Title: **Montane mammals moving upward in the Rocky Mountains as temperature warms**

**Short title:** Upward elevational shifts in montane mammals

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**Abstract**

The Southern Rocky Mountains, the largest and tallest mountain range in the contiguous United States, have warmed considerably in the past several decades due to anthropogenic climate change. Herein we examine how the elevational ranges of 47 mammal species (42 rodents, 5 shrews) have changed between their historical (pre-1980) and contemporary distributions (post-2005) in the Front Range Mountains and San Juan Mountains of Colorado. Historical elevational ranges were based on more than 4580 geo-referenced museum specimen and publication records. Contemporary elevational ranges were based on 7444 records from systematic sampling efforts and museum specimen records. We constructed Bayesian sampling models to estimate the probability a species was present, but undetected, due to undersampling at each 50 m elevational bin for each time period and mountain range. These models leveraged individual-level detection probabilities, the number and patchiness of detections across 50 m bands of elevation, and a decaying likelihood of presence from last known detections. The 95% likelihood elevational ranges were then compared between historical and contemporary time periods to detect directional change. Responses were variable as 23 mammals shifted upward, 10 did not change, 10 shifted downward, and 4 were locally extirpated. The average range shift was 122 m upward, although exclusively montane species shifted upward more often (83%) and displayed larger average range shifts (337 m). Changes in upper range limits were best predicted by increases associated with (a) montane species, (b) species with higher maximum latitude in their geographic range, and (c) the study mountain in the southern edge of their geographic range (stepwise multivariate linear regression: r2 = 0.4705, p < 0.0001). Thus, mammals in the Southern Rocky Mountains serve as harbingers of more changes to come particularly for montane, cold-adapted species in the southern portion of their ranges.

**Introduction**

Earth is warming at an unprecedented rate from human-created emissions ([Duffy & Tebaldi, 2012](#_ENREF_19), [Trenberth *et al.*, 2007](#_ENREF_51), [USGCRP, 2009](#_ENREF_52)). Anthropogenic impacts are also affecting precipitation trends as well as increasing the variability and severity of extreme weather events ([Duffy & Tebaldi, 2012](#_ENREF_19), [Trenberth *et al.*, 2007](#_ENREF_51), [USGCRP, 2009](#_ENREF_52)). Essentially the planet and all its inhabitants are in a climate crisis of unknown magnitude. One urgent imperative is tracking the impacts of these climate changes on living organisms to better mitigate the damages and to improve predictions of foreseeable conservation catastrophes. Unfortunately, there are still more predictive papers than empirical publications describing species responses ([e.g., Dawson *et al.*, 2011](#_ENREF_18), [review in McCain & King, 2014](#_ENREF_33)). Reasons for this disconnect are many-fold, but foremost are the paucity of detailed historical and repeatable surveys across gradients of change (e.g., latitude, elevation, depth), and the significant and long term effort and quantity of data needed to detected organismal responses. As a research community we need to embrace creative ways to compile historical and contemporary records to robustly track how organisms are currently changing and monitor these changes through time ([Dawson *et al.*, 2011](#_ENREF_18), [Grytnes *et al.*, 2014](#_ENREF_24)).

The published resurveys of historical montane gradients do provide strong evidence that some organisms are shifting their ranges to higher elevations. For example, many small mammals have shifted upwards in California ([Moritz *et al.*, 2008](#_ENREF_37), [Rowe *et al.*, 2015](#_ENREF_43)) and Utah ([Rowe *et al.*, 2010](#_ENREF_45)). Many alpine plants in Europe have shifted higher with climate change ([Engler *et al.*, 2011](#_ENREF_20), [Grabherr *et al.*, 1994](#_ENREF_23), [Lenoir *et al.*, 2008](#_ENREF_31), [Pauli *et al.*, 1996](#_ENREF_42)), butterflies on Mt. Kinabalu in Borneo have shifted upwards by an average of 67 m ([Chen *et al.*, 2009](#_ENREF_15)), and a review of montane shifts detected an 11 m increase in elevational ranges per decade across organisms ([Chen *et al.*, 2011](#_ENREF_14)). But the upward shifts are not the whole story; one critical element is the variability in responses on these gradients. Overall the shifts are upward, but individual species also demonstrate unexpected responses like downward shifts or no detectable changes ([Crimmins *et al.*, 2011](#_ENREF_17), [Lenoir *et al.*, 2010](#_ENREF_30), [McCain & King, 2014](#_ENREF_33), [Rowe *et al.*, 2015](#_ENREF_43)). The location of the mountain appears important. For example, American pika on small, isolated sky islands in the western US are experiencing local extirpations linked to higher temperatures, decreased precipitation, and lack of rock ice features ([Beever *et al.*, 2003](#_ENREF_5), [Beever *et al.*, 2010](#_ENREF_6), [Beever *et al.*, 2011](#_ENREF_7), [Millar & Westfall, 2010](#_ENREF_36)). But the same species in the more expansive, taller, and interconnected southern Rocky Mountains appear to have few, if any, local extirpations ([Erb *et al.*, 2011](#_ENREF_21)). Unfortunately, that is the only multi-site climate change study on mammals in the US Rocky Mountains ([McCain & King, 2014](#_ENREF_33)).

