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ECOSPHERE

Evaluating mechanisms of plant-mediated effects on herbivore persistence and occupancy across an ecoregion

JENNIFER L. WILKENING [1,†] EVAN J. COLE,[2] AND ERIK A. BEEVER [3,4]

[1]*Southern Nevada Fish and Wildlife Office, U. S. Fish and Wildlife Service, 4701 N. Torrey Pines Drive, Las Vegas, Nevada 89130 USA*
[2]*Department of Environmental Science, University of San Francisco, 1843A Powell Street, San Francisco, California 94133 USA*
[3]*Northern Rocky Mountain Science Center, U.S. Geological Survey, 2327 University Avenue, Suite 2, Bozeman, Montana 59715 USA*
[4]*Department of Ecology, Montana State University, Bozeman, Montana 59717 USA*

Citation: Wilkening, J. L., E. J. Cole, and E. A. Beever. 2019. Evaluating mechanisms of plant-mediated effects on herbivore persistence and occupancy across an ecoregion. Ecosphere 10(6):e02764. 10.1002/ecs2.2764

Abstract. Contemporary climate change is rapidly creating one of the greatest challenges for management and conservation during the 21st century. Mountain ecosystems, which have a high degree of spatial heterogeneity and contain numerous habitat specialists, have been identified as particularly vulnerable. We used data from multiple years across sites spanning a >40 million ha ecoregion to test hypotheses regarding how community-level characteristics of vegetation may affect a mammalian generalist herbivore, the American pika (*Ochotona princeps*). We examined patterns of pika persistence across sites in the hydrographic Great Basin, and occupancy within a subset of these sites. We used mixed-effects logistic regression models to compare evidence in support of competing explanations for each pattern within an information–theoretic framework (using Akaike's information criterion). Models reflected four hypothesized classes of mechanisms related to nutritional ecology, ecosystem function, indirect indication of climatic effects, and (synergistic) combinations of these three classes. At the site level, models reflecting synergistic effects received the most support. At the within-site level, support appeared to be split equally among hypotheses containing predictors related to either nutritional ecology or indirect climate effects. Well-supported predictors included cover of invasive plant species, cover of more-xeric plant species, species evenness, and proportion of graminoid species. Our results both (1) identify important aspects of vegetation communities that may influence herbivore distribution in mountainous areas across a large, diverse geographic region, and (2) contribute to an improved understanding of how mountain ecosystems may be affected by ongoing climate change, more broadly.

Key words: Akaike's information criterion; climate change; Great Basin; mechanistic hypotheses; mixed-effects models; Pika; plant–animal interactions.

Received 8 November 2018; revised 1 April 2019; accepted 16 April 2019. Corresponding Editor: Joseph D. Holbrook.
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† **E-mail:** jennifer.wilkening@colorado.edu

INTRODUCTION

Contemporary climate change is widely considered one of the most-pervasive and strongest influences on ecosystem composition and function in the 21st century (Araújo et al. 2011, Beever et al. 2017, Pacifici et al. 2017). Such change has been associated with alterations in species distribution, abundance, behavior (including phenology), morphology, and genetics (Staudinger et al. 2013, Nicotra et al. 2015, Carlo et al. 2018). Although a preponderance of reviews and meta-analyses has shown similar responses that suggest fingerprints of a warming climate (e.g., upward or northward range shifts, earlier emergence from hibernation in spring, earlier arrival of long-distance migrants), magnitude and direction of effects can vary across taxa, across years, and across geographic areas (Root et al. 2003, Beever et al. 2013, Rowe et al. 2015,

MacLean and Beissinger 2017). This variability may reflect differences in a species' life-history strategy, weather conditions across particular seasons and years, and a location's biogeographic position within species ranges.

