sampling was not random. Therefore, we verified that patterns in the elevational distribution of pinyon–juniper woodland that were apparent from our data were consistent with evidence recently compiled from satellite data and aerial photographs. Between 1986 and 2005, cover and density of pinyon–juniper woodland in the central Great Basin were most likely to increase at elevations below 2,000 m (Weisberg et al. 2007; Bradley & Fleishman 2008). Those changes reflect increased densities in locations currently occupied sparsely by trees, as well as local expansion of the trees' distributional range. The probability of an increase in density or cover of pinyon–juniper woodland at low to intermediate elevations (2,000–2,600 m) between 1986 and 2005 was 0.25 (Bradley & Fleishman 2008).

Across species and at the level of individual species, birds associated with pinyon–juniper woodland tended to occur at higher elevation in the Toquima and Monitor ranges than in the Shoshone Mountains and Toiyabe Range. Our field data indicated that pinyon–juniper woodlands also occurred at higher elevation in the Toquima and Monitor ranges than in the Shoshone Mountains or Toiyabe Range. These results may seem self-evident, but past work has demonstrated that well-established natural history or expert knowledge about relationships between birds and vegetation sometimes is insufficient to develop reliable explanatory or predictive models (Mac Nally et al. 2008). More broadly, and irrespective of ecosystem, we think it is critical to empirically support expert judgment about relationships among species and their abiotic and biotic environment.

Post hoc analyses of data from the Southwest ReGAP project (http://earth.gis.usu.edu/swgap/landcover.html) supported the hypothesis of a longitudinal gradient in the elevational distribution of pinyon–juniper woodlands (B. Bradley unpublished data). When additional mountain ranges were included in the analysis, two to the west and one to the east of our study area, there was a decreasing longitudinal trend in the presence of pinyon–juniper woodland. That is, high-density pinyon–juniper woodland was more likely to occur at higher elevation in the east-central Great Basin than in the west-central Great Basin. After normalizing by topography (i.e., correcting for total area at different elevations among mountain ranges), presence of high-density pinyon–juniper woodlands in the Toquima and Monitor ranges was skewed toward higher elevations compared with the Shoshone and Toiyabe. This distribution is consistent with our finding that the Brewer's Sparrow, which frequently nests in treeless sagebrush-dominated landscapes (Rotenberry et al. 1999), was the only species to not have its highest mean elevation of occurrence in the Toquima Range. Brewer's Sparrow also was the least likely of the eight species to occur in higher density pinyon–juniper woodlands (Fleishman and Dobkin unpublished data).

