



## Research Article

# A drying climate and habitat availability drive extirpations of a southward advancing ground squirrel

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### Abstract

Ground squirrels act as important members of grassland ecosystems by serving as both ecosystem engineers and as a prey base for carnivores. There is mounting evidence that climate change is driving ground squirrel population declines. We resurveyed 54 historical localities throughout the Wyoming Basin and western Colorado where Wyoming Ground Squirrel (*Urocitellus elegans*) specimens were collected to investigate if climate change was driving extirpations at these historically occupied sites. We detected extirpations at 12 sites and used binomial generalized linear models in an information-theoretic framework to investigate if climate change was associated with these extirpations. Additionally, we investigated if land cover change was associated with persistence and if land cover ameliorated or exacerbated the effects of climate change. We found that changes in climate, especially increasingly dry summer air and increasing mean summer temperatures, were associated with a reduced probability that *U. elegans* persisted at a historically occupied site. In addition, we found that current forest cover at a site and increasing rangeland cover at the regional level were associated with reduced probability that *U. elegans* persisted, although these associations were weaker than the climate associations. The effects of climate change and land cover change did not interact. Our findings build on mounting evidence that montane-associated ground squirrels throughout the Western United States are negatively impacted by climate change. The reduction in ground squirrel abundance or their extirpation due to climate change could lead to changes in ecosystem structure or reductions in trophic complexity.

**Key words:** climate change, ground squirrel, land cover change, resurvey, *Urocitellus elegans*, vapor pressure deficit (VPD).

As the climate of the Earth warms and becomes more variable due to anthropogenic change, many species are shifting their distributions across landscapes (Tingley et al. 2009; Rowe et al. 2010; McCain et al. 2021). This era of biotic redistribution presents unique conservation and management challenges to understand which species are shifting, the underlying mechanisms driving these shifts, and how practitioners can respond to these changes (LeDee et al. 2021). The spatially heterogeneous impacts of climate change and differing trends of change across conditions, such as precipitation and temperature, generate diverging organismal responses (Moritz et al. 2008; McCain and Colwell 2011; Yang et al. 2011; Tingley et al. 2012; Rowe et al. 2015). For instance, birds in the Sierra Nevada have been driven upslope by warming temperatures and downslope by increasing precipitation, resulting in differing responses to climate change within the group (Tingley et al. 2012). In addition to birds, mammal range shifts due to climate change have been idiosyncratic, with some species responding to climate by shifting their geographic or elevational range while other species have not (McCain and King 2014; Rowe et al. 2015; McCain et al. 2021). Even sympatric, congeneric species can exhibit dramatically different climate change responses.

In Yosemite National Park, the pinyon mouse, *Peromyscus truei*, shifted its upper elevational range limit higher by 1,032 m in response to climate change (1914 to 2005) while the more habitat generalist Deer Mouse, *P. maniculatus*, did not exhibit an elevational range shift response (Moritz et al. 2008; Yang et al. 2011; Rowe et al. 2015).

A leading approach to solving the challenge of predicting these contrasting responses is determining which species traits predict responses to climate change (Chessman 2013; McCain and King 2014; Pacifici et al. 2017). Key traits that determine vulnerability to climate change have been identified in plants (Butterfield et al. 2019), insects (Halsch et al. 2021; Nervo et al. 2021), fish (Chessman 2013), reptiles (Cabrelli et al. 2014), birds (Pacifici et al. 2017), and mammals (McCain and King 2014; Pacifici et al. 2017; McCain et al. 2021). While many species in a geographic location may be subject to the same changes in climate, the biological traits of these species determine the extent to which climatic changes are experienced by the organism (Dawson et al. 2011). For example, body size can determine the experienced climate of an organism by constraining the microclimates that organisms can access, such as tree holes that buffer amphibians from

extreme heat (Scheffers et al. 2014), and is a strong predictor of mammal responses to climate change (McCain and King 2014).

Impacts of climate change on several North American ground squirrel species have been detected (Morelli et al. 2012; Falvo et al. 2019; Cordes et al. 2020; McCain et al. 2021), suggesting that this group may be especially vulnerable. Activity time, fossoriality, and hibernation are 3 important traits that mediate the climate to which ground squirrels are exposed. A trait-based understanding of what aspects of climate ground squirrels have the greatest exposure to could allow for informed predictions of climate change responses in species not yet tested for climate change effects. Ground squirrels cannot substantially shift their activity time to avoid stressful environmental conditions as they are obligately diurnal, a trait that is predictive of increased vulnerability across all mammals (McCain and King 2014). Contrastingly, fossoriality reduces organismal exposure to climate change, as burrows provide a microclimate that buffers inhabitants from ambient temperatures in both summer and winter (Pike and Mitchell 2013) and reduce vulnerability to climate change in mammals (Pacifci et al. 2017). Since ground squirrels can shelter from extreme weather events in their burrows, we would expect them to better resist acute physiologically stressful events such as extremely hot days. Contrastingly, increases in chronic physiological stress such as increases in mean temperature should pose a greater risk to ground squirrels as these chronic changes are harder to avoid through inactivity in a suitable microclimate such as a burrow. In the Sierra Nevada, *Urocitellus beldingi* has experienced drastic extirpations in the lower elevation parts of its range associated with warming mean winter temperatures (Morelli et al. 2012), supporting a greater vulnerability of ground squirrels to chronic physiological stressors.

Hibernation dramatically influences exposure to climate change, as many ground squirrels are active and foraging aboveground in summer while dormant in burrows in winter. In summer, ground squirrels can actively access food and water resources, move to more suitable locations, and behaviorally thermoregulate by entering burrows to avoid extreme weather events. In winter, hibernating ground squirrel exposure to climate change is influenced primarily by the insulative capacity of the burrow and snowpack, although some behavioral thermoregulatory strategies exist such as group hibernation (Patil et al. 2013). In yellow-bellied marmots (*Marmota flaviventris*; Cordes et al. 2020), Belding's ground squirrels (*U. beldingi*; Morelli et al. 2012), and Uinta ground squirrels (*U. armatus*; Falvo et al. 2019), seasonal effects of climate change have been detected. In all 3 species, changing winter climates negatively impacted adult survival, while changing summer conditions improved yearling survival in yellow-bellied marmots, demonstrating the importance of accounting for both summer and winter climate effects on survival.

Predicting the vulnerability of ground squirrels to climate change is critical due to their role as an ecosystem engineer (Davidson et al. 2012), major prey source for raptors and other carnivores of conservation concern (Olson et al. 2017), and an agricultural pest species (Davidson et al. 2012). Ground squirrels modify grasslands and shrublands by generating unique plant communities around their burrows and opening underground microclimates to other animals (Davidson et al. 2012; Newediuk and Hare 2020). Through this sheltering effect, small mammal burrows can increase arthropod diversity by 3-fold (Davidson et al. 2012). Mounds of Richardson's Ground Squirrel (*U. richardsonii*) have unique seed assemblages and higher nitrate concentrations than artificial disturbances, creating heterogeneity in plant

community assemblages across landscapes (Newediuk and Hare 2020). Accurate predictions of climate change impacts will allow for proactive management measures to ensure that these ecosystem functions are not lost.