Despite calls (Root and Schneider 2006) over a decade ago for improved understanding of the causal mechanisms underlying patterns of association among climatic and ecological variables, a relative dearth of such research articles in the climate-change literature remains. For example, a recent global review (Cahill et al. 2013) found that out of 136 papers associating climate change with extinction or population decline, only 14 case studies established a causal mechanistic relationship and unequivocally identified mechanism(s) underlying these processes. In contrast, Ockendon et al. 2014 identified 146 studies from terrestrial and freshwater ecosystems that spanned ≥20 yr and related population time series to aspect(s) of climate. Among these studies, a slight majority (n = 87; 59.6%) tested proximate mechanisms to explain relationships between population demography and climate. Given the ever-expanding effort and cost involved in climate-adaptation efforts, understanding how and why these patterns have arisen is of utmost importance (Beever and Belant 2012). Without solid mechanistic understanding, management and conservation efforts can often resort to trial-and-error approaches to address climate-related changes in ecosystems or communities.

Mountain ecosystems represent not only landscapes where contemporary climate changes are occurring rapidly, but, owing to a large percentage (>90%) of strongly protected ecosystems in these regions (Joppa and Pfaff 2011, Sanderson et al. 2015), one of the landscapes where the broadest palette of species movements and future conservation opportunities are possible. The sharp abiotic gradients of mountains make them natural arenas (sensu Beier and Brost 2010) for novel species interactions and corridors for potential re-shuffling of species ranges as climatic shifts continue (Real et al. 2010, Moyer-Horner et al. 2016). Furthermore, such gradients typically mean that beta diversity across all elevations and aspects of mountains is comparatively higher than nearby valley-bottom systems (Meffe and Carroll 1994, Liu et al. 2018). Mountain ecosystems fulfill a range of aesthetic, recreational, and resource-production values (e.g., photography, bird watching, backpacking, skiing; and timber harvest, mining, livestock production, hunting, etc.), in addition to providing critical water resources via snowpack storage and subsequent runoff (Diaz et al. 2003). Although species in mountain ecosystems around the world have been shown to be responsive to changing climatic conditions (Moritz et al. 2008, Sekercioglu et al. 2008, Rowe et al. 2015, Beever et al. 2016), fewer studies have specifically investigated the apparent mechanisms underlying observed changes in species' biological response. Whereas some studies have found that alpine vegetation communities are nitrogen-limited (Bowman et al. 1993, Jaeger et al. 1999), other research suggests that alpine plants can be more strongly limited by available water, amount of solar gain, or number of snow-free days (White and Nemani 2003, Trujillo et al. 2012, Harpold and Molotch 2015, Blume-Werry et al. 2016).

Ecologists have been investigating the relative strength of direct and indirect effects of climate change on both the composition and the function of ecosystems for several decades. For mountain-dwelling animals, direct effects of climatic extremes are often physiological and can include freezing, dehydration, hyperthermia, and starvation due to increased energy loss (Wunder 1992, Mathewson et al. 2017, Penczykowski et al. 2017). In contrast, indirect effects of climate-induced changes in mountains can entail a wide diversity of dynamics, including altered disease dynamics (Pounds et al. 2006), increased susceptibility to pests and pathogens (Rosenzweig et al. 2001), alteration or degradation of food resources (Waite and Strickland 2006), or changes resulting from altered species compositions and interactions such as the introduction of novel predators or competitors (Cahill et al. 2013, Ockendon et al. 2014). However, for mammals, which can store gametes for long periods, delay implantation of embryos, and suspend or terminate reproductive attempts in response to limited resources, nutritional ecology remains a largely unexplored frontier for ascribing changes in animal distribution and abundance to one or more aspects of climate (Post et al. 2009). Further complicating matters, some individual predictors may reflect both direct and indirect mechanisms,

and patterns may often be most accurately described by a combination of synergistic factors.