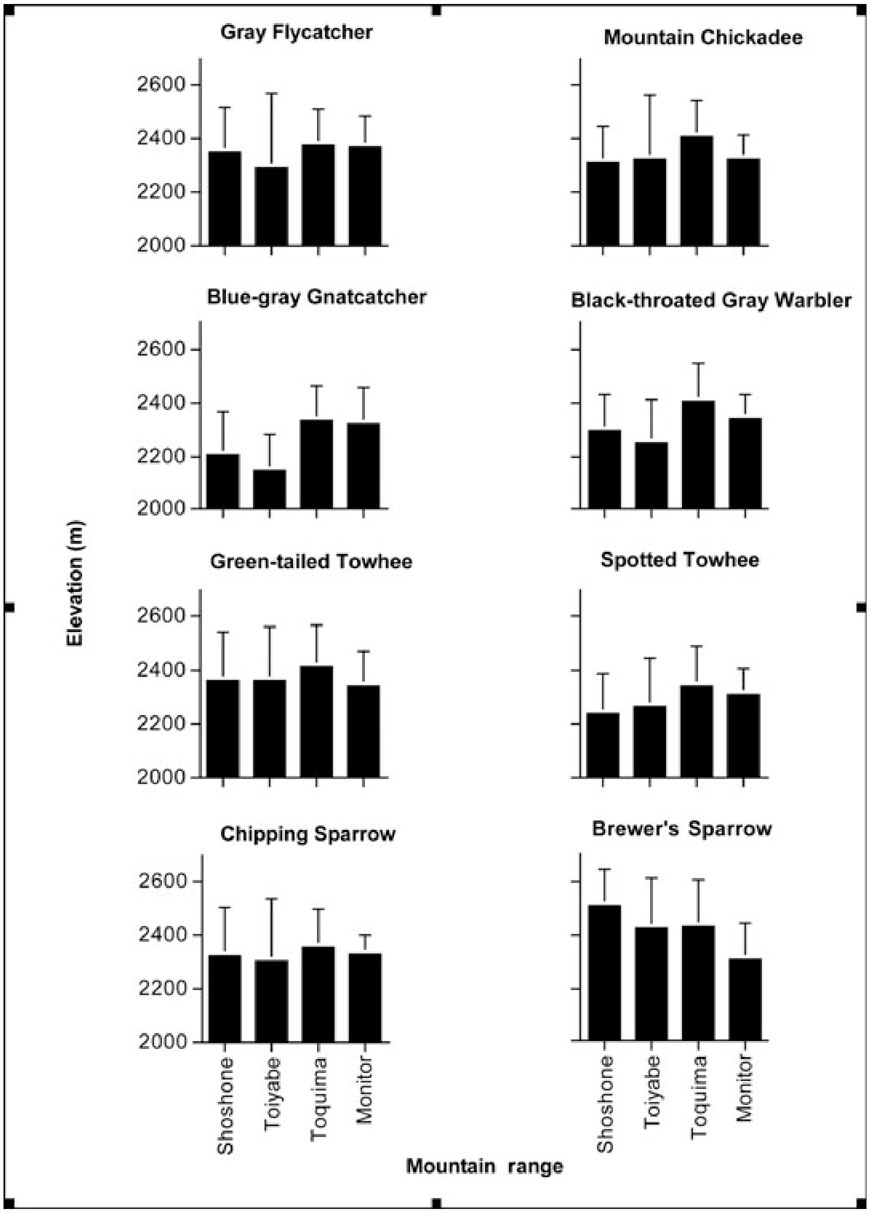

Figure 3. Mean elevation (± SD) of the presence of eight bird species associated with pinyon–juniper woodlands in four adjacent mountain ranges in the central Great Basin of the western United States.

Regional gradients in precipitation and temperature likely play a key role in driving elevational and longitudinal patterns in the distribution of woodlands. Precipitation generally decreases from west to east across the central Great Basin although some ranges that are unusually tall, such as the Toiyabe, also are relatively wet. As elevation increases, temperature decreases and precipitation increases. We did not find a difference in the elevational distribution of riparian and non-riparian survey locations. Nonetheless, our observations over many years suggest that low elevations in the Toquima Range are drier than comparable elevations in the Shoshone Mountains and Toiyabe Range, perhaps too dry to facilitate recruitment of an appreciable number of conifers (Miller & Wigand 1994; Gray et al. 2006). As regional climate warms, expansion of pinyon–juniper woodlands at lower elevations across the central Great Basin is likely to diminish (and perhaps retract upward in elevation) due to limited availability of water, whereas expansion at upper elevations is likely to increase. With regional warming, even if the seasonal distribution of precipitation remains fairly constant, mortality rates of pinyon and juniper at lower elevations may increase. Similarly, a shift to increased summer precipitation and decreased winter precipitation (i.e., reduced snowpack), as predicted by some global circulation models (Bradley et al. 2009), likely will increase mortality rates of pinyon and juniper at lower elevations.

If current trajectories of land-cover change persist, and pinyon–juniper woodland continues to increase in density across the Great Basin and expand its distribution at lower elevations now dominated by shrubs, then it initially may seem that the breeding ranges of many species of pinyon–juniper associated birds will expand. But several caveats are warranted. First, the species of birds most strongly associated with pinyon–juniper woodland (Gray Flycatcher, Blue-gray Gnatcatcher, Black-throated Gray Warbler, Chipping Sparrow [also Mountain Chickadee]) are associated with mature trees, not early successional stages in which trees are not much taller than the surrounding shrubs. Accordingly, breeding habitat for such species may not be available in expansion woodlands for several decades. In addition, recent fires in mature woodlands have been of higher severity due to changes in regional disturbance regimes. Second, increasing aridity may limit not only the abundance of trees (and duration of the growing season) at lower elevations but also the abundance of forbs and grasses, thus potentially reducing the abundance of some insects on which many birds feed. Third, increases in density of pinyon–juniper woodlands are negatively associated with probability of occurrence of some species of birds (e.g., Spotted Towhee, Green-tailed Towhee, Brewer's Sparrow) in the central Great Basin (Dickson et al. unpublished data), which are dependent on the shrub component of open pinyon–juniper woodlands (Greenlaw 1996; Dobbs et al. 1998; Rotenberry et al. 1999).

We found several similarities in among-range and among-year elevational distributions across bird species, especially with respect to the mountain ranges or years that corresponded to the highest mean elevation of species presence. However, differences among species in the rank order of elevational distribution among ranges and years also were apparent. Substantial variation in elevational distribution among species similarly has been documented in butterflies across the Great Basin (Fleishman et al. 2000, 2001).

A growing body of work from multiple continents suggests that responses to biotic and abiotic variables within guilds of birds are sufficiently diverse, and responses of a given species across space and time heterogeneous enough, that a given management intervention may not meet the needs of most, let alone all, species in the group (Mac Nally et al. 2008; Dickson et al. 2009; Thomson et al. 2009). Our results illustrate the importance of examining not only assemblage-level patterns like species richness, but also responses of individual species to major environmental gradients.

Implications for Practice

- Climate change may arrest current expansion of pinyon–juniper woodlands at relatively low elevations in the Great Basin, rendering human intervention to constrain the expansion less necessary.
- It is unwarranted to assume that a bird species distributed widely across montane regions has similar local responses to elevation and other major environmental gradients.
- Management to maximize species richness of birds along elevational gradients and to maximize persistence of individual species of concern requires consideration of different sets of factors.
- A given management intervention likely will not meet the needs of all or most species in a guild of birds.

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