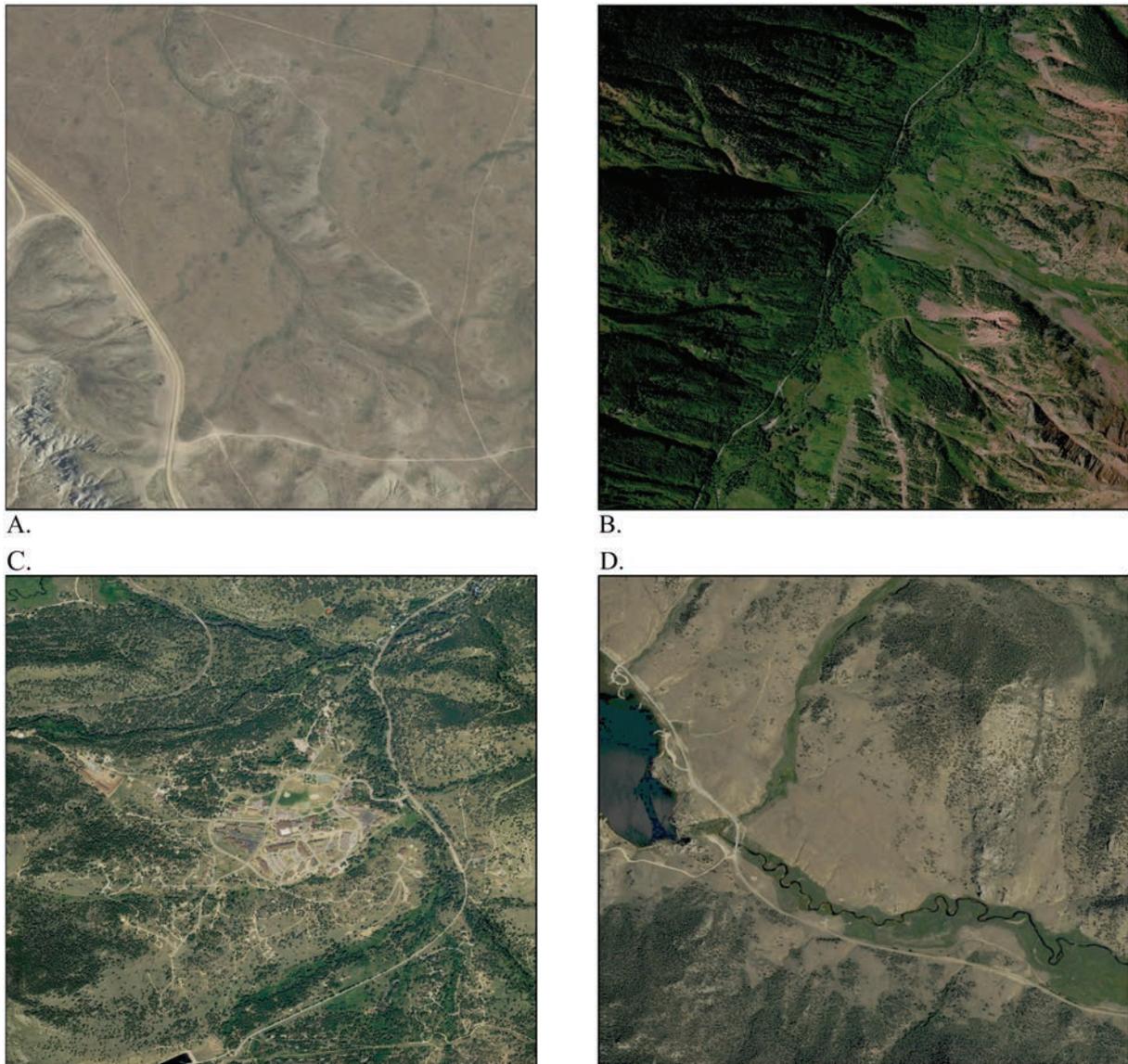
Unlike congeners *U. beldingi* and *U. armatus*, the Wyoming Ground Squirrel (*U. elegans*) has yet to be investigated for a response to climate change. Based on how hibernation, fossoriality, and diurnality modify exposure to climate change, we can predict if and how climate change will impact *U. elegans* and evaluate if these predictions are upheld. When considering the effect of climate change on the persistence of *U. elegans*, we hypothesized that: (H1) extirpation of *U. elegans* at a site would be associated with the magnitude of change from historical climate values more so than current climate conditions, indicating a climate change response, as diurnal mammals are more likely to respond to climate change; (H2) extirpation of *U. elegans* would be associated with chronic physiological stressors such as mean temperature over acute physiological stressors such as maximum temperature, as *U. elegans* is fossorial and can escape acutely stressful weather events in the microclimate of a burrow; and (H3) extirpation of *U. elegans* would be more associated with winter climate conditions than summer climate conditions as they have a broader range of physiological regulation strategies for summer environmental stress than while they are hibernating, which is supported by negative winter climate effects in 2 other *Urocitellus* species (Morelli et al. 2012; Falvo et al. 2019).

In addition to changes in climate, land cover change is a pervasive worldwide threat that can interact with the effects of climate change (Cardillo et al. 2008; Mantyka-Pringle et al. 2015; Betts et al. 2018). Reductions in habitat area should in itself lead to a higher probability of extirpation through neutral processes (Dennis 2002; Hylander and Ehrlén 2013) and can exacerbate or buffer the impacts of changes in climate (Mantyka-Pringle et al. 2015). For example, Belding's ground squirrels persisted throughout changes in climate at sites 255 m lower in elevation when anthropogenic subsidies of forage and water were present (Morelli et al. 2012). When considering how land cover change might influence *U. elegans*, we hypothesized that: (H4) higher percent cover of appropriate habitat (rangeland, agricultural land, barren land; Olson et al. 2017) at the site scale and the regional scale would be positively associated with persistence by supporting larger populations that would be less susceptible to stochastic extirpation; and (H5) higher percent cover of appropriate habitat (rangeland, agricultural land, barren land) at the site scale would reduce the impact of changes in climate on persistence through an interaction effect.

## Materials and methods

### Study system

The Wyoming Ground Squirrel (*U. elegans*) is a medium-sized (~400g), diurnal, fossorial ground squirrel inhabiting open shrub and grassland habitats in the Intermountain West and can be identified from other co-occurring *Urocitellus* species by distinctive alarm calls and tail coloration (Armstrong et al. 2011). Appropriate habitats include sagebrush steppe, montane meadows, grass- and forb-dominated mountain lowlands, barren or unvegetated areas near these habitats, and disturbed margins of human-developed areas (Fig. 1). Within these habitats, deep soils are preferable, with *U. elegans* displacing other ground squirrels to rockier habitat (Zegers 1984). *Urocitellus elegans* are commonly found in large aggregations of individuals and are active aboveground from April to late August, although time