Theory underlying plant–herbivore interactions, community structure, niche packing, and patterns of species richness all have rich histories of trying to understand how and why organisms respond to changes over space and time (Shmida and Ellner 1984, Olff and Ritchie 1998, Crawley 2009). Although plant composition at multiple scales broadly reflects the intersection of precipitation and temperature (Whittaker 1970), plant composition and structure at finer spatial scales can strongly reflect the species and density of herbivores present. Conversely, animals often track availability of plant resources across space and time. In mountains, the GLORIA plant-monitoring research network has shown that most species distributions in Europe are moving upslope; however, effects of these shifts were mixed during recent decades. Species richness increased on boreal and temperate-region summits (mean = +3.9 spp.) but decreased on Mediterranean-region summits (mean = −1.4 spp.; Pauli et al. 2012). Using resurveys of ten mountain summits in the Swiss Alps in 1905, 1985, and 2003, Walther et al. (2005) similarly found increasing species richness on summits and that the pace of upslope shift of distributions increased markedly after 1985. Even when upper- and lower-elevation bounds of plant species occupancy remain unchanged, the distribution of individuals between those bounds can lead to species' distributions leaning upslope (Breshears et al. 2008).

In the Great Basin ecosystem of the western United States, cheatgrass (*Bromus tectorum*)—a non-native annual grass whose introduction radically alters fire cycles and the phenology of available forage for herbivores—is forecasted to undergo continuing changes in distribution and abundance under contemporary global change (Bradley et al. 2016). Given that vegetation may indirectly affect herbivore fitness and persistence via several mechanisms, including (1) spatiotemporal availability (due to phenological mismatches, melt–refreeze tissue death, and altered water availability; e.g., Penczykowski et al. 2017), (2) nutritional-quality effects on herbivore fitness, and (3) effects to plant-community composition and structure, we created hypotheses that mirrored these three pathways.

Herein, we used data from multiple years to test whether aspects of plant communities predicted patterns of American pika (*Ochotona princeps*) persistence across sites spanning ~40 million ha of the hydrographic Great Basin, and at a finer scale, patterns of pika occupancy across talus patches within sites in this same ecoregion. We created a small suite of a priori models reflecting mechanisms related to plant-community characteristics that we hypothesized reflected nutritional ecology, a site's (or patch's) aridity or moistness, ecological functioning of the plant community, or synergistic effects of climate change. We compared evidence in support of these competing mechanistic explanations in an information–theoretic framework (Akaike's information criterion [AIC], Burnham and Anderson 2002). Although the influence of vegetation on pikas has been previously discussed (Rodhouse et al. 2010, Erb et al. 2014, Yandow et al. 2015, Ray et al. 2016), to date there have been no analyses investigating competing models of community-level attributes of vegetation as predictors of pika occupancy or persistence. Our results represent the first ecoregional-scale effort to analyze patterns of distributional change in a mountain-dwelling vertebrate using fine-scale (1-m) field sampling of vegetation.

Methods

Study organism

American pikas (hereafter, pikas) make an excellent study system to determine whether climate may be acting via any of several classes of indirect mechanisms on species distribution. Pikas are small (125–200 g) lagomorphs that typically occur on talus patches and other broken-rock features (e.g., lava flows) at higher elevations throughout mountainous areas of western North America. Because pikas can be locally abundant and highly detectable, researchers are afforded greater statistical power to understand patterns and identify mechanisms underlying any changes. When pikas were prevented from behavioral thermoregulation in experiments, individuals perished from acute heat stress within 6 h (Smith 1974). Persistence, distribution, abundance, and range shifts have all been shown to correspond to aspect(s) of climate at one or more spatial resolutions.

Pikas are dietary generalists (Dearing 1996), though they primarily consume herbaceous species with some inclusion of non-vascular plants (e.g., mosses; but see Varner and Dearing 2014 for an exception of pikas primarily consuming mosses). Pikas are active year-round, in contrast to other mountain-dwelling species that hibernate, enter torpor, or migrate during the winter. During the snow-free season, pikas consume forage directly and cache vegetation in haypiles that they territorially defend from conspecifics that sometimes engage in kleptoparasitism (McKechnie et al. 1994). Pikas consume the stored vegetation throughout the winter, when access to non-cached vegetation is limited. Although conflicting evidence exists regarding whether haypiles are necessary for overwinter survival, pikas living in areas where snow is infrequent and rarely persists (e.g., low elevations of the Columbia River Gorge and Lava Beds National Monument) typically do not have detectable haypiles. Haypiles may be considered an insurance policy to permit overwinter survival when snow cover is unusually heavy or long-lasting.