Variability in individual species responses is expected if the climatic conditions and anthropogenic changes varies on each mountain ([e.g., Grytnes *et al.*, 2014](#_ENREF_24)). Other important biogeographic factors may include the latitude of the mountain, the location of the mountain in relationship to the species’ geographic range, and the size, height and isolation of the mountain ([McCain & King, 2014](#_ENREF_33)). Traits of the species themselves like body size, activity times, and physiology may also mediate who responds as predicted to climate change and who does not (e.g., [Angert *et al.*, 2011](#_ENREF_2), [McCain & King, 2014](#_ENREF_33), [Moritz *et al.*, 2008](#_ENREF_37)). So far, such mediating traits are rarely detected in individual montane gradient studies. But for mammals, despite some initial lack of trait detection ([e.g., Angert *et al.*, 2011](#_ENREF_2), [Moritz *et al.*, 2008](#_ENREF_37)), McCain and King ([2014](#_ENREF_33)) detected that body size, activity patterns, and locations of latitudinal and elevational ranges were important to determining which North American mammal species responded as predicted to climate change. Surely if traits were important to mediating responses, we would also detect them on individual mountain gradients or particular regional studies encompassing multiple species. Strong associations in species traits and biogeographic trends with climate change responses would enable better predictions and improve conservation outcomes for the types of species most at risk from large, fast, detrimental environmental change.

Thus, herein, we examine how 47 mammal elevational ranges have changed in response to warming in two regions of the largest, tallest and most interconnected mountains in the contiguous US, the Southern Rocky Mountains. We compile historical elevational ranges for each species based on museum specimens and literature before climate change (<1980), and contemporary elevational ranges based on more than a decade of extensive trapping surveys and supplemental museum specimens (>2005). We develop Bayesian undersampling models to accommodate species-, mountain-, and time-period-specific 95% probability elevational ranges. Then we assess how elevational ranges have changed with climate change, testing for biogeographic and species-trait effects that may mediate which species are and are not moving higher in elevation with increasing temperatures.

**Materials and methods**

The Rocky Mountains extend from northern New Mexico, USA to northwestern, British Columbia, Canada reaching their highest elevations in Colorado, USA. The two mountainous regions studied in the Colorado Rockies, the San Juan Mountains (1414–4286 m) and the Front Range Mountains (1438–4346 m), were chosen for their contrasting climates and geography (Figure 1; [Armstrong *et al.*, 2011](#_ENREF_4), [Fitzgerald *et al.*, 1994](#_ENREF_22), [McCain *et al.*, 2018](#_ENREF_34)). Temperature decreases and precipitation increases with elevation on both gradients ([McCain *et al.*, 2018](#_ENREF_34)). Climatically, the southwestern San Juans are warmer and wetter than the more northeastern Front Range. Both mountains receive precipitation as snow in the winter months, but the San Juans intercept substantial rainfall from summer monsoons predominately at mid- and high-elevations, as the base of the San Juans is semi-arid desert habitat. The Front Range is less arid at the base, characterized by the western-most extension of eastern plains grassland. Temperatures have increased on both mountains since the 1980s, but the San Juans are getting increasingly wetter, while the Front Range is becoming increasingly drier (Mote et al. 2005).

Mammal surveys and collecting began in the mid-to-late 1800s in both regions, but the Front Range is more intensively sampled (Figure 1) due to its easier access, the closer proximity of the two largest universities in the state, and the inclusion of Rocky Mountain National Park. We, specifically CMM, began trapping small mammals in the San Juan Mountains in 2007 and the Front Range Mountains in 2010; thus we have over a decade of mammal surveys and experience in the two ranges (Appendix S1). The two ranges have similar small mammal richness (rodents and shrews) with 35 species in the Front Range and 31 species in the San Juans among which 22 are shared ([McCain *et al.*, 2018](#_ENREF_34)).