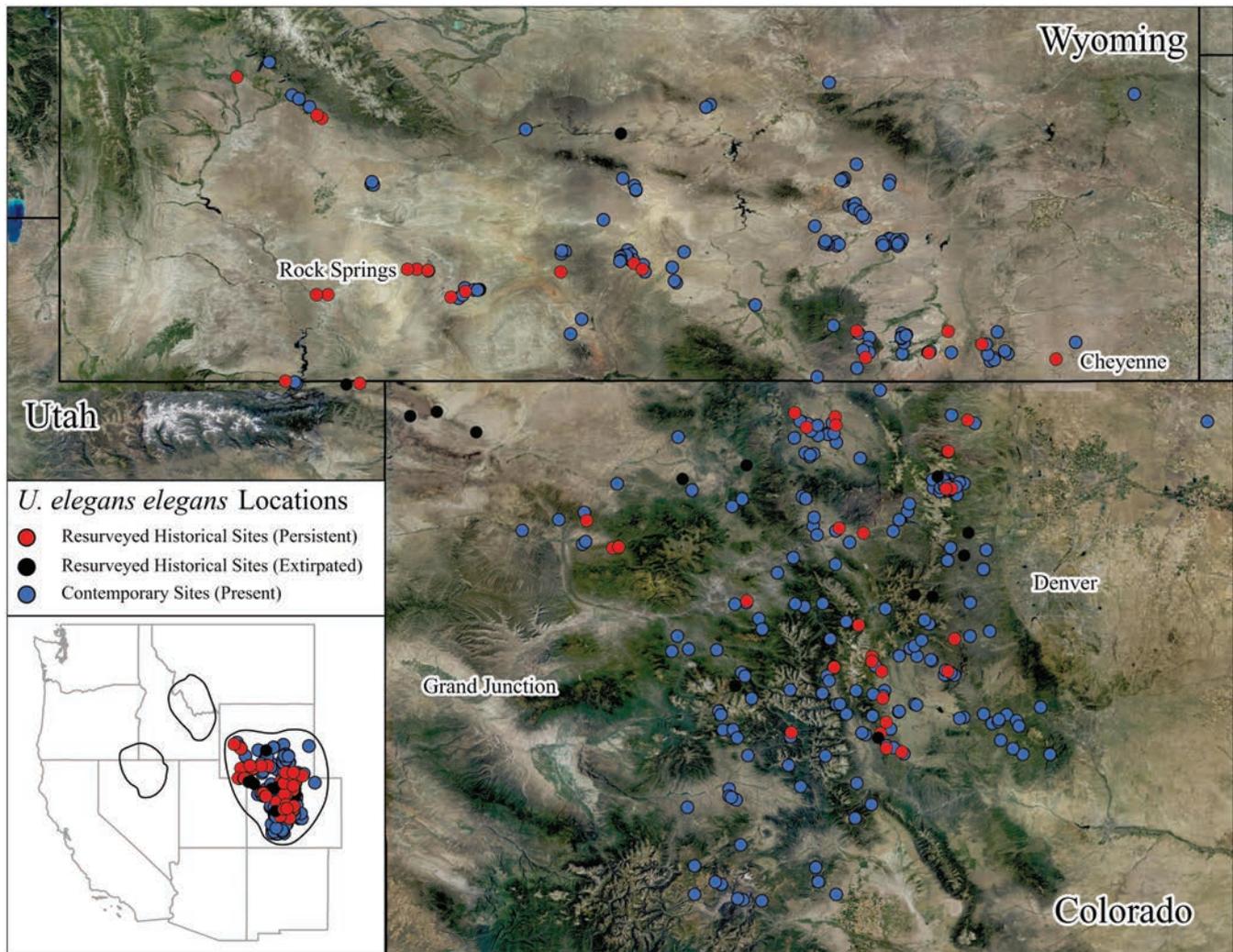
**Fig. 1.** Habitat variation of resurveyed sites. *Urocitellus elegans elegans* resurvey sites varied greatly across their geographic range. The northern part of the range mainly consists of sagebrush steppe, such as site A near Pinedale, Wyoming. In contrast, some sites were located in montane meadows, containing lush herbaceous cover. Site B is located in the Elk Mountains near Aspen, Colorado. *Urocitellus elegans elegans* can be associated with moderate levels of human disturbance, such as in site C near Estes Park, Colorado. Lastly, *U. elegans elegans* can be found in complexes of shortgrass, sagebrush, and other vegetation types depicted in site D, near Fairplay, Colorado.

spent in hibernation varies across their range (Fagerstone 1988; Armstrong et al. 2011). *Urocitellus elegans* feed primarily on forbs followed by grasses with no significant variation between sexes (Zegers 1984). As with other burrowing small mammals, *U. elegans* are both an ecosystem engineer and a prey source to larger mammals and raptors (Armstrong et al. 2011; Davidson et al. 2012) and are considered an agricultural pest species at excessive densities (Zegers 1984; Davidson et al. 2012). All fieldwork was conducted in accordance with American Society of Mammalogists guidelines for work with live mammals (Sikes et al. 2016) and was approved by the University of Colorado Boulder IACUC #2548.

### Study area

*Urocitellus elegans* is composed of 3 geographically distinct subspecies (Fig. 2): *U. elegans nevadensis* in northeastern Nevada; *U. elegans aureus* in southwestern Montana and southeastern Idaho; and *U. elegans elegans* in western Wyoming and Colorado

(Zegers 1984; Armstrong et al. 2011). This study focuses on *U. elegans elegans* (hereafter, UEE), whose range consists of the sagebrush-dominated Wyoming Basin of western Wyoming in addition to the sagebrush–grassland lowlands and grass–forb montane meadows of western Colorado. This southernmost subspecies could serve as a signal for future range dynamics in more northerly and colder parts of the species range in a changing climate (Bradshaw and Holzapfel 2006; McCain et al. 2021). *Urocitellus elegans elegans* has a unique distributional history. First detected around 1890, UEE began expanding its range southwards from the Wyoming Basin into Colorado, with the first Colorado specimen collected in 1893 (Hansen 1963). The mechanism behind this expansion—that occurred before major effects of climate change were detected—was likely some combination of release from competition with prairie dogs as the latter were eradicated, and land cover change (Armstrong et al. 2011).



**Fig. 2.** Map of *Urocyon elegans elegans* occurrences. Blue points represent occurrences of *U. elegans elegans* generated from citizen science data, opportunistic observations by ALN, and raptor prey base surveys by the US Forest Service Rocky Mountain Research Station (Olson et al. 2017). The black outlines reflect the *U. elegans nevadensis*, *U. elegans aureus*, and *U. elegans elegans* subspecies ranges, from left to right, adapted from Zegers (1984). Red points represent historical specimen localities resurveyed for this study that persisted while black points represent extirpated localities. *Urocyon elegans elegans* are present across a variety of habitat throughout this geographic range including sagebrush steppe, lowland grasslands, and montane meadows.

### Historical collection localities

We georeferenced museum specimen locality data from UEE specimens collected prior to 1980, when climate change signatures were first detected in the Rocky Mountains (USGCRP 2009; McGuire et al. 2012). UEE localities collected prior to 1980 were gathered from the Global Biodiversity Information Facility portal (<http://www.gbif.org/>) on 11 December 2019, and locality data were georeferenced based on the MaNIS point-radius georeferencing method (Wieczorek et al. 2004). Specimen localities were constrained to those present in the range of UEE, south of 43°N latitude and east of 110°W longitude. We georeferenced each locality and retained localities at 2 nested criteria of spatial uncertainty. First, localities with an overall spatial uncertainty radius (including named place uncertainty, directional offset uncertainty, etc.) summed to less than 1 km were retained (strictest criteria). Second, localities where the named place uncertainty (uncertainty generated by the size of the locality attributed to the specimen) was less than 1 km and directional offsets (ex. 1.5 km north of “Named Place”) located likely sampling sites generated by historical surveys including historical sampling transects, localities alongside linear features

such as highways or railroads, or meadows surrounded by unsuitable forest and mountainsides were retained (strict criteria). This resulted in 2 nested data sets—our strictest criteria data set with the lowest level of spatial uncertainty, and the total data set that included sites meeting the strict or strictest criteria. Not all localities that were retained by our selection criteria were able to be surveyed due to lack of land access permission or spatial non-independence from other resurvey localities (i.e. <1 km apart). All localities visited were separated by at least 1 km to maintain spatial independence of sites. This is a conservative distance for separation between sites as 1 km is substantially greater than the typical 500 m dispersal distance of *Urocyon* squirrels (Holekamp 1986). In total we visited 54 UEE localities recorded prior to 1980 that met our strict criteria (Supplementary Data SD1), 41 of which met the strictest quality criteria.