Study area and site classification

The Hydrographic Great Basin is an area of internal drainage, located roughly between the Rocky Mountains to the east and the Sierra Nevada to the west. This arid region occurs across parts of Nevada, Utah, Oregon, California, Idaho, and Wyoming, USA. Numerous mountain ranges with peaks as high as 4342 m are oriented along a north–south gradient and are separated by wide, lower-elevation (1220–1830 m) valley bottoms. Vegetation communities at lower elevations tend to be dominated by sagebrush (*Artemisia* spp.) or salt-scrub species, whereas at higher elevations, dominant plant species resemble those found in the Rocky Mountains or the Sierra Nevada, depending on proximity.

The hydrographic definition of the Great Basin was used for this study because it is the only one with a definitive border. Historical records of pika sightings were obtained from multiple sources; we used these records to compile a list of 25 discrete sites across the Great Basin (Fig. 1). We used data from pika-occupancy surveys of the same sites during 1994–2004 to classify these 25 sites as extant, extirpated, or transitional (Appendix S1: Table S1). Extant sites ($n = 12$) were areas where pikas still occurred at the same locations and elevations recorded by historical surveys. Extirpated sites ($n = 8$) contained no evidence of current occupancy in any talus patch within 3 km of the historic collecting location, indicating that pikas had become locally extinct at some time since the historic survey (average = 72 yr). Transitional sites ($n = 5$) consisted of areas where pikas still remained, but populations had moved upslope, both within and across talus areas, since the historical survey. Within transitional sites, minimum elevation of current pika occupancy (which contained $n = 23$ pika-occupied vegetation-survey locations) occurred >200 m higher than the minimum elevation of occupancy recorded historically. Detection probabilities for pikas are often quite high ($P > 0.90$; Beever et al. 2008, 2010, Rodhouse et al. 2010, Erb et al. 2011, Moyer-Horner et al. 2012, Ray et al. 2016), and individuals leave conspicuous signs of presence, such as mounds of collected fresh vegetation (e.g., haypiles), distinctive piles of fresh fecal pellets (scat), or both. These indirect signs, in combination with the high probability of visual and/or aural detection, allowed for the current occupancy status of patches and sites to be confidently determined.

Vegetation surveys

Vegetation-survey locations were randomly selected from among a larger group of pika survey points. Selection of vegetation-survey locations was stratified to ensure that vegetation surveys within each site (be it extant, extirpated, or transitional) spanned the complete elevation range of pika habitat. Additionally, information from the historical sighting(s), such as geographic coordinates or physical descriptions of areas, was used to confirm that data were collected from areas of historical pika occupation for all sites. Within extant sites, vegetation surveys were conducted adjacent to fresh hay piles in currently occupied pika territories. Within extirpated sites, vegetation surveys were conducted in unoccupied territories at locations of indicators of historical pika occupancy (e.g., old hay piles or scat). Within transitional sites, vegetation surveys were conducted at a mixture of locations within each site: Higher-elevation areas currently occupied by pikas and (typically) lower-elevation areas of past pika occupancy, as evidenced by fresh or old sign, respectively.

