Range dynamics of small mammals along an elevational gradient over an 80-year interval

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Abstract

One expected response to observed global warming is an upslope shift of species elevational ranges. Here, we document changes in the elevational distributions of the small mammals within the Ruby Mountains in northeastern Nevada over an 80-year interval. We quantified range shifts by comparing distributional records from recent comprehensive field surveys (2006–2008) to earlier surveys (1927–1929) conducted at identical and nearby locations. Collector field notes from the historical surveys provided detailed trapping records and locality information, and museum specimens enabled confirmation of species' identifications. To ensure that observed shifts in range did not result from sampling bias, we employed a binomial likelihood model (introduced here) using likelihood ratios to calculate confidence intervals around observed range limits. Climate data indicate increases in both precipitation and summer maximum temperature between sampling periods. Increases in winter minimum temperatures were only evident at mid to high elevations. Consistent with predictions of change associated with climate warming, we document upslope range shifts for only two mesic-adapted species. In contrast, no xeric-adapted species expanded their ranges upslope. Rather, they showed either static distributions over time or downslope contraction or expansion. We attribute these unexpected findings to widespread land-use driven habitat change at lower elevations. Failure to account for land-use induced changes in both baseline assessments and in predicting shifts in species distributions may provide misleading objectives for conservation policies and management practices.

Keywords: binomial model, climate change, elevational gradient, Great Basin, likelihood ratios, Nevada, range limits, range shifts, Ruby Mountains, small mammals

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Introduction

Ecological response to recent climate change has been significant across taxa, ecosystems, and regions (Parmesan & Yohe, 2003; Root et al., 2003; Walther et al., 2005). One such response is the displacement of range boundaries. Under climate warming, species are expected to track changing temperature by shifting their latitudinal distributions poleward and/or their elevational distributions upslope. Range shifts may be most evident in montane systems, where species can more readily respond to changing conditions along a local elevational gradient (Wilson et al., 2007; Lenoir et al., 2008). Although studies that span a species entire geographic range are relatively uncommon (Parmesan, 2006), elevational gradients often encompass the entire local range, permitting examination of local upper and lower range limits. Concordant with recent warming, montane studies (both local and larger-scale composites) have documented expansions of upper range limits and, to a lesser degree, upslope contractions of lower limits for temperature-sensitive species (Grabherr et al., 1994; Parmesan, 1996; Pounds et al., 1999; Beever et al., 2003; Wilson et al., 2005; Lenoir et al., 2008; Moritz et al., 2008; Raxworthy et al., 2008; Crimmins et al., 2009).

In this analysis, we use historical records and recent resurveys to document elevational shifts for nonflying small mammals in the Ruby Mountains of the Great Basin over an 80-year interval. The Great Basin is one of the most threatened ecosystems in North America (Noss et al., 1995). Climate change, land use, and invasive species have altered the structure and ecological dynamics of native plant communities in this region (Miller & Wigand, 1994; Knapp, 1996). Although studies have documented decline in individual species, such as *Erethizon dorsatum* (Sweitzer et al., 1997), *Brachylagus idahoensis* (Larrucea & Brussard, 2008), and *Ochotona princeps* (Beever et al., 2003; Grayson, 2005), the impacts of these changes remain poorly understood. This

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analysis represents the first multispecies investigation of elevational range shifts in response to recent environmental change for Great Basin small mammals. Over this 80-year interval, change in the placement of elevational range limits, midpoint, and extent are assessed for both individual species and groups of species with similar ecologies. We evaluate whether climate warming has resulted in systematic upslope shifts or expansions in elevational range, or whether potential interactions between change in climate and land use have resulted in a more complex set of responses.

To account for potential sampling biases in comparison of ranges over time (Hill *et al.*, 2002; Shoo *et al.*, 2006; Tingley & Beissinger, 2009), we introduce a binomial likelihood model that estimates whether the failure to detect a species outside of its observed range limit represents an artifact or a true 'absence.' Using data on abundances and an estimate of sampling intensity, we calculate confidence intervals around observed elevational range limits for each species in both time periods. Our model is derived from others used in paleontology to determine whether the last observation of a taxon in a stratigraphic section accurately reflects extinction (e.g., Strauss & Sadler, 1989; Marshall, 1990; Weiss & Marshall, 1999; Wagner, 2000a).

Other approaches have been proposed that account for potential sampling biases in estimating range shifts. Most commonly, survey data are subsampled to account for sample size differences across time periods (Hill *et al.*, 2002; Wilson *et al.*, 2005, 2007; Lenoir *et al.*, 2008; Raxworthy *et al.*, 2008). Although subsampling can avoid biases attributed to uneven effort over time, it is a presence-only method and may overestimate range expansion and contraction. More effective approaches account for both observations and nondetections (Tingley & Beissinger, 2009), such as occupancy modeling (MacKenzie *et al.*, 2006), which has recently been applied to estimate changes in range boundaries for historical/modern comparisons (Moritz *et al.*, 2008; Tingley & Beissinger, 2009).

Our binomial likelihood model also distinguishes between nondetection and true absence in defining species' range limits. Although it contains some assumptions which occupancy modeling can test (see 'Materials and methods'), it requires fewer ancillary data (e.g., daily trapping records) and therefore has broader potential application (e.g., for natural history collections data where sampling strategies may vary or effort data may be unavailable). The conservation community will benefit from a diversity of approaches to account for sampling biases in documenting range shifts, especially those that can be readily applied to historical data.

Materials and methods

Study system

The Ruby Mountains are located in northeastern Nevada (Fig. 1). Here, we follow Borell & Ellis (1934) and Hall (1946), including the East Humboldt Range within our study system. The Ruby Mountains span approximately 130 km in length, covering $>1821\,km^2$, and constitute one of the largest mountain systems within the Great Basin. The entire region lies within the rain shadow of the Sierra Nevada, and is generally arid, although interior mountain ranges do receive variable amounts of precipitation at higher elevations. The elevational gradient extends from between 1700 and 1800 m in adjacent valleys to 3470 m at the highest peak (Ruby Dome).
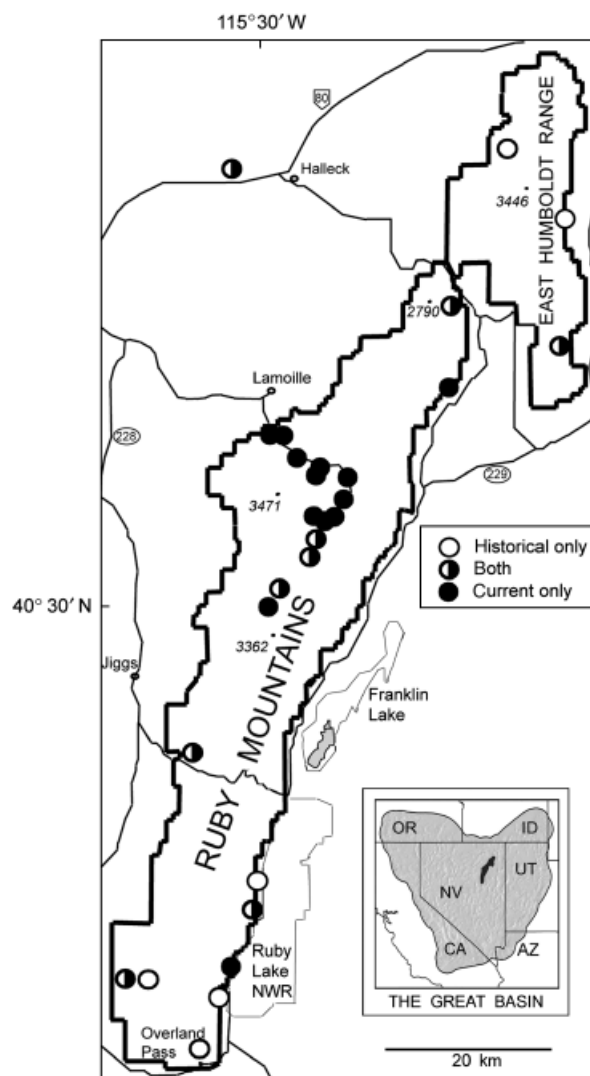