### Persistence resurveys

*Urocyon elegans elegans* presence at resurvey sites was established by visually scanning with binoculars for individuals and additionally confirming species identity by listening for

diagnostic alarm calls. ALN conducted field resurveys in May through July of 2020 and 2021. Survey bouts lasted approximately 4 h and occurred in the morning (07:00 to 11:00) and the afternoon (14:00 to 18:00). All habitat (NLCD Classes: 1, 2, 3, 7) within a 1-km radius around the historical locality was surveyed, in addition to nonhabitat areas crossed while traversing between patches of habitat. ALN used a handheld land cover GIS overlay with real-time GPS tracking to ensure that all habitat areas were surveyed once per resurvey. Resurvey sites on private land were accessed with landowner permission. Resurveys were conducted in an occupancy framework with a removal sampling design to account for imperfect detection and the reliable resighting of individuals at the same location after being initially observed (MacKenzie et al. 2002, 2017). In a removal sampling design, detection probability is estimated by only revisiting absence sites until a presence is detected or the number of revisits provides sufficient power to robustly estimate true occupancy (MacKenzie et al. 2017). Absence sites were visited multiple times (min = 2, avg = 2.46, max = 3), providing a robust estimate of occupancy given that no sites had a detection of UEE after an initial non-detection (MacKenzie et al. 2017). Absences recorded in 2020 were resurveyed again in 2021 to ensure recolonization had not occurred. The observed detection probability of UEE,  $P = 1$ , is likely due to the visual and auditory conspicuousness of this species and is supported by the relatively high detection probability of other *Urocyon* species surveyed in a similar framework (Morelli et al. 2012).

### Climate data

To investigate how changes in climate might drive local extirpations of UEE from historically occupied sites, we used historical and modern climate data from PRISM, a commonly used source of gridded climate data that covers a wide temporal range (1895 to present; Daly et al. 2000) and is frequently used in ecological studies (Tingley et al. 2009; Rowe et al. 2011; MacLean et al. 2018). Temperature, precipitation, and vapor pressure deficit (VPD) values were downloaded from PRISM. For temperature and VPD, values representing chronic and acute physiological stress were used (Johnston et al. 2020): mean temperature (chronic temperature stress); minimum and maximum temperature (acute temperature stress); minimum VPD (chronic air dryness); and maximum VPD (acute air dryness).

While temperature and precipitation values are commonly used in climate change studies, VPD—a measure of the drying effect of air on organisms—represents an important and relatively understudied aspect of climate change on animals (Johnston et al. 2019, 2020; Grossiord et al. 2020). VPD is measured as the difference between the current vapor pressure of the air and vapor pressure at saturation (Grossiord et al. 2020). As the value of VPD increases, the drying effect of air on organisms increases, which can lead to physiological stress due to water loss and can exacerbate the effect of other stressors (Johnston et al. 2020). Because VPD can be influenced by temperature, 2 values of VPD are provided by PRISM. As air warms during the day, its capacity to hold moisture increases, leading to an increase in VPD. Therefore, maximum VPD values in a day reflect acute drying stress while minimum VPD reflects the baseline drying stress throughout the day (Johnston et al. 2020).

First, climate data were downloaded as monthly averages for 1951 to 1980 (historical values) and 1991 to 2020 (modern values). The historical climate data were downloaded in individual years at 4 km resolution, as this is the highest spatial resolution

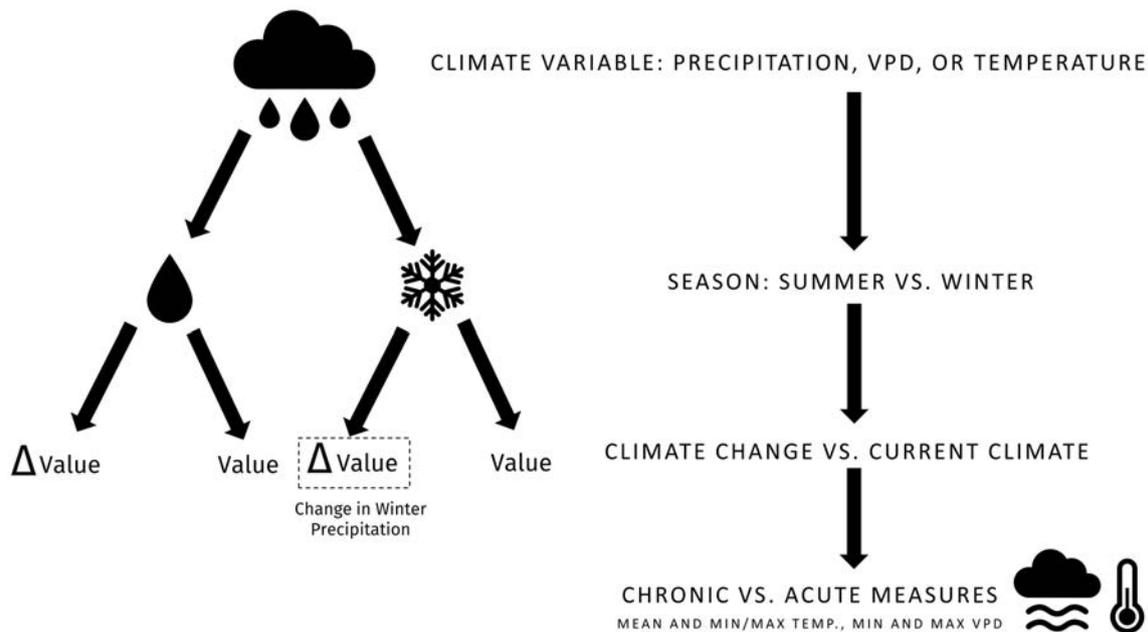
publicly available. Historical monthly values were averaged from 1951 to 1980 and downscaled from 4 km to 800 m using bilinear interpolation (Phillips et al. 2006). The modern climate data were downloaded as a 30-year average from 1991 to 2020 at 800 m resolution. Second, to generate seasonal averages of each climate variable, values were averaged across the most active quarter of the year (May, June, July) and the coldest quarter of the hibernating period for UEE (December, January, February; Zegers 1984). Third, measures of the degree of change in each climate variable were generated by subtracting the historical climate value from the modern climate value. Thus, each of the 20 final climate variables represented a combination of a type of climate variable (temperature, precipitation, VPD), a season (active season or dormant season), and reflected either climate change or a modern climate variable (Fig. 3). Variables were standardized using z-scores to allow for meaningful interaction terms and comparable beta estimates (Schielzeth 2010).

### Land use and land cover data

To investigate the impact of land cover and land use change on the persistence of UEE at a historically occupied site, historical and modern gridded land use and land cover data were obtained. Historical land use and land cover data (1970 to 1985) were obtained at 100 m resolution from the Enhanced Historical Land Use and Land Cover Dataset developed by the US Geological Survey (Price et al. 2007). This data set represents land cover at the end of our historical period and thus serves as a conservative baseline for historical land cover. Modern land use and land cover data (2019) were obtained from the National Land Cover Database and aggregated to 100 m resolution (Yang et al. 2018). Both data sets use the Anderson land use classification codes, allowing for direct comparisons between modern and historical data. Historical and modern land use and cover (hereafter referred to as just land cover) at each site were calculated at both the site (1 km) and regional (10 km) scale (Riitters et al. 1997). To capture the amount and change in UEE habitat, the percentages of land classified as developed (Class 1), agricultural (Class 2), range (Class 3), forest (Class 4), and barren (Class 7) were separately calculated in a 1 km and 10 km circular buffer around the site for both historical and modern land cover. The other 4 land cover types (e.g. wetlands, perennial snow) were not included in analyses. The land cover types we included (Classes 1, 2, 3, 4, 7) are important determinants of habitat quality for UEE (Armstrong et al. 2011; Olson et al. 2017). UEE abundance was positively associated with bare ground (“barren”) in the Wyoming Basin (Olson et al. 2017) and many ground squirrels associate with open ground (Aliperti et al. 2022). Grasses and forbs (range) are the main diet of UEE (Armstrong et al. 2011) and can often include agricultural crops. Low levels of human development have been shown to positively influence *U. beldingi* (Morelli et al. 2012) and may increase resources for UEE as well. UEE are not found in forests (Armstrong et al. 2011). Change in each land cover type for both the site level and regional scale was calculated by subtracting the historical percent cover value from the modern percent cover value.