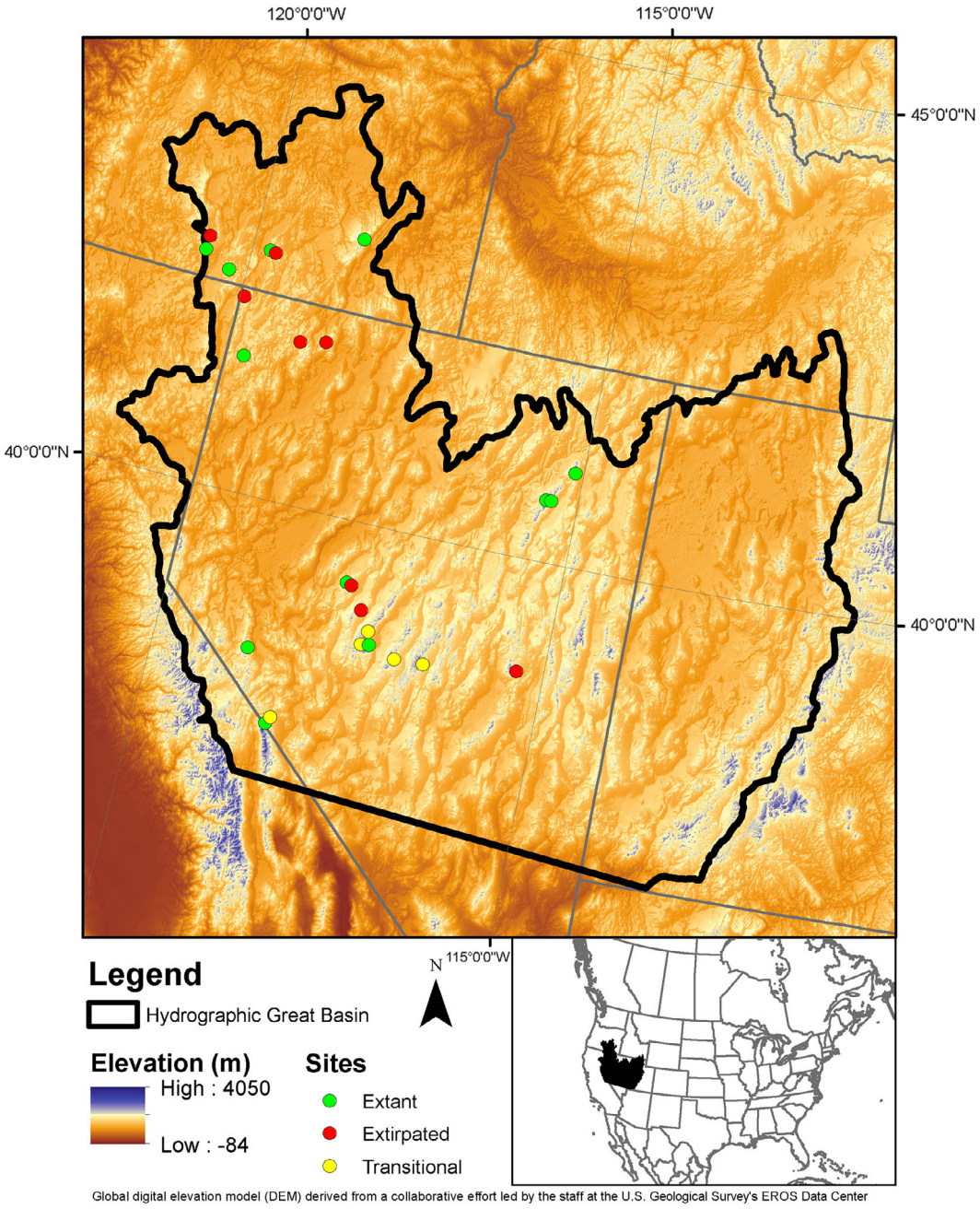


Fig. 1. Map of extant, extirpated, and transitional sites in the Great Basin.

Numerous vegetation surveys (n_{total} = 159) were conducted at all sites from 2005 to 2006 during the months of peak plant biomass—July and August. Surveys were conducted at 3–4 locations per site, and each location was surveyed in 2005 and 2006. Vegetation was quantified using the line-point intercept method (sensu Herrick et al. 2017) using 50-m transects. A transect was placed along the isocline (contour) with the fresh hay pile or other indicator of pika sign as the center point (e.g., at the 25-m mark). A pin flag was dropped at every meter along the transect on

both sides of the center point and all vegetation layers were recorded. An additional 50-m transect was placed both above and below the middle line. Thus, each vegetation survey consisted of three parallel, 50 m long transects, spaced 15 m apart, which resulted in 150 points per vegetation survey. At all sites, approximately half of the points (i.e., location where pin flag was dropped and vegetation layers recorded) occurred over talus areas, while the other half occurred in adjacent-vegetation areas; this ensured that the full range of available forage was captured by each survey. All vegetation was identified to species or genus level in the field when possible, and unknown species were collected and later identified by specialists at the University of Nevada-Reno Herbarium.