*Historical Mammal Data*

We amassed specimen data from all museum collections with mammal specimens from Colorado, USA (Figure 1 circles). We downloaded data from or contacted 75 museums, and received records for 58,709 specimens from 45 of these institutions with Colorado holdings (2009–2012; Appendix S1). These specimen records were updated to the current scientific names following Wilson and Reeder ([2005](#_ENREF_55)), and were georeferenced following the MaNis protocols with quantified error estimates ([Chapman & Wieczorek, 2006](#_ENREF_13), [Wieczorek *et al.*, 2004](#_ENREF_54)). For quality assurance, we restricted analyses to rodent and shrew specimens with (1) a reliable species-level identification by an expert, re-verified by CMM, and/or in a plausible locality based on current, known state distributions; (2) a documented year or time period of collection; (3) an elevation provided by the collector or a locality specific enough to be georeferenced (latitude, longitude, elevation) with a horizontal error <1000m (designated as usable) or <5000m (designated as marginal) with the stricter criteria used in the final lowest and highest known sites; and (4) a location within the northeast portion of the Front Range (Boulder and Larimer counties) or the southwestern portion of the San Juans (Dolores, La Plata, Montezuma, San Juan counties). Each species’ historical elevational range on each gradient was based on the vetted specimen records dated before 1980. These data were augmented by historical specimens or trapping records in the literature that we did not encounter from the museums, including from the *Colorado Biological Survey* ([Cary, 1911](#_ENREF_12)), *Mammals of Mesa Verde National Park, Colorado* ([Anderson, 1961](#_ENREF_1)), and *Distribution of Mammals in Colorado* ([Armstrong, 1972](#_ENREF_3)) with a particular emphasis on lowest and highest historical records in each mountain region. The most rigorous vetting was implemented for the lowest and highest known localities for each species, in which case records were not used if any significant error was plausible in the locality, the elevation, or the identification.

*Contemporary Mammal Data*

All specimens from our Colorado mammal database and contemporary surveys that met the accuracy criteria and were collected or documented after 2005 were included in the contemporary data (Figure 1 stars). The Colorado database was augmented in 2018 using searches on GBIF (Global Biodiversity Information Facility: www.gbif.org) and Arctos (https://arctos.database.museum) for more recent specimens (2006–2018) of just our target species that had been added or collected since our original database construction. These were georeferenced (if not originally) and vetted as were all previous records.

For systematic, contemporary mammal surveys, two elevational transects were established in the southwestern San Juan Mountains and two in the northeastern Front Range ([Figure S1.1; McCain *et al.*, 2018](#_ENREF_34)). Each transect consisted of eight sites placed every 200−300m in elevation between the base of the range (1400−1700m) and the upper limit of vegetation on the mountain top (3600−3800m) (Figure S1.1). At each of these 32 sites, we conducted small mammal surveys between 2010–2012 using live-trapping, pitfall traps, and visual surveys. We chose sites that reflected the main habitats at that elevation and were anthropogenically undisturbed. Mark and recapture live-trapping was based on 300 Sherman live-traps open for 5 consecutive nights placed across habitat types (1500 trap-nights per site). Additionally, 40 pitfall traps, which better detect shrew species, were sampled across habitats for 90 days (~3600 pitfall trap-nights per site). For diurnal rodents that do not readily enter live-traps, five visual transect surveys were conducted for one hour during each of the trapping days. Visual surveys were stratified by time and location, and each sighted mammal was geo-referenced with a hand-held GPS unit. Trapping data from nine sites in the San Juans in 2007 were also included (Figure S1.1), consisting of 100 live-traps and 10 pitfall traps for 3 consecutive nights per site. Additional strategic trapping and visual surveys were conducted in sites and elevations with critical potential areas of undersampling contemporarily, including Mesa Verde National Park in 2018 with live-trapping at two sites (200 traps for 4 nights per site), pitfall traps at 9 sites (20 traps for 3 weeks per site), and standardized visual surveys at 13 sites (Figure S1.1). We also conducted additional live-trapping (200 traps for 3 nights per site), pitfall trapping (10 pitfall for 3 weeks per site), and visual surveys in three low elevation sites in the Front Range in 2017. Species were identified in hand, based on collected specimens, or with DNA sequences in cases of problematic identifications ([McCain *et al.*, 2018](#_ENREF_34)). Lastly, all mammal sightings while in camps, in transit between sites, scouting sites, or during climate and vegetation data collection were also geo-referenced and elevation recorded.

*Bayesian Undersampling-Detection Models*

The documented elevational range of the species was assumed to be between the lowest and highest known localities per time period (i.e., interpolated ranges). But the sampling along each elevational gradient in each time period was patchily distributed (Figure 1, S1.2), and species are not always detected when present (MacKenzie et al., 2002). Therefore, to estimate elevations in which each species had a high probability of occurrence beyond the observed range, we developed a Bayesian model. Occupancy models typically rely on repeated surveys and local environmental data to predict a species’ probability of presence when undetected in a particular locality (MacKenzie et al., 2002, Kéry & Royle, 2008, Szewczyk & McCain, 2019). Such data are unavailable in many cases, including for typical compiled historical datasets. Consequently, we employed a modified conceptual framework to evaluate the probability of sampling error rather than directly considering species’ environmental preferences.