Fig. 1 Map of sites surveyed in the Ruby Mountains during the historical (1927–1929, $n=15$) and current (2006–2008, $n=22$) periods, relative to the Forest Service boundary (ca. 1800 m). Inset shows the location of the mountain range within the Great Basin.

The western slope is gradual with lower base elevations than that are present along the more precipitous eastern slope. The ecosystem is cold-temperate semi-desert with habitats across the gradient varying from desert shrublands to alpine tundra, with mid and higher elevations characterized by cirque basins and glacial lakes. Direct human activity has dramatically transformed this landscape through livestock grazing, agriculture, the arrival and spread of exotic annual species (primarily cheatgrass), and fire suppression (Miller *et al.*, 1994; Noss *et al.*, 1995; Knapp, 1996). The highest 364 km^2 are currently protected wilderness.

We extend our study area to include a nearby low-elevation site (1590 m), west of the mountain range proper, which was sampled during both historical and current surveys (Fig. 1). By establishing this site as the low point of our gradient, we can better investigate both changes at the lower elevational limit for montane species, and determine whether desert-adapted species typically restricted to the lowland valleys have expanded their ranges upslope.

This study focuses on small (<500 g) nonvolant mammals (shrews, rodents, and lagomorphs) that are readily documented using standard trapping techniques. There are 27 small mammal species within the study area. These species can be classified based on microhabitat occupancy (Brown, 1971; Grayson, 2000; Rickart, 2001; Rowe, 2007) as mesic specialists (12 species), xeric specialists (8), or habitat generalists (7). Grouping species by common environmental requirements can indicate whether there is a consistent signal in direction and magnitude of response that may provide greater generalization.

Survey data

We used diversity and distribution data collected during two discrete survey periods (1927–1929 and 2006–2008) to create two faunal 'snapshots' separated by 80 years. Both surveys were comprehensive and used comparable trapping methods. The historical surveys, conducted by Borell & Ellis (1934) from the Museum of Vertebrate Zoology, University of California, covered the extent of the mountain range (Fig. 1) and spanned elevations from 1590 to 3014 m. The objectives of the historical surveys were to document the distributions, habitat associations, and life histories of mammals from all local microhabitats (Borell & Ellis, 1934). We used their detailed field notes to reconstruct survey effort and results. Importantly, for each site we can reconstruct the number and type of traps used, and accurate abundance data (numbers and identity of all captured individuals, including those not preserved as specimens). They conducted surveys at 15 sites, capturing 2249 individuals (2155 trapped and 94 shot, 866 preserved as museum specimens), representing 37 species, 25 of which are small mammals. Records indicate 187 days of trapping, with an estimated 11 165 trapnights (one trap, set one night). Complete data on captures and trap effort were available for 167 days (89%). Incomplete data were limited to individuals processed as specimens (rather than the entire catch), or involved uncertainty in trapping effort. Species identifications were verified for potentially problematic taxa (e.g., *Microtus*, *Sorex*, and

Tamias) by direct examination of Borell's specimens housed at the Natural History Museum, University of Kansas.

Between 2006 and 2008 we conducted comprehensive surveys at 22 sites (Fig. 1). These included resurveys of nine of the 15 historical sites (those which could be precisely relocated using field notes and photographs), including the lowest- and highest-elevation sites. The remaining 13 sites were distributed along the elevation gradient. We surveyed each site for a minimum of 500 trapnights over at least four consecutive days, with traps checked twice daily. At each site, we trapped across microhabitats, using a variety of trap types (Sherman live-traps, Museum Special traps, Victor rat-traps, shrew pitfall traps, and Macabee gopher traps) to ensure sampling of the entire community. At three additional sites we only targeted gophers or shrews. In total, 16 170 trapnights resulted in the capture of 1518 individuals representing 25 species, two of which were not target taxa. Voucher specimens were deposited at the Utah Museum of Natural History, the Field Museum of Natural History, and the Monte L. Bean Museum at Brigham Young University.

We used capture data distributed across the elevational gradient to document observed lower and upper range limits for each species for both time periods. We parsed the elevational gradient into 100-m bins using the highest elevation (3470 m) as an upper, hard boundary (i.e., 1571–1670, 1671–1770, and 1771–1870 m, etc.), resulting in 19 bins, 15 of which fall within the sampled gradient (1590–3014 m). The four highest bins (3070–3470 m) were not sampled during either time period, but encompass <2% of the area of the mountain range and are principally high-alpine rock outcrop. For each time period, survey sites and associated species data were placed within their respective elevational bins. If trap lines at a given site fell within more than one 100-m bin, survey data were parsed at this finer scale. Sites were surveyed within 11 and 13 bins during the historical and current surveys, respectively (Appendices S1 and S2).

Changes in climate

Climate data were obtained at a spatio-temporal resolution comparable to the survey data. We examined changes in winter/spring (November–April) precipitation (i.e., the rainfall associated with the following growing season), summer (June–August) maximum temperature, and winter (December–February) minimum temperature. These metrics provide general indicators of climate trends, and seasonal extremes which may have a direct impact on thermal tolerances of species. For each variable, we obtained data for the 3 years of the survey period (1927–1929, 2006–2008) and the three preceding years. For each time period, we used data extracted at all survey sites (historical and current) to avoid potential biases due to variation in the distribution of sites over time. We obtained monthly gridded data sets (at ca. 4 km resolution) from PRISM Climate Group (Daly *et al.*, 1994, 2002; http://www.prismclimate.org), and interpolated values when extracting data from these grids. Although we extracted the climate data at the site level, we evaluated climate change contingent on elevation by grouping data within low (1590–2064 m),

mid (2065–2539 m), and high (2540–3014 m) elevation zones. These zones are equal in extent and roughly correspond to major transitions from desert shrub and piñon juniper woodland, to aspen and mountain mahogany woodland, to limber pine and subalpine meadow.