Predictor variables

Prior to analysis, all data were checked for outliers and no data were omitted. Collected vegetation data were summarized to estimate 11 vegetation-related predictor variables we hypothesized would influence herbivore persistence and/or indicate climate-driven shifts in vegetation community composition (Table 1). These included relative cover of different groups of plant species, characterizations of vegetation species composition, and various ratios (Table 1).

Invasive species (*Bromus tectorum, Brassica* spp.) were removed from the species richness measures, to avoid artificial inflation of richness values as a result of non-native species (Mooney and Cleland 2001). Invasive species were retained in calculations of species evenness, however, in order to test the hypothesis that invasive cover would be more prevalent at extirpated sites. Similarly, invasive species were removed for the final three predictors (RatioGramToChem, RatioGramPlusForbToChem, RatioGramToForb) to ensure accurate representation of selected vegetation parameters and maintain consistency across vegetation predictors. Species evenness was obtained by calculating the exponential of the Shannon-Wiener-Index, as this value is considered an index of true diversity because it counts all species according to their frequency (Jost 2006). Mosses were the only non-vascular plant encountered at vegetation-survey locations. We were unable to identify mosses to the level of individual species; however, mosses were relatively rare across our sites and averaged far <1% cover within each site. Absolute cover of ocean spray (*Holodiscus discolor*) and fernbush (*Chamaebatiaria millefolium*) was selected based upon decades of anecdotal evidence and recent analyses suggesting co-occurrence of both plant species and pikas (E. A. Beever, *unpublished data*), and this relationship was recently confirmed for fernbush in an adjacent region (Ray et al. 2016).

Numerical values for each predictor were calculated from each vegetation survey (n = 159).

Table 1. Predictor variables for models related to vegetation communities and pika persistence and occupancy in the hydrographic Great Basin, western North America.

Predictor	Effect	Definition
SpecRich	+	Vegetation species richness (excluded non-vascular plants because these were not identified to species)
SpecEven	+	Vegetation species evenness (excluded non-vascular plants because these were not identified to species)
CovInvasives	−	Relative cover of all invasive plant species as defined by Hickman (1993)
CovRiparian	+	Relative cover of all riparian plant species as defined by Hickman (1993)
CovNonVasPlant	+	Relative cover of non-vascular plants, which was only mosses
CovOceanPlusFern	+	Absolute cover of ocean spray (*Holodiscus discolor*) + fern bush (*Chamaebatiaria millefolium*)
CovRabbitPlusSage	−	Relative cover of gray rabbitbrush (*Ericameria nauseosa*) + sage brush (*Artemisia tridenta*ta)
CovPinyonPlusJuniper	−	Relative cover of pinyon (*Pinus monophylla*) + juniper (*Juniperus occidentalis*)
RatioGramToChem	−	Relative cover ratio of native graminoid species to all other vegetation species
RatioGramPlusForbToChem	+	Relative cover ratio of native graminoid + native forb species to all other vegetation species
RatioGramToForb	−	Relative cover ratio of native graminoid species to native forb species

Note: The sign associated with each predictor indicates the hypothesized effect on pika persistence and occupancy.

These predictors were then used in two different model sets, one at the site level and one at the within-site level. For the site-level analysis, data from all 25 sites (extant, extirpated, and transitional) were used and each vegetation-survey location was classified as extant (n = 97) or extirpated (n = 51). Within transitional sites, only occupied vegetation-survey points were included (i.e., n = 11 unoccupied locations were excluded) for the site-level analysis. For the within-site-level analysis, data from the 5 transitional sites were used, and each vegetation-survey location was classified as occupied (n = 23) or unoccupied (n = 11).

A set of 26 candidate models was generated using one or several predictors (Table 2). To contextualize and interpret the potential mechanistic significance of each predictor and combination of predictors, we categorized our models according to a set of a priori hypotheses, defined below. Each predictor represents a potential mechanism by which vegetation communities may influence pika persistence and/or occupancy, and a predictor is not limited to a single hypothesis group because predictors may reflect or relate to more than one hypothesis.