### Model-building and selection process

To elucidate the influences of climate and land cover change on the persistence of UEE, we employed an information-theoretic approach to assess the degree of support for our hypotheses (Burnham and Anderson 2002). To address the influence of climate, land cover, and the potential interaction of both, we built 3 groups of models. First, we built models solely with climate



**Fig. 3.** Conceptual diagram of how broad climate phenomena were decomposed into more specific predictors to capture distinct aspects of climate that have empirically documented, unique impacts on ground squirrels. Each climate variable was decomposed into the summer season and winter season, reflecting conditions experienced by ground squirrels while active (summer) and hibernating (winter). A current value and a measure of the amount of change from historical to current conditions were generated for each seasonal climate variable. Lastly, VPD and temperature measures included measures of chronic physiological stress (minimum VPD and mean temperature) and acute physiological stress (maximum VPD and min/max temperature).

variables to address our climate hypotheses. Second, we built land cover models with solely land cover variables to address our land cover hypotheses. Lastly, we built combined models to investigate if the effects of land cover and climate change interacted. Our detection probability of  $>0.99$  indicates that imperfect detection is not a concern and single-season occupancy models are not needed (MacKenzie et al. 2002; Erb et al. 2011). Instead, we built binomial generalized linear models of persistence as these models provide simpler interpretation than single-season occupancy models (Williams et al. 2006; Erb et al. 2011).

For each of our climate-only and land cover-only groups of models, we built models through a 2-step process of variable screening and model selection (Olson et al. 2017). We used an initial screening approach as models including all predictors fit improperly and contained many correlated predictors. First, univariate binomial generalized linear models for all variables in that group were run in R (R Core Team 2021) using the “glm” package with the persistence or extirpation of UEE as the response variable. Next, we built AICc (Akaike’s Information Criteria, corrected for sample size) screening tables to determine which univariate models performed better than a null model ( $>2 \Delta AICc$ ; Burnham and Anderson 2002). An intercept-only model was used as the null model. This screening process was conducted with the strictest inclusion criteria (41 sites), and with the total resurvey data set (54 sites). In both the land cover and climate screenings, all variables that performed better than a null model in the total data set also performed better than the null with only the strictest criteria data set. Therefore, for all subsequent analyses the total resurvey data set ( $n = 54$ ) was used. After this screening process (Supplementary Data SD2), we built more complex models to evaluate our hypotheses. For any model with more than 1 predictor variable, we ensured that there were no pairwise correlations greater than our a priori cutoffs of  $>|0.4|$  between predictors, and no predictor had a variance inflation factor (VIF)  $> 5$  (a measure

of multicollinearity) to avoid biasing parameter estimates with correlated predictors (Zuur et al. 2010).

We retained 5 climate variables after the univariate screening process: change in summer minimum VPD; modern summer minimum VPD; change in winter minimum VPD; change in minimum winter temperature; and change in mean summer temperature (in order of AICc ranking). We built these candidate models by first generating a univariate model with the highest ranked climate variable. Next, the second highest ranked climate variable was added to the model if the addition did not result in pairwise collinearities of  $>|0.4|$  between predictors and no predictor had a VIF  $> 5$ . We repeated this process until there were no more uncorrelated climate variables in the set left to include. For our land cover variables, only 2 land cover variables were retained after screening: change in rangeland cover at the regional scale (10-km radius) and current forest cover at the site scale (in order of AICc ranking), and were uncorrelated ( $r = 0.35$ ). We built a single model for land cover consisting of change in rangeland at the regional scale and forest cover at the site scale. We explored interactions between these 2 land cover variables, but no interactions were significant.

To test for interactions of climate and land cover variables, we used the top-performing climate model and systematically checked for significant interactions with the 2 land cover variables retained in the land cover model. We ran a bivariate model with elevation and latitude as predictors to investigate if extirpations were associated with a directional range shift across elevation or latitude. However, our historical sites do not cover the full contemporary latitudinal range of UEE and thus should be interpreted conservatively. Lastly, we built a model that encompassed both land cover change and climate change to model the additive effects of both aspects of global change on UEE persistence. First, we built a single model with the variables from the best-performing climate model and the best land cover model. Next, we removed the predictor with the beta estimate of the smallest

magnitude, reran the model, and continued this process until AICc did not decrease. Once we had built our sets of candidate models, we used AICc screening tables to evaluate the degree of support for each model using both AICc scores and AICc weights. The best candidate model was selected as the model with the lowest AICc score. We used the package “DHARMA” in R (Hartig 2017) to evaluate the fit of the model and test for overdispersion, outliers, and violations of distributional assumptions.

To ensure that information gained from resurveying historical localities of UEE represented conditions across the range of the subspecies, we used 3 independent data sets of recent UEE occurrences ( $n = 306$ ) to compare the distribution of important predictors of persistence between all observations and resurvey sites (Supplementary Data SD3).

## Results

### Site resurveys

Of the 54 historical sites resurveyed, 42 were contemporarily occupied with UEE individuals, resulting in a contemporary occupancy rate of 78%. There was no difference in occupancy between the strictest and strict criterion data sets (Fisher’s exact test, 2-tailed  $P = 0.45$ ). Our observed detection probability was  $P = 1$ , as no presences were detected at sites where UEE was not detected during an earlier survey. Thus, we conclude that not detecting UEE at a site represents true absences. Local abundance at persistence sites varied from single individuals to large aggregations of greater than 20 individuals. Absence sites were spread throughout the range of sites surveyed; elevation ( $z = 1.15$ ,  $P = 0.25$ ) and latitude ( $z = 1.43$ ,  $P = 0.15$ ) were not significantly associated with persistence at a site. Sites where UEE were contemporarily present varied widely in both natural habitat type and level of human development. Presences occurred in sagebrush shrublands, montane meadows, and agricultural lands. The degree of human development at occupied sites ranged from 0% (total absence of human infrastructure) to 81% (on the side of a highway off-ramp in downtown Green River, Wyoming; Fig. 1).

### Univariate climate and land cover variable screening

Of the 20 climate variables, 5 variables passed initial screening (Table 1; Supplementary Data SD2). VPD variables were ranked highest, followed by temperature variables. No precipitation variables passed the univariate screening process. Of the VPD variables, change in minimum summer VPD, minimum summer VPD, and change in minimum winter VPD passed univariate screening. Of the temperature variables, change in minimum winter temperature and change in summer mean temperature passed univariate screening. Of our land cover variables change in rangeland cover at the regional scale and current forest cover at a site passed univariate screening (Supplementary Data SD2). Subsequent models were built with uncorrelated combinations of these variables (Supplementary Data SD2).

### Climate and land cover model

After running our climate and land cover variable selection process, the variables included in our combined model consisted of change in minimum summer VPD, change in mean summer temperature, change in rangeland cover at the regional scale, and change in forest cover at the site scale (Fig. 4). The final best-fit model of climate and land cover consisted of change in summer minimum VPD, change in rangeland cover at the regional level,

**Table 1.** Univariate models of *Urocyon v. elegans* persistence at historically occupied sites throughout western Wyoming and Colorado. Models that are within 2  $\Delta$ AICc are considered similar in explanatory power. An intercept-only model was used as the null model. Regional land cover variables refer to percent cover of a land cover class in a 10-km radius from the sample site while site land cover variables refer to a 1-km radius. Changes in VPD and temperature reflect the difference between the current and historical value of that climate variable.