Occasionally, trap lines at a given site fell within different grid cells or different elevational zones. In these instances, we extracted the data for one survey site at multiple points, resulting in six additional readings [total of 37 climate data points: low ($n = 18$), mid (10), and high (9)]. Within each time period (historical or current), we computed the average climate value at each site over the representative months and years. These data were then summarized for each time period and elevational zone (low, mid, high) using box-plots. We used Wilcoxon's signed-ranks tests to identify consistent trends across sites in the direction of change in a given variable over time. We also examined statewide trends in mean annual, January, and July temperatures from 1895 to 2008, obtained from the National Climate Data Center, regressing temperature data against year to determine the extent of increase over time.

Estimating range limits

Valid comparisons between historical and current distributions require accounting for uncertainty in observed range limits. To address this problem, we introduce a binomial likelihood model to estimate confidence intervals around observed elevational range limits. This model is analogous to paleontological models used to determine whether the last observation of a taxon in a stratigraphic section accurately reflect its true extinction (e.g., Strauss & Sadler, 1989; Marshall, 1990; Weiss & Marshall, 1999; Wagner, 2000a). Similar models have been employed in conservation biology to estimate how much time must elapse after the last sighting of a species before it should be considered extinct (e.g., McCarthy, 1998; Solow & Roberts, 2003; Solow, 2005; McInerny et al., 2006; Solow et al., 2006; Rivadeneira et al., 2009). An important aspect of both problems is that the last observation of a species can either exactly reflect or underestimate the true extent of the range; it cannot overestimate it. Therefore sampling tends to obscure range endpoints, causing observed ranges to be shorter than true ranges. The likelihood that a species extends beyond the observed range is affected by two factors: the length of the proposed extension and the intensity of sampling along the gradient (Wagner, 2000a; Holland, 2003; Solow & Roberts, 2003). We apply this approach to establish a conservative estimate as to how many 100-m elevational bins a species may occupy beyond its observed upper and lower range limits.

Observed range limits represent the points beyond which the number of observations for a given species is zero, but beyond which sampling has occurred. Our model tests the hypothesis that the apparent absence of a species beyond its observed range boundary accurately reflects the range endpoint. Likelihoods are computed based on the abundance of the species in question measured across its observed range, relative to the overall sampling effort across those same elevational bins, plus the bins for which the range extension is being hypothesized. Sampling effort can be estimated using either the total number of individuals captured across all species or the trap effort employed; we compare the findings

of both measures below. Captures are often highly correlated with effort and can therefore be used as a proxy for sampling in instances where effort data are unknown or incomplete.

We adopt a binomial model, where the likelihood (L) that the observed endpoint is the true termination of the range is (Wagner, 2000a):

$$L \propto (1 - \theta)^G, \text{ with } \theta = \frac{F - 2}{S - 2}. \tag{1}$$

This model calculates the likelihood of failing to find a species beyond its observed range with G sampling opportunities. The expected proportion of success for each opportunity is θ, where F is total captures of the species over its observed range, and S is the sum of sampling opportunities across both the observed range of the species in question *and* the range extension (i.e., the total sampling over the observed range + G); Fig. 2.

We adopt as our null hypothesis, H_0, the observed range for a species is accurate, or that the sampling gap, G, is 0. From Eqn (1), $L(H_0)$ always equals 1, and the likelihood for any alternate hypotheses, H_i, proposing a sampling gap, must be <1. Therefore the most likely hypothesis is always the observed range. By adopting the observed range as the null hypothesis, we assess how well the empirical data support the inference that the observed range reflects the true range for each species. From Eqn (1), increased sampling effort beyond the last appearance of a species increases G, and lowers the likelihood of a range extension. Because G is also included in S, as G increases, θ decreases. We could estimate a constant θ, however, we adopt the more conservative approach of estimating θ as a function of the hypothesis under consideration (Edwards, 1992; Wagner, 2000a, b). This is warranted as the null hypothesis, 'The true range of Species A ends at the last observation,' implies a θ of F finds over a range of potential finds, R. The alternate hypothesis, 'Species A actually ranges to a point beyond the observed range, despite our failure to observe it,' implies a different θ: F finds over the extended range, $S = R + G$. An important aspect of this model from Eqn (1) is that it requires that a species be observed at least three times before range extensions can be calculated, conservatively eliminating inferences of range extensions for very poorly sampled species.

To determine to what extent a species may occur beyond its observed range boundary, we evaluate the strength of support in the abundance data for alternate hypotheses using likelihood ratios (LR) (Edwards, 1992; Royall, 1997), adopting Royall's (1997) cutoff of LR ≥ 8 as strong evidence in favor of a hypothesis. This value is similar to other proposed values, ranging from 7.4 (log-likelihood difference of 2) to 9.0 (Edwards, 1992; Schluter et al., 1997; Burnham & Anderson, 2002; Wagner et al., 2006; Finarelli, 2008). For simplicity, we place $L(H_0)$ in the numerator, thus the LR for a species at elevational bin i, beyond the observed range becomes

$$LR = \frac{L(H_0)}{L(H_i)} = \frac{1}{(1 - \theta_i)^{G_i}} = (1 - \theta)^{-G_i}. \tag{2}$$

LR increases with increasing θ and G, indicating progressively stronger evidence in favor of the null hypothesis relative

Sampling for
entire section
[total # captures]

Observed
Species A
[# of captures]

Elevational bin

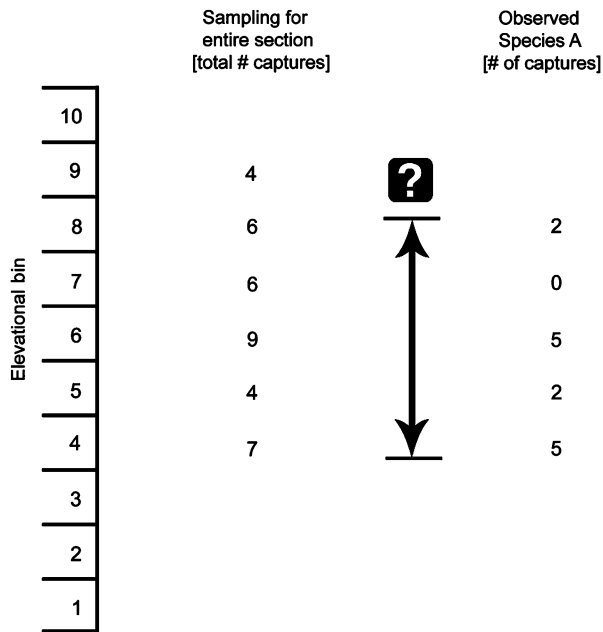|		
10		
9	4	**?**
8	6	2
7	6	0
6	9	5
5	4	2
4	7	5
3		
2		
1		

Fig. 2 Hypothetical capture data for demonstration of the binomial likelihood model (see 'Materials and methods'). Species A has an observed elevational range (double arrow, using the range-through assumption) between bins 4 and 8. However, the captures of Species A make-up a subset of the total sampling effort for the survey along the gradient. We wish to test the hypothesis that, the observed range of Species A accurately reflects its true range and therefore it is truly absent at elevational bin 9 (question mark). For a hypothesized range extension of Species A to elevational bin 9, $G = 4$. From Eqn (1), for Species A, $F = 14$ and $S = 36$, therefore $\theta = 0.35$, and the likelihood of a hypothesized extension to bin 9 is $L = (1-0.35)^4 = 0.18$. The likelihood ratio for this range extension, from Eqn (2), is LR $= (1-0.35)^{-4} = 5.60$. An LR < 8 indicates that the evidence is not strong enough to support the hypothesis that Species A's range ends at bin 8, and that a range extension through elevational bin 9 is warranted by the empirical data. See text for details.

to the alternative hypothesis of a range extension. This makes sense, in that we should always be less confident in range extensions for very common species or for intervening gaps that are well sampled or very long (Wagner, 2000a; Solow & Roberts, 2003). LR ≥ 8 represents strong evidence in favor of the null hypothesis over the alternative, such that we are confident that the species is not present at bin i. Elevational bins for which LR ≤ 8, represent points along the gradient where the data are ambiguous, and therefore constitute range extensions supported by the empirical data (Fig. 2).