Within each time period, mountain range, and elevational bin, we considered the detected individuals as a draw from a multinomial distribution (Fig. S1.2), representing a sample from the community of individuals at those elevations. The number of observed individuals from each species depends on the species’ relative abundance and the probability of detecting a given individual of the species. Thus, for each elevational bin *i*, the number of observed individuals belonging to species 1–*J*, represented as the vector ***yi***, was modeled as:

where ***pj*** is a vector of the probabilities that a random observed individual from elevational bin *i* belongs to each species, *Yi* is the total number of individuals detected across all species in elevational bin *i*, *λij* is the relative abundance of species *j* in elevational bin *i*, *Zij* is a latent binary parameter indicating the true presence (1) or absence (0) of species *j* in elevational bin *i*, and *δj* is the probability of detecting a given individual of species *j*. Note that *pij* is a probability ranging from 0 (species *j* is not present at elevation *i*) to 1 (only species *j* is present at elevation *i*). We used the repeated survey data in the contemporaneous dataset to calculate the individual-level detection probability, *δj*, for each species.

The unobserved parameter *Zij* is Bernoulli distributed with probability , which is the probability that species *j* was present but unobserved due to sampling error, and is calculated as a function of the elevational distance to the nearest detection, the patchiness of the interpolated range (i.e., the proportion of elevational bins without detections within the interpolated range), and their interaction:

where *aj* is the species-specific intercept, *β* are the slopes. The intercepts among species were distributed normally with community-level mean *α* and standard deviation *σ*, while the slopes were community-level with one value for all species.

For each elevational bin beyond each species’ interpolated range, we calculated the probability of occurrence as the posterior probability of *Zij* = 1 (i.e., the proportion of posterior samples predicting *Zij* = 1). A species was assumed absent at an elevation if the probability of occurrence was < 5%, indicating ≥ 95% posterior probability of absence. Based on this dichotomy, we calculated Bayesian interpolated ranges incorporating sampling uncertainty to then use as the elevational range of each species for each mountain in each time period. Only those species with at least 10 historical records per mountain that were also detected in the contemporary sampling were included in the range shift analyses.

The model was run with JAGS 4.3.0 in R 3.6.1 using the *rjags* package. For each dataset partition, we ran 3 chains for 20,000 iterations, with the first 10,000 iterations discarded as burn-in, and then retained every 10th iteration for the final posterior distributions. We used uninformative prior distributions for *α*, *β*, and *σ*, and a diffuse normal prior distribution constrained to be positive for each *λij* where the mean was the overall abundance of each species (Appendix S4).

*Statistical Analyses*

A significant change from the Bayesian historical to the Bayesian contemporary elevational range limits was determined if the change was ≥ 100m. The size of the shift upward (positive) or downward (negative) was calculated for the (1) lower limit; (2) upper limit; and (3) overall elevational change in range upward or downward based on the direction of range midpoint shift and the combined lower and upper shifts. To assess whether range losses and range gains were associated with particular areas on the mountains, we calculated the number of species losing or gaining range at each 50m band up each mountain. If anthropogenic habitat change, which declines with elevation on both mountains, is the dominant factor causing range reductions, then range losses should be concentrated at the lower elevations. In contrast, if anthropogenic climate change is the dominant factor causing lower range reductions and upper range expansions, then losses and gains would be expected across the lower-middle elevations, with the majority of expansions concentrated at the higher elevations. Because the number of species per elevational band differs (unimodal with highest richness of included species between 1900–2000m), counts of range losses and range gains summed across all species for each 50m elevation on each mountain gradient is biased towards elevations with more species. Thus, we examined the percentage of range losses and range gains for each 50m elevation on each mountain gradient by dividing the species counts by the historical number of species present at each band. This created an elevational heat-map of the range changes. We used non-parametric Spearman’s rank correlation tests to assess whether the trend in percent range losses decreased with elevation or percent range gains increased with elevation on each mountain gradient.