Model	AICc	$\Delta$ AICc	Weight
Change in minimum summer VPD	46.25	0	0.68
Change in regional rangeland cover	48.40	2.15	0.23
Minimum summer VPD	52.16	5.92	0.04
Site forest cover	53.01	6.76	0.02
Change in minimum winter VPD	53.76	7.51	0.02
Change in winter minimum temperature	56.02	9.77	0.01
Change in summer mean temperature	56.28	10.03	0.004
Null model	59.29	13.04	0.001

and forest cover at the site level. Increasing chronically dry air and increases in forest cover reduced the probability of UEE persisting at a site. The strength of the association of forest cover was half the strength of the association of increases in chronically dry summer air. With 95% of the AICc weight, our climate and land cover model performed better than any other top model from all analyses (Table 2). The best climate change model marginally outperformed the best land cover model,  $\Delta$ AICc = 1.65. None of the systematic interactions of our best-performing land cover and climate variables were significant, all  $P > 0.05$ . Model diagnostics supported proper model fit in all tests, all  $P > 0.53$  (Supplementary Data SD3).

### Climate hypotheses

For all 3 climate hypotheses, the same model performed best. The top-performing climate model consisted of change in minimum summer VPD and change in mean summer temperature. Chronically drying summer air and warming summer mean temperatures were both associated with a reduced probability of persistence, although the strength of the latter was approximately one-quarter the strength of the former. This best model supports the importance of changes in chronic, summer climate conditions over acute, winter, and modern climate conditions. Additional models of acute, winter, and modern climate conditions failed to outperform our best model (Supplementary Data SD4).

### Land cover model

Only 2 land cover variables were retained after our univariate screening process, change in rangeland cover at the regional scale and current forest cover at a site. Increasing rangeland cover at the regional scale and higher forest cover at the site scale were both negatively associated with persistence at a site, although change in regional rangeland cover had a slightly stronger negative association (Table 3).

## Discussion

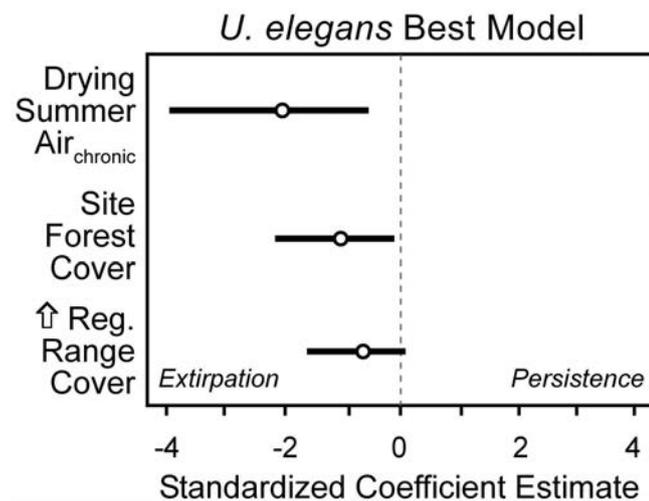
We resurveyed localities where Wyoming ground squirrels (*U. elegans*) were historically collected to investigate if changes in

climate or land cover were associated with extirpations throughout the Wyoming Basin and western Colorado and if impacts of climate change followed trait-based predictions. We detected associations of both changes in climate conditions and land cover with extirpations of UEE from historically occupied sites, adding to evidence that ground squirrels may be particularly vulnerable to climate change (Morelli et al. 2012; Falvo et al. 2019; Cordes et al. 2020; Johnston et al. 2020; McCain et al. 2021). While extirpations from climate change are often thought of in an upslope retraction perspective, we found that extirpated sites reflected areas where the greatest increase in atmospheric dryness occurred. These sites did not neatly align with range margins at the lower end of elevation. By using the presence of traits previously investigated in mammals and ground squirrels for associations with climate change, we were able to make specific hypotheses about how different aspects of climate might influence the persistence of UEE.

*Urocitellus* squirrels are diurnal, which robustly predicts greater risk of climate change impacts in North American mammals (McCain and King 2014). Additionally, other diurnal North American ground squirrel species including the yellow-bellied marmot (*M. flaviventris*) and Belding's ground squirrel (*U. beldingi*) have been negatively impacted by changes in climate (Morelli et al. 2012; Cordes et al. 2020). Therefore, we hypothesized that

UEE would respond negatively to climate change (Morelli et al. 2012; Falvo et al. 2019). Our prediction of an effect of climate change was supported as models of climate change significantly outperformed models using contemporary climate values. This result suggests that there could potentially be some degree of local adaptation occurring, which could lead to the magnitude of change from historical conditions predicting extirpation better than the contemporary climate value. This contrasts with what one would predict if physiological limits were relatively identical across a species range. In those cases, one would expect sites at the environmental extremes—such as the lowest elevation populations—to become extirpated first, leading to an upslope or up-latitude retraction pattern of extirpation (Rowe et al. 2010; Morelli et al. 2012; McCain et al. 2021). However, we found that not only were measures of the magnitude of change in climate variables more important than extreme values, but also that extirpations did not follow archetypal biogeographic patterns such as upslope or up-latitude range shifts. The magnitude of change in summer minimum VPD at a site was not associated with the historical value, indicating that historical conditions were not overly constraining the possible values of change in summer minimum VPD at a site, while modern conditions were positively associated (Supplementary Data SD3). This result indicates that sites that have reached the driest states were not necessarily the driest sites historically, which may explain why extirpations are not occurring in predictable biogeographic patterns and supports the identification and monitoring of areas within a management unit that are experiencing the greatest changes in climate or land cover, even if they have not experienced the greatest disturbance or been of marginal suitability in the past. Measuring the physiological tolerances of UEE across its range could further clarify why measures of change in climate were much stronger predictors of extirpation than the climate values themselves. Increasing chronically dry air in summer and warming mean summer temperatures both reduced the probability that UEE persisted at a site over time. These 2 climate variables are measures of chronic physiological stress on organisms at these sites, including ground squirrels (Johnston et al. 2020).

Associations of chronic as opposed to acute physiological stressors to extirpation events matched our predictions for how changes in climate would impact UEE due to its fossoriality. UEE individuals can remain underground in burrows to shelter from extremely hot days (Pacifci et al. 2017) or shift their activity time earlier or later in the day to avoid acute heat stress. However, chronic heat stress from increasing mean temperatures throughout an entire active season is less easily avoided by entering burrow microclimates. This pattern more generally reflects the different temporal scales that climate change can act upon and in turn, the scale dependency of organismal responses to climate



**Fig. 4.** Coefficient estimates for the best-fit model for *Urocitellus elegans* persistence at historically occupied sites. Estimates are standardized to allow for direct comparisons between predictors. Bars represent 1 standard error. Increasing minimum VPD (drying summer air chronic), percent forest cover in a 1-km radius of a resurvey site (site forest cover), and increasing percent cover of rangeland in a 10-km radius of a resurvey site (↑ regional rangeland cover) were all negatively associated with the probability of *U. elegans* persisting at a site.

**Table 2.** Top-performing models for climate, land cover, and combined effects of climate change and land cover change on the persistence of *Urocitellus elegans* at historically occupied sites. Coefficient estimates are z-score-transformed. Change in value is represented by  $\Delta$ . Bold text is highlighting the best model.

Model	$\Delta$ Summer minimum VPD	$\Delta$ Mean summer temp.	Forest 1 km	$\Delta$ Rangeland 10 km	AICc	$\Delta$ AICc	Weight
Best combined model	<b>-2.05</b>		<b>-1.04</b>	<b>-0.65</b>	<b>39.83</b>	<b>0.00</b>	<b>0.73</b>
Complete combined model	-2.08	-0.15	-1.00	-0.63	42.13	2.30	0.23
Climate model	-1.82	-0.53			46.39	6.55	0.03
Land cover model			-0.65	-1.21	48.04	8.21	0.01
Null model					59.29	25.72	<0.001

**Table 3.** Final model and screened univariate models for the association of land cover change with the probability of *Urocyon v. elegans* persistence at historically occupied sites. Coefficient estimates are z-score-transformed. Change in value is represented by  $\Delta$ .