Analyzing range shifts

Temporal changes in species elevational ranges were evaluated using the estimated confidence intervals as the upper and lower range endpoints for each species. Failure to account for uncertainty in observed range endpoints results in invalid comparisons between historical and current distributions. We

employed regression analyses to identify patterns of change in the placement of the upper and lower range limits, the mid-point and the overall range extent. We also discuss range shifts in reference to species-specific patterns of occurrence along the gradient over the 80-year interval. Using Fisher's exact test (two-sided), we assessed the significance of differences in proportions of occurrence over time within the three elevation zones.

Results

Changes in climate

Data at the state level indicate an increase in annual mean temperature of 1.11 °C between 1927 and 2008 (Fig. 3a). Seasonal values are similar, ranging from 1.03 to 1.32 °C for July and January, respectively. Increases in temperature are also evident within the study region, although the extent of change varies along the elevation gradient. We documented significant increases in summer maximum temperature at low (Wilcoxon's signed-ranks tests: 18 increases, 0 decreases, $Z = -3.724$, $P < 0.001$), mid (9 increases, 1 decrease, $Z = -2.701$, $P = 0.007$), and high (9 increases, 0 decreases, $Z = -2.668$, $P = 0.008$) elevations (Fig. 3b), as well as for mean summer maximum temperature (paired-sample t-tests, low: 1.33 °C, $t = -14.110$, $P < 0.001$; mid: 0.58 °C, $t = -4.815$, $P < 0.01$; high: 0.58 °C, $t = -6.050$, $P < 0.001$). Across all sites, summer maximum temperature increased 0.94 °C ($t = -11.017$, $P < 0.001$), with site-specific values ranging from -0.02 to 1.76 °C. Changes in winter minimum temperatures were more ambiguous (Fig. 3c). Among sites within each elevational zone, the number of increases relative to decreases was not significant, however, the relative number of increases does rise with elevation (Wilcoxon's signed-ranks tests, low: 9 increases, 9 decreases, $Z = -0.697$, $P = 0.486$; mid: 6 increases, 4 decreases, $Z = -0.051$, $P = 0.959$; high: 7 increases, 2 decreases, $Z = -0.77$ $P = 0.441$). When means are examined, there is a significant increase in winter minimum temperatures at high elevation (paired-sample t-tests: increase of 1.01 °C, $t = -7.365$, $P < 0.001$), a marginal increase at mid elevation (0.55 °C, $t = -2.230$, $P = 0.053$), and no change at low elevation (0.06 °C, $t = -0.433$, $P = 0.671$). We can estimate expected displacement in species' ranges using adiabatic lapse rates. Conditions along an elevation gradient are variable, with lapse rates changing seasonally and different relationships present along windward and leeward mountainsides. Therefore, we calculate a range of estimates using the extreme dry (9.8 °C km^{-1}) and moist (5 °C km^{-1}) lapse rates. If species are simply tracking temperature increases, range margins at low elevations should have shifted upslope between 136

and 266 m, and between 103 and 202 m at high elevations.

Winter/spring precipitation increased along the elevational gradient between the two survey periods (Fig. 3b). At each site, precipitation is currently greater than
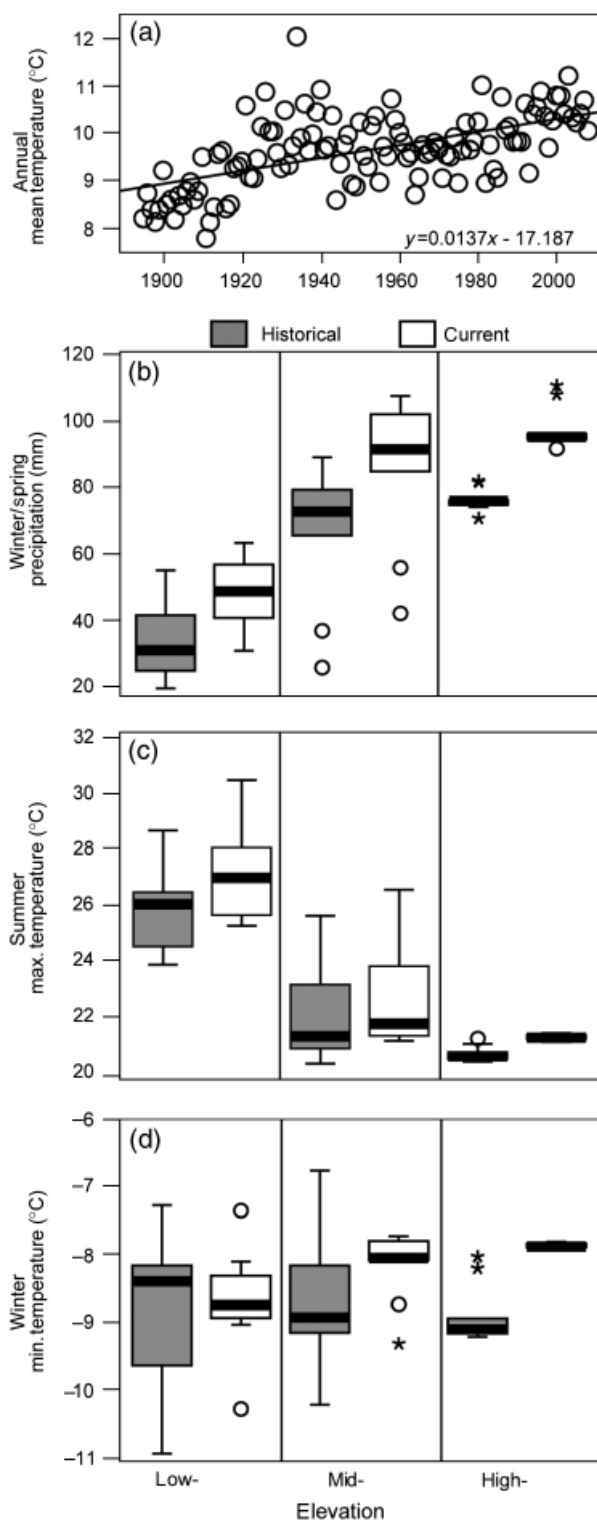
it was historically (Wilcoxon's signed-ranks tests, low: 18 increases, 0 decreases, $Z = -3.724$, $P < 0.001$, mid:10 increases, 0 decreases, $Z = -2.803$, $P = 0.005$, high: 9 increases, 0 decreases, $Z = -2.666$, $P = 0.008$). Increases in mean precipitation among sites within each elevational zone were significant, and rose with elevation (paired-sample t-tests, low: 14.62 mm, $t = -13.239$, $P < 0.001$; mid: 19.65 mm, $t = -13.925$, $P < 0.001$ high: 21.59 mm, $t = -18.111$, $P < 0.001$).