To assess how species traits influenced the responses to anthropogenic climate change, we examined several traits empirically linked or hypothesized to be important to differential responses to climate change in mammals (e.g., [Angert *et al.*, 2011](#_ENREF_2), [McCain & King, 2014](#_ENREF_33), [Moritz *et al.*, 2008 and references therein](#_ENREF_37)), including body size, activity times, elevational affiliations, high latitude ranges, location of study area within the species biogeographic range (i.e., southern third, middle third or northern third of its range), or whether the study area was near the species range edge (e.g., western-most populations of a plains species). Many more traits were possible, but we were limited by our species sample size as well as the similarity or correlation in many other traits considered here (e.g., body size and reproductive traits). Body sizes in grams were taken from the PanTHERIA and MOM databases ([Jones *et al.*, 2009](#_ENREF_27), [Smith *et al.*, 2003](#_ENREF_46)). Daily activity times (obligate diurnal, obligate nocturnal, and flexible) were from the PanTHERIA database ([Jones *et al.*, 2009](#_ENREF_27)) or species accounts in the journal *Mammalian Species*, and were checked against additional literature sources ([Armstrong *et al.*, 2011](#_ENREF_4), [Hall, 1981](#_ENREF_25), [Nowak, 1991](#_ENREF_39)). Each species was denoted as a low elevation species, a montane species, or cosmopolitan (across most habitats and elevations on the mountain) by its known habitat affinities in Colorado ([Armstrong *et al.*, 2011](#_ENREF_4)), but also based on its individual historical distribution on each mountain (all or most of its range below or above the midpoint of the mountain). Latitudinal ranges and study locations within North American geographic ranges were calculated from the PanTHERIA database ([Jones *et al.*, 2009](#_ENREF_27)) but modified to only include distributions within North America ([Hall, 1981](#_ENREF_25), [IUCN, 2011](#_ENREF_26)).

Trends in lower and upper range shifts were analyzed to detect if particular traits were associated with differential increases or decreases using multivariate linear regressions on each mountain. We used stepwise models, the lowest AICc weights, and all variables that were individually significant to detect the best-fit model ([Burnham & Andersen, 2002](#_ENREF_11)). A second set of trait analyses were conducted on expected (upward) and non-expected responses (downward, no change) on each mountain using stepwise multivariate, logistic regressions and the lowest AICc weights to detect the best-fit model as in McCain and King ([2014](#_ENREF_33)). Because phylogenetic relatedness could impact the robustness of these analyses (e.g., [Blomberg & Garland, 2002](#_ENREF_9), [Blomberg *et al.*, 2003](#_ENREF_10)), we estimated a phylogenetic signal in the lower and upper range shifts on each mountain. Phylogenies were from the mammal supertree ([Bininda-Emonds *et al.*, 2007](#_ENREF_8)) pruned to the taxa included in each mountain dataset. Phylogenetic signal was calculated with *phylosignal* ([Keck *et al.*, 2016](#_ENREF_28)) in *R* ([Team, 2019](#_ENREF_48)) using all five significance tests (*Cmean*, *I*, *K*, *K.star*, and *Lambda*). Because no significant phylogenetic signal was detected for the lower or upper elevational range shifts on either mountain (p >> 0.05; Table S1.1), we only used the non-phylogenetically corrected analyses.

**Results**

Our compiled databases for historical and contemporary distributions of small mammals (rodents, shrews) included 35 species in the Front Range Mountains (FR) and 33 species in the San Juan Mountains (SJ). Those species used in the analyses (28 FR, 19 SJ) were well sampled both historically and contemporarily with an average of 97 specimens historically and 158 specimens contemporarily per mountain (Appendix S2). The empirical elevational ranges for each species were based on these data for each mountain and time period (Figure 2: thick bars). Several species were not used in the range shift analyses because they were deemed to be insufficiently detected historically (<10 specimens; 6 FR, 13 SJ) or under-sampled with contemporary trapping methods (3 FR, 1 SJ; see Figure S3.1). The sampling across each elevational gradient in each time period was not uniform (Figure 1; Figure S1.2). This is expected given the historically compiled efforts across multiple generations of researchers. Nonetheless, the number of specimens and localities is quite high both historically (4580 specimen-localities) and contemporarily (7444 specimen-localities) for these two regions. Importantly, the sampling effort is underestimated from these specimen sums. It represents only the successful captures of our target species, but not the captures of non-target mammals, any individuals not saved as specimens, nor the trapping efforts that resulted in no or few specimens. Nonetheless, to compensate for the patchy distribution of specimens and sampling across the two mountains and time periods, we constructed Bayesian sampling models.