Model	$\Delta$ Rangeland 10 km	Forest 1 km	AICc	$\Delta$ AICc	Weight
Land cover model	-1.21	-0.65	48.04	0	0.52
$\Delta$ Rangeland 10 km	-1.49		48.40	0.36	0.43
Forest cover 1 km		-0.96	53.00	4.97	0.04
Null model			59.29	11.25	0.002

change. At the scale of a single day, animals can respond to physiologically stressful conditions by shifting activity times (Levy et al. 2019), lowering physiological rates (Nowack et al. 2017), engaging in thermoregulatory behaviors (Moyer-Horner et al. 2015), or utilizing microclimates (Potter et al. 2013). Other responses that are required to manage changes in climate at larger time scales include plastic changes in tolerance to changing physiological stressors (Boutin and Lane 2014), microevolutionary responses (Tejeda et al. 2016), and movement across landscapes to suitable conditions (Scheffers et al. 2017). In burrowers and other groups that can readily avoid acute physiological stress, changes in climate at larger time scales will likely be more consequential, as was detected in UEE with chronic measures of air dryness and temperature most strongly predicting extirpation. Whether these chronic stressors are impacting UEE and other ground squirrels directly through physiological stress or indirectly by reducing forage quality warrants further inquiry.

Changes in VPD, the drying effect of air on organisms, are an emerging driver of animal population declines; we and Johnston et al. (2020) found that increasingly dry air negatively impacted the persistence of hibernating mammal populations. In addition to overwinter effects of dry air (high VPD) found by others, we found evidence of effects during summer (Fig. 5). Changes in VPD could act on animal populations through indirect pathways, in addition to directly raising physiological water demand. Increasing VPD has been implicated in drought-induced plant mortality and may lead to reductions in forage availability and water content of forage (Grossiord et al. 2020), reducing resource availability during summer. Increasing physiological water demand can also interact with other aspects of an animal's physiology, potentially increasing vulnerability to other climate stressors—lacertid lizards had reduced thermoregulatory ability when dehydrated (Sannolo and Carretero 2019). For hibernating mammals, Johnston et al. (2020) posited that negative impacts of increasing winter air dryness could be due to dehydration in the hibernacula. Fresh forage with water content is not available to hibernators and consuming snow would lead to additional energetic costs, creating a period of water limitation that is becoming anthropogenically intensified.

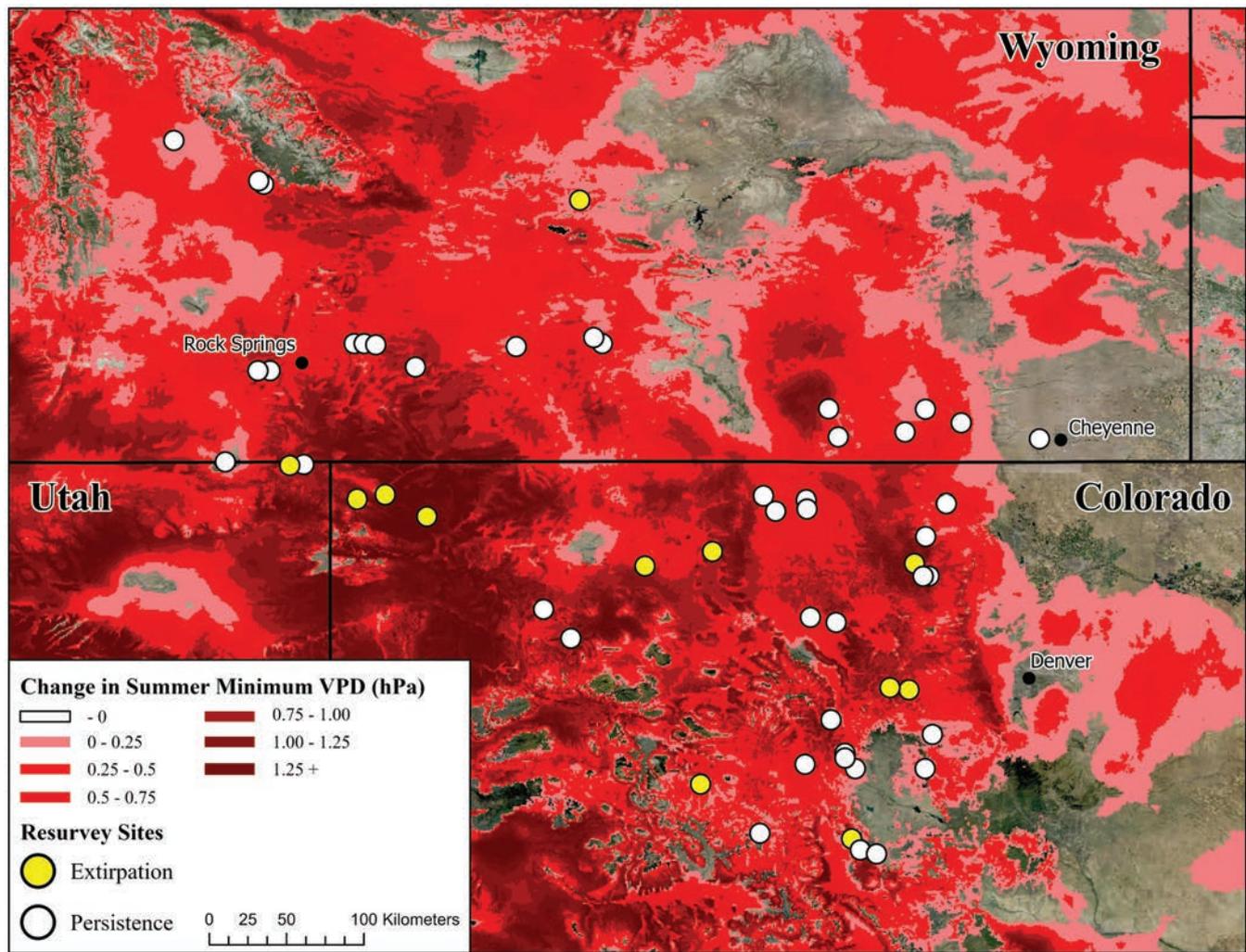
While historical measures of forage quality were unavailable at our resurvey sites, long-term wildlife study sites with similarly long-term vegetation monitoring such as those at field research stations could begin untangling the direct and indirect effects of changes in atmospheric dryness. Forage quality could be impacted both in the degree of moisture available per gram of mass and in the total quantity of forage on the landscape (Falvo et al. 2019) and could lead to extirpations in UEE at sites with increasing atmospheric dryness. In Uinta ground squirrels,

population density at a long-term study site increased over time, even as the population experienced reduced adult survival rates from warmer winters and springs, with increases in forage availability suggested as a probable cause (Falvo et al. 2019). Future paired studies of both the direct impacts of climate change on the physiological processes of wildlife and on their resource availability could allow managers to target conservation efforts toward protecting climate refugia if direct impacts are more important, or could supplement resource availability in extreme years if indirect impacts are driving extirpations.

In recent years, the importance of changes in both winter climate and summer climate to hibernator populations has been recognized (Morelli et al. 2012; Falvo et al. 2019; Cordes et al. 2020). We hypothesized that UEE persistence would be more strongly associated with winter climate conditions than summer conditions because other ground-dwelling squirrels and 2 other *Urocyon* species (Morelli et al. 2012; Falvo et al. 2019; Cordes et al. 2020; Johnston et al. 2020) demonstrated strong negative associations with warming winter climates. However, we found that changes in summer climate conditions were more strongly associated with UEE extirpations. Possibly, UEE may be experiencing less winter change (e.g. more consistent snowpack) compared to the study sites of these other ground squirrel species, may have greater physiological tolerance to extreme cold temperatures, may be experiencing greater losses of forage in summer due to desiccation, or may be constructing burrows or using behavioral thermoregulation in a way that buffers hibernating individuals more effectively. Comparable data sets of historical and modern snowpack in measures relevant to insulative capacity, i.e. thermal index, could help in investigating if UEE are exposed to stressful hibernacula conditions. Further investigation into mechanisms leading to the differing seasonal responses of *Urocyon* species to climate change could further understanding of the drivers of divergent climate change responses between organisms with otherwise similar traits.