Estimates of range limits

Of the 25 target species in the historical data set, there were sufficient data to calculate confidence intervals for 24 species. Of these, eight show perfect and 13 near-perfect (within one elevational bin) correspondence between observed and estimated range limits (Appendix S1). Among species for which extensions were documented, the average upper and lower range extensions were 210 and 100 m, respectively. Although our focus is on small mammals, captures of larger mammals are incorporated into sampling effort (Appendix S1) because the traps used to collect those individuals could potentially have captured members of the target group (i.e., 45% of captures from steel leg-hold traps used during the historical period were small mammals). The historical data set also includes individuals that were shot (at precise localities) or caught by hand. We analyzed the data without these individuals (4.3% of all captures), and incorporating them did not impact estimated confidence intervals for the remaining species. Using trap effort as the measure of sampling intensity affected the estimated ranges of two species, *Sorex monticolus* and *Ochotona princeps*, expanding the lower range limit of each by 1 bin (*S. monticolus*: bin 1970; *O. princeps*: bin 2570).

For the current data set, we estimated range extensions for 18 of the 21 focal species. Of these, seven show perfect and seven near-perfect (within one bin) correspondence between observed and estimated range limits (Appendix S2). Among the species for which extensions were documented, the average upper and

Fig. 3 Statewide (Nevada) data on annual mean temperature from 1895 to 2008 (a). Changes in Winter/spring (November–April) precipitation (b), summer (June–August) maximum temperature (c) and winter (December–February) minimum temperature (d) over the past 80 years in the Ruby Mountains. Time periods include the 3 surveyed years plus 3 years preceding: historic (1923–1929) and current (2002–2008). Trends are presented for broad elevation bins (low: 1590–2064 m, $n = 18$; mid: 2065–2539 m, $n = 10$; high: 2540–3014 m, $n = 9$). Data sources provided in 'Materials and methods.'

lower range extensions were 300 and 140 m, respectively. During our surveys we captured two species outside of our target group. As with the historical data we included these in the calculation of sampling effort (Appendix S2). Using trap effort only affected the estimated range limit of *Peromyscus truei*, extending its lower limit by one additional bin (bin 1670). Agreement between the two measures of sampling intensity is unsurprising, as trap effort and total number of individuals captured are significantly correlated during both survey periods [Historical: $n = 18$ (sites surveyed multiple times are separated by year), $r = 0.822$, $P < 0.01$; Current: $n = 77$ (traplines), $r = 0.591$, $P < 0.01$]. Removal of specialized trap types (shrew pitfall traps and gopher traps) does not affect the results.

Here we provide a detailed explanation for the estimated range extensions in one of the historical data sets (Appendix S1); results are similar for other data sets. For many species [e.g., *Perognathus parvus* and *Dipodomys ordii*) range extensions were not postulated despite sampling in adjacent elevational bins (Appendix S1), suggesting that the survey data for these species accurately reflects their ranges. In several cases a lower range extension of one bin was estimated only because the observed range endpoint was adjacent to a bin without sampling (i.e., bin 1770 Appendix S1). Because $G = 0$ for any bin with no sampling, LR = 1 [Eqn (2)]; that is, the LR correctly reflects ignorance when an observed range boundary is defined by a lack of data in the adjacent bin.

The observed range for *P. truei* appeared to be narrowly distributed in the historical data set, however, the estimated upper range limit extends to the edge of the study system (Fig. 4, Appendix S1), suggesting the available data are insufficient to estimate the historical elevational range, and therefore interpretations of change over time at this upper range limit cannot be made with any confidence. Magnitudes of range extensions are influenced by the relative number and distribution of captures across the observed range. Fewer observations and greater patchiness tend to lower estimates of θ for a given species, as captures for that species contribute less to the total number of finds across those elevational bins. Abundant species, such as *P. parvus* and *D. ordii*, have no hypothesized extensions because they constitute large proportions of the total finds where they occur (Appendix S1), and when one fails to find these species outside their observed ranges, it represents strong evidence that their ranges have indeed ended. Conversely, rare species represent only a small proportion of the captures at any given elevation, and failure to find these species does not constitute strong evidence for their absence beyond their observed range limits.

Range shifts

A total of 27 small mammal species were recorded in the study region from the historical (1927–1929) and current (2006–2008) surveys, with 19 documented during both periods. *O. princeps* were sighted during the current surveys, but not targeted because recent studies document substantial population declines and local extinctions in this region (Beever *et al.*, 2003; Grayson, 2005). Of the seven species documented during only one survey period, appropriate sampling methods were used during both periods, and therefore failure to detect them suggests either occurrence at very low densities or local extinction/colonization between surveys. Few observations (≤ 6) were made for five of these seven species (Appendix S1: *Microdipodops megacephalus*, *Spermophilus mollis* and *Peromyscus crinitus*; Appendix S2: *Sorex preblei* and *S. tenellus*), whereas two species, *Perognathus longimembris* and *L. curtatus*, were more abundant (Appendix S1).

Here, we discuss temporal range dynamics for 17 of the 19 species documented during both survey periods. We exclude the two gophers, *Thomomys talpoides* and *T. townsendii*, because their capture generally requires specialized trapping, the incidence of which cannot be verified across all historical sites. Of these 17 species, there were sufficient data [Eqn (2)] to calculate confidence intervals for all but one, *Onychomys leucogaster* (Appendix S2). The elevational distributions during each survey period are shown in Fig. 4 (see also Appendices S1 and S2). Because observed ranges may reflect sampling biases we incorporate the estimates of confidence intervals in all discussions of range limits, midpoints and extents.

The results show no consistent directional trend in shifts at either the upper (Fig. 5a; Wilcoxon's signed-ranks tests: 4 decreases, 2 increases, 9 ties, $Z = -0.632$, $P = 0.527$) or lower (Fig. 5c; 4 decreases, 4 increases, 8 ties, $Z = 0.000$, $P = 1.000$) range margins. Displacement at the lower range limit was slightly more common (50%) than at the upper limit (40%), although all lower limit shifts were relatively minor, with the median shift both upslope and downslope of 200 m (Figs 4 and 5c). Median expansion and contraction at the upper range limit were 350 and 200 m, respectively. The magnitude of upslope vs. downslope shifts pooled for upper and lower range limits were not significantly different (Mann–Whitney U-tests: $U = 21$, $Z = -0.454$, $P = 0.755$), nor were the magnitude of pooled upslope and downslope shifts for upper vs. lower range limits ($U = 22$, $Z = -0.303$, $P = 0.852$). Similarly, directional trends across species in range midpoint (Fig. 5b; 5 decreases, 4 increases, 6 ties, $Z = -0.241$, $P = 0.809$) and range extent (Fig. 5d; 6 decreases, 4 increases, 5 ties,

$Z = -0.466$, $P = 0.641$) were not evident. These results were generated using total number of individuals as the measure of sampling intensity. As mentioned above, model results using trap effort to measure sampling intensity expanded the lower limit of only one species for each survey period, and only by a single elevational bin, and do not alter these results.