The Bayesian sampling models utilized the number of observations per 50m elevational band, the estimated probability of detection based on our mark-recapture statistics, the patchiness of the elevational distribution for the species, and a declining probability of undersampling away from the last known detection to estimate a probability of distribution. The changes in the range limits between the empirical data and the Bayesian model varied from 0 to 392 m historically and 60 to 657 m contemporarily. The elevational limits based on the 95% probability for both the lower limit and the upper limit on each species elevational range per mountain per time period was then compared to assess range shifts with climate change (Figure 2: thin bar extensions; Appendix S2). Species that significantly shifted their lower or upper elevational limit contemporarily (≥100m change) included 23 species that shifted upwards and 10 species that shifted downward (Figure 2 blue and red bars, respectively). Another 10 species did not significantly shift either range limits (Figure 2 grey bars), and four species known historically were undetected contemporarily and thus considered locally extirpated (zeros in place of contemporary range bars).

The average elevational range shift across all species was upward by 122 m. The Front Range species shifted higher on average (152 m) than did the San Juan species (80 m). These shifts varied across species with both losses and gains in lower limits and upper limits (Figure 2). Elevational heat maps display the non-random distribution of range losses and gains (Figure 3). The percentage of range gains increased significantly with elevation on both gradients (Spearman’s rank correlations: FR r = 0.42, p = 0.0399; SJ r = 0.53, p = 0.0077). Whereas, the percentage of elevational losses occurred across both elevational gradients rather uniformly (Spearman’s rank correlation FR r = -0.23, p = 0.2827; SJ r = 0.245, p = 0.2485). All four species detected as locally extinct were low elevation rodents with relatively small elevational ranges and all associated with dry desert, grassland or canyon habitats.

A combination of species traits and biogeography influenced the trajectory and magnitude of the range shifts, particularly for the changes in the upper range limits (Figure 4, 5). Montane species shifted higher more often (83%) and with larger upward shifts (337 m) than low elevation (31%, -31 m) or cosmopolitan species (42%, 150 m). The best multivariate linear regression model for the upper range limit shifts based on the lowest AICc weight and all variables individually significant (r2 = 0.4705, p < 0.0001, AICc weight = 605.2) consisted of an increase in upward shifts for montane species (Figure 4A, 5A), for species with high maximum latitude in their geographic range (Figure 5A), and species in which the study mountains were at the southern edge of their geographic range (Figure 5B). The best multivariate linear regression model for the lower range limit shifts was less conclusive (r2 = 0.1025, p < 0.0363, AICc weight 626.9) and only included an increase in upward shifts for species where the study mountain was at the eastern edge of their geographic range (Figure 5C). Lastly, the best multivariate logistic regression model for the expected responses to climate change (upward shifts) versus the unexpected responses (downward, no responses) detected a greater preponderance of unexpected responses in the low elevation species compared to the montane and cosmopolitan species (Fig. 4B; χ2 = 8.5582, p < 0.0136, AICc weight = 57.4).

**Discussion**

Small mammals are moving to higher elevations in the Colorado Rocky Mountains on average by over 120 m with slightly larger upward shifts in the northwestern Front Range Mountains (180 m) than the southwestern San Juan Mountains (80 m). Since temperatures have warmed across Colorado and within each of these mountains ([McGuire *et al.*, 2012](#_ENREF_35), [Mote *et al.*, 2005](#_ENREF_38), [Trenberth *et al.*, 2007](#_ENREF_51), [USGCRP, 2009](#_ENREF_52)), this confirms the expected response to anthropogenic climate change—species sensitive to temperature will track cooler temperatures at higher elevations as temperatures increase ([Parmesan & Yohe, 2003](#_ENREF_41), [Pauli *et al.*, 1996](#_ENREF_42), [Thomas *et al.*, 2004](#_ENREF_49), [Walther *et al.*, 2005](#_ENREF_53)). This trend is most pronounced in the montane mammals—those with elevational ranges predominately in montane habitats at mid- to high-elevations—who are shifting upward by an average of over 330m (Fig. 2, 4A, 5A).

Physiological and biogeographic traits mediate who is responding as expected by shifting higher and which species are not responding as expected by shifting downward or not changing. In particular, the distance shifted upward by small mammals appears to be a function of cold-adaption. This is inferred by the factors associated with increased upper range limits, including species with (a) a montane affiliation, (b) geographic ranges extending to higher maximum latitudes, and (c) the Front Range and San Juan Mountains occurring in their southern, lower geographic limits (Fig. 5A, B; r2 = 0.4705, p < 0.0001). The species least likely to respond as expected were the lower elevation species, which in these areas include mostly semi-arid desert, canyon land, and grassland species adapted to higher temperatures and lower rainfall than their montane counterparts ([Armstrong *et al.*, 2011](#_ENREF_4)) (Fig. 4B; χ2 = 8.5582, p < 0.0136). Changes in lower range limits were more enigmatic and variable across species than upper limits. Species in which the Front Range and/or the San Juan Mountains were at the eastern edge of their geographic range moved their lower elevational limit higher (Fig. 5C; r2 = 0.1025, p < 0.0363). Again, this may be an indication of montane, cold-adapted species, since most of the species with the southern Rockies as their eastern geographic range edge are species distributed only in the intermountain west or western North America ([Armstrong, 1972](#_ENREF_3), [Armstrong *et al.*, 2011](#_ENREF_4), [Hall, 1981](#_ENREF_25)). For example, some of the eastern edge species that shifted their lower limit upward include Red-back voles (*Myodes gapperi*), Water shrews (*Sorex palustris*), Yellow-bellied marmots (*Marmota flaviventris*), and Golden-mantled ground squirrels (*Callospermophilus lateralis*)(see Appendix S2).