The composition of land cover types at a site or changes in land cover could interact with climate or separately influence population dynamics of UEE at our sites (Mantyka-Pringle et al. 2015). While we found that forest cover and increases in rangeland habitat were associated with an increased probability of extirpation, we found no evidence of interactions between land cover and climate. Additionally, all land cover associations were weaker than climate associations. Logically, sites with greater unsuitable forest cover had a greater probability of extirpation, but this reduction in habitat did not exacerbate the effects of climate. However, resurveys were limited by the number of quality specimen localities, and greater statistical power could better detect subtle interactions and smaller effects of more climate and land cover variables. It is puzzling that increases in rangeland habitat at the regional scale decreased the probability of persistence, as increases in available habitat should lead to larger populations that are more resilient to random extinctions (Dennis 2002).

One possible driver of increased probability of extirpation with regional habitat gains is juvenile dispersal of individuals from the historical site to more suitable surrounding habitat. If regional habitat quality improves, dispersing UEE juveniles could colonize the larger region, with the population at the historical site of lower habitat quality eventually becoming extirpated. Another possible mechanism may be that increases in regional habitat have altered biotic interactions. Biotic interactions such as competition and predation can play a major role in UEE population dynamics (Zegers 1984). For example, white-tailed prairie dogs, *Cynomys leucurus*, are a competitor with UEE and show stronger



**Fig. 5.** We resurveyed 54 localities where *Urocitellus elegans elegans* specimens had been collected prior to 1980 to determine if individuals were still present. The Wyoming Basin and western Colorado regions are visible in the map with a VPD surface. Warmer (redder) colors reflect drying air conditions since 1980.

increases in abundance in response to increasing herb cover than UEE (Olson et al. 2017). White-tailed prairie dogs will kill UEE individuals (Hoogland and Brown 2016) and increases in forb-rich rangeland habitat could lead to larger populations of white-tailed prairie dogs and thus reduce UEE abundance through direct mortality. Identifying sites where historical records of small mammals and their associated biotic communities are available could allow for investigations into the relative roles of changes in climate and biotic interactions on the persistence of these species. While the mechanism of this regional landscape habitat effect requires further study to determine the causal mechanism, our findings suggest that the larger landscape context in which UEE colonies are situated influences long-term persistence.

When estimating the impact of climate change on populations, stochastic interannual population variability can bias estimates of trends generated from resurveys (McCain et al. 2016; Stuble et al. 2021). For groups with high degrees of population growth rate variability including insects and small mammals, population trends of metrics such as abundance can be biased unless resurvey sampling occurs over many years. We addressed these concerns by using persistence at a site, which is more resistant to high variation in population growth rates than abundance trends (McCain et al. 2016). If the amount of habitat at a site was the only

significant predictor or had standardized coefficient estimates that were substantially larger than any measure of climate, population variability would be the most parsimonious explanation for observed extirpations. The presence of climate and land cover variables with larger or similar standardized coefficient estimates suggests that population fluctuations in a short time window of the resurveys is not the sole driver of observed extirpations.

While many studies have found broad elevational trends in extirpations (Moritz et al. 2008; Lenoir and Svenning 2015; McCain et al. 2021), extirpations of UEE were not associated with elevation and instead reflected sites throughout the range where chronic air dryness has increased, there is higher forest cover, and regional rangeland cover has increased. The sites we resurveyed span across the historical (preclimate change) southward range expansion of UEE into western Colorado from the Wyoming Basin (Armstrong et al. 2011). As climate change continues, it appears that the southern range expansion could continue as long as refugia of suitable habitat with sufficient air moisture are available (Morelli et al. 2017). If montane populations experience less change in air dryness than lower elevation populations, UEE could become isolated in montane areas of the Southern Rocky Mountains. Spatially explicit predictive species distribution models could provide a better prediction

of how this novel range extension might shift as global change progresses.

Burrowing herbivorous mammals are key members of grassland and shrubland ecosystems, supporting biodiversity both through modification of the landscape and through trophic interactions (Davidson et al. 2012). It is clear that climate change is impacting a number of these species in North America (Morelli et al. 2017; Falvo et al. 2019; Cordes et al. 2020). These effects might lead to changes in both grassland ecosystem structure (Newediuk and Hare 2020) and trophic complexity (Davidson et al. 2012) at sites where ground squirrel extirpation is occurring. Future work investigating other aspects of sites with altered communities from historical assemblages could help to investigate the consequences of loss of these ecosystem engineers. UEE are experiencing local extirpations that are strongly associated with drying air moisture, and to a lesser degree changes in land cover, and these climate conditions will likely become more physiologically stressful, with the Western United States becoming warmer and drier in the future (Overpeck and Udall 2010). Understanding possible community-level consequences of these extirpations will allow ecologists to better understand how climate and land cover change drive the extirpation of species and how consequential those extirpations are to the biological community present.

## Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**—Specimen identification information for sites resurveyed. All sites ( $n = 54$ ) correspond to specimen localities of *Uroditellus elegans elegans* collected prior to 1980.

**Supplementary Data SD2.**—Results from the variable screening process for both climate and land cover predictors. Univariate binomial generalized linear models of whether a resurveyed site still had *Uroditellus elegans elegans* individuals present were generated for each climate and land cover predictor. An intercept-only model of persistence was generated as a null model. Climate and land cover predictors whose AICc score was 2 AICc less than the intercept-only null model were retained.

**Supplementary Data SD3.**—Firstly, we present additional model diagnostics of the best-fit model testing for overdispersion and outliers generated by the package “DHARMA” in R (Hartig 2017). We then generate boxplots of the variables retained in the best-fit model that compare the range of conditions covered by our resurvey sites and the entire subspecies range using 3 independent data sets. These 3 data sets are, expert-vetted community science observations gathered from iNaturalist ( $n = 178$ ), opportunistic observations of *Uroditellus elegans elegans* individuals collected by ALN during the study period ( $n = 53$ ), and occurrence locations generated from a raptor prey base study conducted by the US Forest Service Rocky Mountain Research Station ( $n = 75$ ; Olson et al. 2017). Next, we present 4 figures that illustrate the range of conditions in both climate and land cover that were observed at our resurvey sites. Lastly, we present a visualization of 2 regression analyses to investigate whether changes in minimum vapor pressure deficit (VPD) are associated with historical or modern minimum VPD values.

**Supplementary Data SD4.**—In addition to the main method of model creation, we generated an additional set of candidate models that reflect the best model created when only using the subset of screened climate variables that represent support or opposition for each hypothesis. For example, to interrogate our hypothesis that winter climate conditions would be stronger predictors of

whether or not *Uroditellus elegans elegans* persists at a historically occupied site, we generated models with variables representing summer climate and we generated models with variables representing winter climate and compared the relative support of each set of models as an additional line of analysis of our hypotheses. Both analytical processes led to the same biological conclusions and this supplementary model-building process is retained here to support the analysis in the main text and to provide representative models of variable combinations not present in the best model generated in the main text.

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## Author contributions

ALN and CMM determined the study objectives and designed the methods. ALN conducted the fieldwork, produced the statistical analyses, and expanded on the historical data originally compiled by CMM. ALN wrote the manuscript with editing by CMM.

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## Conflict of interest

None declared.

## Data availability

The data that support the findings of this study are available from the corresponding author, ALN, upon reasonable request.

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