We categorized species by microhabitat preference as generalist, xeric or mesic. Comparing range shifts for species across categories is complicated by the low number of xeric species captured during both time periods (Fig. 4), and as a result, our discussion is largely qualitative. Historically, the ranges of all but one generalist extended to the upper limit of the gradient, therefore precluding possible upslope expansion. Stasis was evident in only two generalist species, *Peromyscus maniculatus* and *Spermophilus beldingi* (Fig. 4). *Tamias minimus*, showed a substantial change at the upper range limit, contracting downslope 300 m. At the lower range boundary, upslope contractions of 200 m were documented for *T. umbrinus* and *S. lateralis*, and a downslope expansion of at most 200 m for *Reithrodontomys megalotis*.

No xeric species showed upslope range expansions between the two survey periods (Fig. 4). The elevational range of *P. parvus* was static, and the range of *D. ordii* contracted downslope by 200 m. Although the historical upper limit of *P. truei* is uncertain, it could not have

expanded upslope (Fig. 4), and its lower range limit expanded downslope either 200 or 300 m (depending on measure of sampling intensity). Two species, *L. curtatus* and *P. crinitus*, were captured during the historical survey but were not taken during the current survey. We also do not observe upslope range expansions in the two xeric species typically restricted to the lowland valleys (*P. longimembris* and *M. megacephalus*, Appendices S1 and S2).

Potential range shifts could be evaluated for seven mesic species. Two mesic species, *Zapus princeps* and *Sorex palustris*, showed upslope contractions at their lower range limits (Fig. 4). *Z. princeps* also expanded its upper range limit 600 m. *Microtus montanus* may have expanded its range upslope one elevational bin. Directionality in the displacement at the upper range limit of *Sorex vagrans* is uncertain due to potential sampling biases during the historical time period (Fig. 4).

Temporal patterns in occurrence across elevation confirm these findings, as xeric species do not occur at more sites now than in the past. In fact, two species have declined in occurrence at their range boundaries (Table 1). Similarly, among mesic species, patterns of occurrence support the expansion of *Z. princeps* into higher elevations. No generalist species increased in occurrence over time, and decreases in occurrence are suggested at the lower limit of *T. minimus*, but are not yet manifest as a range contraction (Table 1, Fig. 4).
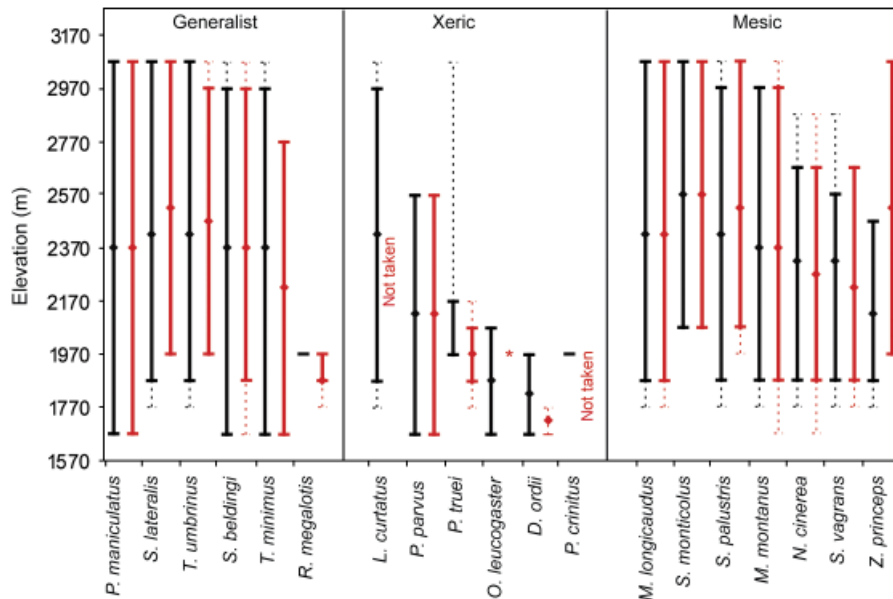

Fig. 4 Observed and estimated range limits for 20 species in both the historical (black) and current (red) survey periods. Solid lines indicate observed ranges and the dotted lines the extensions using number of individuals as the measure of sampling intensity. Diamonds represent range midpoints. Extensions could not be computed for *Onychomys leucogater*, indicated by *. For clarity not all species are pictured. Three species (*Spermophilus mollis*, *Perognathus longimembris*, and *Microdipidops megacephalus*) restricted to lowlands during the historical surveys were not captured during the current surveys and are not shown (Appendices S1 and S2). *Ochotona princeps* was not targeted during the current surveys and is therefore not pictured. Gophers (*Thomomys talpoides* and *T. townsendii*) also are not shown. Elevations represent each upper bin boundary.
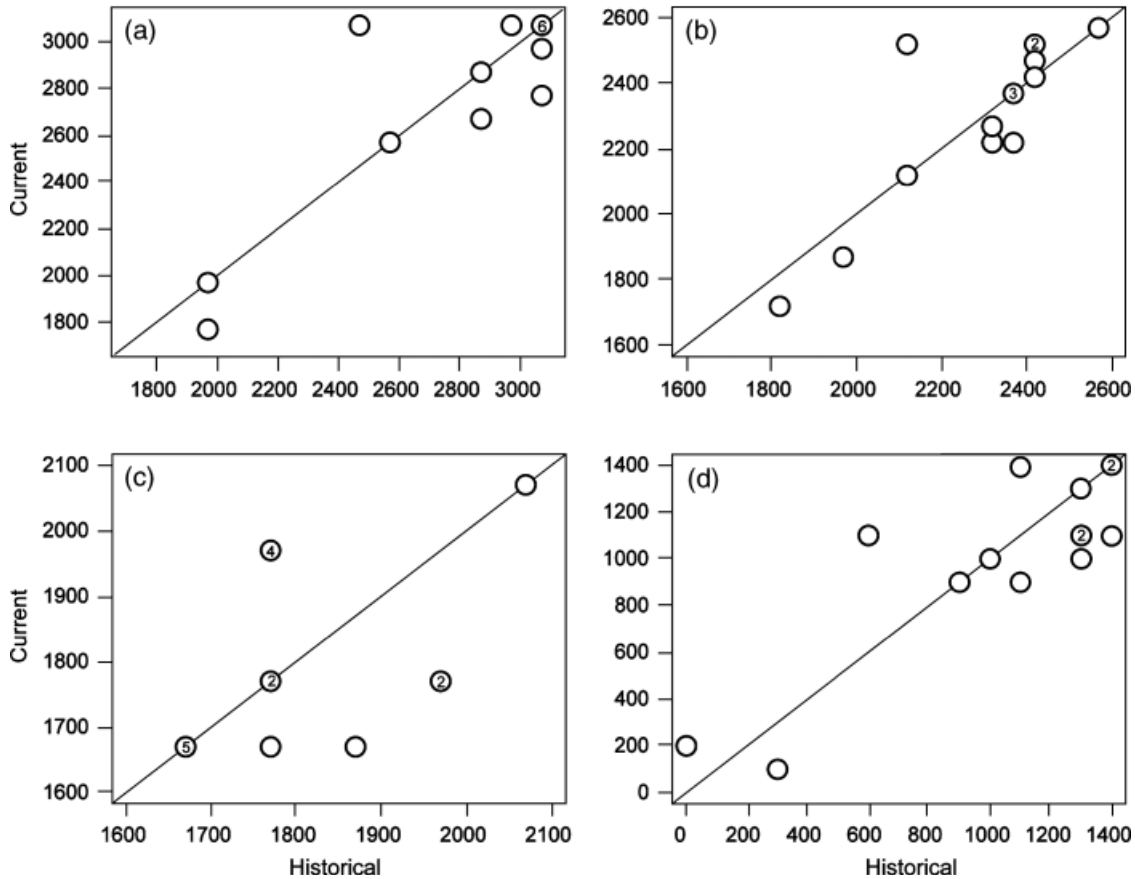
Fig. 5 Summary of the changes in species' upper (a) and lower (c) range limits, the range midpoint (b), and the range extent (d) between the historical and current time periods. Data reflect those provided in Fig. 3, with the exceptions of *Lemmiscus curtatus* and *Peromyscus crinitus*, which were not documented during the current surveys. Each circle represents one species unless multiple species with an identical pattern are indicated by an enclosed number. Because of the uncertainty in its upper range limit, *Peromyscus truei* was only included in the lower range limit panel. Similarly, *Onychomys leucogaster* was excluded from all panels.