Most resurveys designed to detect elevational range shifts take advantage of well-sampled, historical studies of a single set of sites along an elevational gradient (e.g., [Moritz *et al.*, 2008](#_ENREF_37), [Nufio *et al.*, 2010](#_ENREF_40), [Rowe *et al.*, 2010](#_ENREF_45), [Tingley *et al.*, 2012](#_ENREF_50)). Then the contemporary researchers resurvey those particular sites as best as possible to detect changes due to climate change or land use change. But those ideal historical datasets are rare and if we limit ourselves to such studies, we will not proceed in detecting climate change effects much beyond published studies. Herein we used a more expansive methodology by building a dataset of historical elevational distributions for two mountain slopes, the southeastern-facing slope of the San Juan Mountains and the northeastern-facing slope of the Front Range, based on specimens and records of multiple generations of researchers. Then, we compared these historical datasets to contemporarily collected data through an extensive trapping effort augmented by specimens and records of additional researchers. This methodology has detractions as the data are not compared at single sites, and the sampling is broader spatially and temporally and thus patchier. But it has its attractions as the elevational ranges are based on many more sites potentially encompassing a more accurate description of the elevational ranges for a mountain and not having as large an influence of the single time period of sampling ([McCain *et al.*, 2016](#_ENREF_32)). And, because the historical ranges are the maximum detected regions, detecting change may be a higher statistical bar than detecting changes at single sites. But, there is also potentially more error in the species identifications and locality information than in a single gradient study.

We combat these sampling issues in multiple ways. First, the specimens, their identifications, their localities, and elevations were vetted extensively, with particular emphasis on records near the elevational margins for each species since historical and contemporary comparisons are essentially comparisons of the lower and upper maximum records. Difficult to identify species (i.e., shrews, chipmunks, voles, and *Peromyscus*) were dealt with special emphasis on re-identifications, molecular analyses, and quantitative morphological models ([e.g., Chinn, 2018](#_ENREF_16), [King & McCain, 2015](#_ENREF_29), [McCain *et al.*, 2018](#_ENREF_34)). Second, we built Bayesian models to estimate sampling-based uncertainty across each gradient tailored to the species’ detections and detectability as well as the overall distribution of sampling sites. This lead to 95% Bayesian limits which were robustly extended beyond the empirical ranges for comparisons between time periods by eliminating some of the undersampling or patchy sampling influences. Lastly, the maximum contemporary elevation for many species was higher than any historical record for either region (southwest quadrant or northeast quadrant of the state), making it unlikely that the upward shifts were due to historical undersampling of high elevations. Similarly, many of the upward shifting species had changes in both their lower and upper limits that were well below the highest elevations on each mountain. The Front Range Mountains were the better sampled of the historical gradients, and still showed the stronger elevational shifts and detected similar patterns as the lesser sampled San Juan Mountain species. Even if you remove all the San Juan analyses, the same conclusions hold.

Anthropogenic land use change is not absent from these gradients ([Szewczyk & McCain, 2019](#_ENREF_47)), and has been shown to influence other small mammal elevational studies (e.g., [Rowe, 2007](#_ENREF_44), [Rowe *et al.*, 2010](#_ENREF_45)). But along these gradients it is most concentrated at the lowest elevations, particularly at the base of the Front Range Mountains, and declines with elevation. It is likely that the three local extirpations in the Front Range, which were all at the lowest elevations, were predominantly due to direct reduction of their habitat. These three heteromyid species (*Dipodomys ordii, Perognathus flavescens, P. flavus*) were previously detected in areas around Boulder and Loveland that are now almost completely developed. But the land use influence on the broader gradient, although localized influences exist, appears to be reduced. There is no signal of greater numbers of range reductions in the lowest elevations that then decline with elevation on either mountain. In fact, range reductions occur rather evenly across both gradients, while range gains do increase with elevation as expected with climate change (Figure 3B, D).