Discussion

Estimating range limits

Evaluating uncertainty associated with range endpoints is necessary for making informed inferences about distributional shifts (Shoo *et al.*, 2006), and both subsampling (Hill *et al.*, 2002; Wilson *et al.*, 2007) and information-theoretic (MacKenzie *et al.*, 2006; Moritz *et al.*, 2008) approaches have been employed to address this issue. Our likelihood technique complements these, providing species-specific assessments of range boundaries, without requiring ancillary information (i.e., daily trapping records), which may not be obtainable for many historical data sets. This then increases the potential pool of data that can be applied to these questions.

The binomial likelihood model calculates confidence intervals around the observed range endpoints using likelihood ratios. Here, we calculated range extensions using abundance data, however, an additional benefit of this approach is that it can be easily applied to situations where only presence/absence is known (Wagner, 2000a). We used both total number of captures and trap effort as proxies for the sampling effort along the gradient, finding high concordance between results. Given the correlation between effort and captures, when effort data are not available, robust findings can be achieved using capture data. We also note that although we demonstrate the model for elevational ranges, this model can be applied to any one-dimensional gradient (e.g., latitude or depth).

Changes in elevational ranges

Over the past 80 years, the Ruby Mountains have become warmer and wetter. There are documented increases in summer maximum temperature across the

Table 1 Occurrence data for species in the historical and current periods

Species	Low			Mid			High		
	H	C	P	H	C	P	H	C	P
Generalist									
Peromyscus maniculatus	8	10		5	4		3	9	
Spermophilus lateralis	3	3		4	3		3	6	
Tamias umbrinus	4	4		4	2		3	8	
Spermophilus beldingi	4	1		2	0		1	4	
Tamias minimus	7	4	0.07 ↓	4	2		1	2	
Reithrodontomys megalotis	1	4							
Xeric									
Lemmiscus curtatus	2	0		3	0		1	0	
Perognathus parvus	8	9		5	1	0.05 ↓			
Peromyscus truei	2	2		1	0				
Onychomys leucogaster	3	1							
Dipodomys ordii	5	1	0.04 ↓						
Peromyscus crinitus	2	0							
Mesic									
Microtus longicaudus	5	4		4	4		2	7	
Sorex monticolus	1	1		1	3		2	7	
Sorex palustris	3	1		2	2		1	3	
Microtus montanus	4	3		2	2		1	1	
Neotoma cinerea	5	4		3	0		1	1	
Sorex vagrans	5	6		2	3		0	1	
Zapus princeps	3	4		4	4		0	8	0.02 ↑
Total number sites	8	10		5	4		3	9	

Sites were divided into three broad elevational zones: low (1590–2064 m), mid (2065–2539 m), and high (2540–3014 m). Significance per zone was determined using Fisher's exact test, because power is low all P values ≤ 0.10 are shown. Direction of change between historical (H) and current (C) surveys is depicted with an arrow.

entire gradient, and significant increases in winter minimum temperature occur at higher elevations. An asymmetric rate of increase in minimum temperatures has been noted along other elevational gradients, (Diaz & Bradley, 1997; Pounds *et al.*, 1999), although this is not universal (Vuille & Bradley, 2000; Pepin & Lundquist, 2008). Such asymmetry may result when a drier adiabatic lapse rate is converted to a moist lapse rate at high elevations, especially if decreased snowpack has lowered albedo, further enhancing warming. Increases in precipitation were gradient-wide. Although climate-based expectations in range response based on temperature without precipitation are likely overly simplistic, based solely on warming, we would predict species' ranges to have generally shifted upslope between the historical (1927–1929) and current (2006–2008) survey periods. For generalists, upslope expansions (where possible) or stasis were expected, whereas among specialists, xeric species should have expanded upper range limits and mesic species should show upslope shifts at one or both range margins, depending on the position of their historical distribution. Because of asymmetric warming in minimum temperatures (Fig. 3), expansions

at the upper range limit should be greater than upslope contractions at lower limits.

However, our results do not provide evidence for such systematic range shifts. While most generalist species could not expand their ranges upslope between sample periods, stasis is only observed for two of six generalist species. Moreover, no xeric species expanded their ranges upslope during this 80-year interval (Fig. 4, Appendices S1 and S2). Rather, xeric species' ranges either remained at historical limits or showed either a lowering of the upper range limit (*downslope* range contraction) or a lowering of lower range limit (*downslope* range expansion). The absence of upslope expansions may reflect a lag between change in environmental conditions and associated range shifts. However, the number of sites occupied at upper range margins either remains static or decreases (Table 1), suggesting that the lack of upslope shifts cannot be attributed to an increase in species occurrences at the upper range margin preceding upslope invasion. Our results also suggest that species typically restricted to lowland valleys (i.e., *P. longimembris* and *S. mollis*) have not moved into montane habitats in response to

increased temperatures, although we cannot comment on patterns of occurrence for these species, as our sampling within the valley bottom was limited. Elevational stasis in some lowland species may be attributed to restricted microhabitat requirements (e.g., based on edaphic features) that may not be available upslope despite suitable climatic conditions.