Other small mammal studies along elevational gradients similarly observed a mixture of species shifting higher and lower as well as those not showing much change ([Moritz *et al.*, 2008](#_ENREF_37), [Rowe *et al.*, 2015](#_ENREF_43), [Rowe *et al.*, 2010](#_ENREF_45)). They each also detected some legacies of land use change. But unlike those studies, we detected species traits that mediated which species shifted upward as expected by climate change and those that did not (Fig. 4, 5). Some reasons for this may include a combination of smaller, less connected mountain systems with an overall less diverse mammal community compared to the southern Rocky Mountains. Although when many of those species and their responses from previous studies were analyzed together, upward contractions were supported in montane species, larger bodied mammals, and obligately diurnal species ([McCain & King, 2014](#_ENREF_33)). In this dataset we did not detect an influence of body size, but likely this was an issue of only including smaller sized mammals in our target group, and unlike previous studies, all shrews (the smallest mammals on these mountains) included in our dataset shifted their ranges upward in elevation.

These data are clear evidence that small mammals, particularly montane and cold-adapted species, are shifting their ranges to higher elevations as temperatures warm regionally. These data provide a warning that our cold-adapted, high elevation, high latitude species are indeed responding to anthropogenic climate change in general by moving higher. The lower limit shift upward appears to be a less pronounced trend than upper limit extensions. This lag may indicated the temporal variability in climate change conditions year to year allowing some populations to exist despite their low viability long-term. Clearly, the type of species and where a species is studied within their range are important. Thus, cold-adapted, montane species in the southern edge of their geographic ranges are critical groups of species of conservation concern as temperature continue to warm based on these data an previous analyses ([McCain & King, 2014](#_ENREF_33)). Take heed—it is only going to continue.

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**Supporting Information Legends**

**Appendix S1. Supplementary Methods: Figure S1.1.** Map of contemporary sampling localities by authors; **Figure S1.2.** Elevational sampling distributions**; Table S1.1.** Phylogenetic signal statistics; **Appendix S2.** Dataset of species, traits, samples, range limits and shifts; **Appendix S3**. **Supplementary Results: Figure S3.1.** Range comparison for rare and under-sampled species.

**Figure Legends**

**Fig. 1.** A map of the historical (circles) and contemporary (stars) sampling localities within the two mountainous regions, the Front Range Mountains (right) and San Juan Mountains (left), in Colorado, USA (greyscale inset). The thin black lines denote the county boundaries in each region. In the Front Range, the counties are Larimer Co. in the north and Boulder Co. in the south. In the San Juans, the counties are Dolores Co. in the northwest, Montezuma Co. in the southwest, San Juan Co. in the northeast of the figure and La Plata in the southeast of the figure. The background gradations of color depict the elevational change in each region with the dark pink as the lowest elevations and the dark green as the highest elevations. For the author’s contemporary sampling sites only, see Figure S1.1.

**Fig. 2.** Paired historical (left) and contemporary (right) elevational ranges of the included small mammal species on the (A) Front Range Mountains, and the (B) San Juan Mountains. The species are arrayed across the x-axis by the contemporary climate change response (local extirpation = zeros, range midpoint shift downward = red, no change = grey, and range midpoint shift upward= blue). The empirical ranges based on the minimum and maximum specimen or literature localities are in thick bars and the Bayesian 95% limits based on the undersampling models are in thin extensions. Species names denoted by first initial of the genus and the first few letters of the specific epithet; for complete taxonomic names, see Appendix S2.

**Fig. 3.** Elevational heat maps of the range gains (black bars) and losses (grey bars) at each 50m elevational band across the studied species. The summed numbers of gains and losses per band (bars) are shown with the number of species in each band (dotted grey curves) for the Front Range (A) and the San Juans (C). To correct for variation in the number of species in each band, the percentages of range gains and losses divided by the number of historical species in a band are shown for the Front Range (B) and the San Juans (D).

**Fig. 4.** A comparison of the differences in elevational range shifts among low elevation, cosmopolitan and montane species. A. Distribution of mean (circle) and 1 standard deviation (bars) of change in lower (L) and upper (U) range limits for each group. B. The number of species with a predicted (upward shift; dark grey) and non-predicted (downward shift, no change; light grey) response to climate change for each group.

**Fig. 5.** The magnitude of range changes in the upper and lower range limits were a function of species traits. A. The upward shift of upper range limits was larger for species whose geographic ranges extended to higher latitudes and this was particularly pronounced among montane and cosmopolitan species. B. The upward shift of upper range limits was larger for species in which the studied mountain range (Front Range and/or San Juans) was at the southern edge of their geographic ranges, but not the north, east, or west edges nor the middle (non-edge) of the range. C. The upward shift of the lower range limits was larger for species at the eastern edge of their geographic range.