A few xeric species were not recorded during the current surveys, many of which were historically rare (Appendix S1). Failure to detect them during the current surveys may not indicate episodes of local extirpation. One species, *L. curtatus* was detected at numerous sites during the historical surveys (Appendix S1), but not in the current surveys. However, this species is known to have irruptive population fluctuations (Carroll & Genoways, 1980), and its absence in the current data set is not strong evidence for absence in the modern system.

Although many mesic species have broad elevational ranges, only two showed upslope shifts at their lower range limits (Fig. 4). Upslope contractions for both *Z. princeps* and *S. palustris* may indicate a direct response to warming (i.e., summer maximum temperatures that are beyond the range of tolerance), and fall within lapse rate expectations. However, indirect responses to warming cannot be ruled out. For example, *S. palustris* has a specialized diet of aquatic invertebrates (Beneski & Stinson, 1987), and its disappearance at low elevations may reflect changes in availability of preferred prey that are restricted to cold stream habitats. Retention of low elevation range boundaries in other mesic species may reflect other factors, such as increased precipitation, recovery of habitat from earlier periods of grazing (Rowe, 2007), or that temperatures have yet to pass beyond critical thresholds.

Z. princeps was the only species to show a substantial upslope range expansion, with an upslope invasion three times that of the contraction at its lower limit (Fig. 4), far exceeding expectation based on lapse rates alone. A greater shift at the upper range margin is concordant with expectations based on the asymmetric rates of warming for minimum temperatures along the gradient. This species is an obligate hibernator with documented sensitivity to temperatures during hibernation, particularly with respect to juvenile survival (Cranford, 1978, 1983). It therefore follows that increases in winter minimum temperatures would permit successful hibernation at higher elevations.

Our results differ from those of the recent Grinnell resurvey in Yosemite National Park, California, USA (Moritz *et al.*, 2008). Both studies compare historical museum survey and recent field data to document changes in elevational ranges in comparable small mammal faunas in the western United States. In accord with climate warming, Moritz *et al.* (2008) documented significant upslope shifts or expansions for many high– and low-elevation species. In our analysis, *Perognathus parvus* showed no change in its elevational range, whereas in Yosemite, Moritz *et al.* (2008) noted upward range expansion in a related pocket mouse *Chaetodipus californicus*, ultimately doubling its range extent. In addition, in our analysis *Peromyscus truei* expanded its range *downslope*, whereas it showed substantial *upslope* shifts for both upper and lower range limits in Yosemite (Moritz *et al.*, 2008).

These differences in response cannot be attributed to variation in resurvey interval (ca. 90 vs. 80 years) or degree of warming documented across regions. Rather, the most notable difference between these gradients is land use. Whereas land use driven changes in habitat are relatively minor in the protected landscape of Yosemite National Park (Moritz *et al.*, 2008), they are widespread at low- to mid-elevations across the Great Basin (Noss *et al.*, 1995). We attribute the downslope range expansions and contractions for species in the Ruby Mountains to floristic changes resulting from climate warming, land use, and the spread of invasive species.

Piñon-juniper range expansion and increased density have been well documented in the Great Basin (Tausch *et al.*, 1993; Miller & Wigand, 1994; Weisberg *et al.*, 2007; Bradley & Fleishman, 2008). Expansion has been both up and downslope, but is greater in the downslope direction, where it displaces sagebrush steppe (Weisberg *et al.*, 2007) (Fig. 6). Expansion of piñon-juniper woodlands began in the late 1880s with a sharp increase by the early to mid 1900s (Miller & Rose, 1999). Both climate and land use have been implicated. Warming has been shown to promote upslope expansion (Miller & Wigand, 1994; Gray *et al.*, 2006), and may contribute to downslope expansion by altering winter thermal inversion layers (Billings, 1954). Increases in precipitation also likely promote downslope movement as establishment in the arid lowlands is moisture dependent (Bradley & Fleishman, 2008). While changes in climate conditions may facilitate tree invasion, it has been argued that the rate and extent of expansion was also initiated by, and continues to be exacerbated by, land-use practices, namely reduced fire frequency and overgrazing (Miller & Wigand, 1994; Miller & Rose, 1999). Grazing can promote piñon-juniper expansion through removal of competing herbaceous cover (which also indirectly suppresses fire by removal of fine fuels), and in the late 19th and early 20th centuries, grazing by domestic livestock was the most widespread form of land use in the West (Fleischner, 1994; Vavra *et al.*, 1994).

Exactly which set of interacting factors has promoted piñon-juniper woodland expansion in the Ruby Mountains is not known, but the consequences for the small

Fig. 6 Repeat photography showing vegetation changes at Flyn Springs (1859 m). Historical photo was taken by A. E. Borell in 1928 (courtesy of MVZ archives) and the current photo by R. J. Rowe in 2006. Most notable is the expansion of piñon-juniper woodland at the expense of shrubland.

mammal fauna are profound. Our results show a downslope range expansion of *P. truei*, which has a close association with piñon-juniper woodland (Hoffmeister, 1951). In contrast, two sage-loving species, *P. parvus* and *T. minimus* decreased in occurrence at low and mid elevations, potentially suggesting range contractions in the near future. Decline in sagebrush habitat may also have decreased the probability of detecting *L. curtatus* during the current surveys. Increases in precipitation also may have contributed directly to the absence of upslope range shifts among the xeric-adapted, low-elevation species.

Other floristic changes have influenced downslope range dynamics for low-elevation species. The downslope range contraction in *D. ordii* may be explained by the encroachment of shrubland into areas previously dominated by grasses and open habitat (Brown *et al.*, 1997). This turnover in vegetation was likely facilitated by earlier periods of overgrazing (e.g., USFS, 1993; Elmore & Kauffman, 1994; Austin & Urness, 1998). Lastly, we document the downslope range expansion of *R. megalotis*, a seed eater often associated with heavy grass cover but found within a broad range of microhabitats. We attribute this result to a combination of factors including the downslope expansion of piñon-juniper woodland (Hope & Parmenter, 2007) and regrowth of herbaceous cover following release from overgrazing (Reynolds & Trost, 1980; Jones *et al.*, 2003).

Conclusions

Over the past 80 years, upper and lower elevations within the Ruby Mountains have been subject to different changes in climatic conditions and land-use histories. As a result, the small mammals within this region do not show systematic range shifts concordant with the predicted effects of climate warming alone. While some mesic species have responded to warming by shifting their ranges upslope, potential range expansions of low-elevation, xeric species have been hampered by land use driven changes in vegetation and perhaps the counter effect of increased precipitation. The continued and combined effects of climate change and land use are likely to result in communities dominated by generalists (Warren *et al.*, 2001), as the distribution of specialists are pushed toward the gradient margins. Predictive distribution models that only incorporate climate thresholds should be interpreted with great caution for regions where the modern landscape has been heavily modified by human activity.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Abundance data and model output for the historical surveys (1927–1929).
Appendix S2. Abundance data and model output for the current surveys (2006–2008).

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