1. Nutritional Ecology: Pika persistence and occupancy are positively associated with the local availability of high-quality forage items (e.g., plant species providing significant protein, micronutrients, or water content: Dearing 1997, Huntly et al. 1986, Smith and Erb 2013). Across the Great Basin, rabbitbrush (*Chrysothamnus* and *Ericameria* spp.) and sagebrush (*Artemisia tridentata*) have high amounts of secondary compounds (e.g., terpenoids, volatile oils) and are consumed sparingly by many herbivores during much of the year (McArthur et al. 1977, Striby et al. 1987, Tirmenstein 1999. We thus predicted persistence and occupancy to

Table 2. Set of candidate models established a priori to test mechanistic hypotheses related to vegetation communities and pika persistence and occupancy in the hydrographic Great Basin.

Number	Model	Hypothesis group
1	CovOceanPlusFern	Nutritional Ecology
2	CovRabbitPlusSage	Nutritional Ecology, Climate—Dry
3	RatioGramToChem	Nutritional Ecology, Climate—Dry
4	CovOceanPlusFern + CovRabbitPlusSage	Nutritional Ecology
5	CovRabbitPlusSage + RatioGramToChem	Nutritional Ecology
6	CovOceanPlusFern + RatioGramToChem	Nutritional Ecology
7	CovOceanPlusFern + CovRabbitPlusSage + RatioGramToChem	Nutritional Ecology
8	SpecRich	Ecosystem Function
9	SpecEven	Ecosystem Function
10	CovInvasives	Ecosystem Function
11	SpecRich + CovInvasives	Ecosystem Function
12	SpecEven + CovInvasives	Ecosystem Function
13	CovRiparian	Climate—Wet
14	CovNonVasPlant	Climate—Wet
15	CovPinyonPlusJuniper	Climate—Dry
16	CovRabbitPlusSage + CovPinyonPlusJuniper	Climate—Dry
17	CovRabbitPlusSage + CovPinyonPlusJuniper + RatioGramToChem	Climate—Dry
18	CovRiparian + CovPinyonPlusJuniper	Climate—Wet and Dry
19	CovNonVasPlant + CovPinyonPlusJuniper	Climate—Wet and Dry
20	CovInvasives + CovRabbitPlusSage	Synergistic Effects
21	CovInvasives + RatioGramToChem	Synergistic Effects
22	CovInvasives + CovPinyonPlusJuniper	Synergistic Effects
23	CovInvasives + CovRabbitPlusSage + RatioGramToChem	Synergistic Effects
24	SpecEven + RatioGramToChem	Synergistic Effects
25	RatioGramPlusForbToChem	Nutritional Ecology
26	RatioGramToForb	Nutritional Ecology, Synergistic Effects
27	Null Model	

be negatively associated with these genera. Initial work on the chemistry of ocean spray and fernbush suggests greater nutritional value and digestibility for pikas (E. Beever and J. Varner, *unpubl. analyses*), and therefore, we predicted that persistence and occupancy would be positively associated with these species.

2. Climate–Dry: Pika persistence and occupancy are negatively associated with xeric conditions (Hafner 1993; Beever et al. 2003, Beever et al. 2011), which are reflected in the vegetation community by associated species (e.g., pinyon, juniper). Similarly, we also selected rabbitbrush and sagebrush as predictors associated with xeric conditions (see Scheinost et al. 2010) and thus with pika absence. Plant communities shaped by xeric conditions tend to be composed of more graminoids and shrubs than forbs and trees (Ray et al. 2016), so we hypothesized that the ratio of graminoids to all other vegetation would negatively predict pika persistence or occupancy.
3. Climate–Wet: Pika persistence and occupancy are positively associated with mesic conditions (Hafner 1993, Beever et al. 2003, 2011, 2016, Erb et al. 2011); therefore, we hypothesized that pika occupancy would be positively predicted by cover of mesic-associated plant species. We indexed wetter microclimates using the combined percent cover of all riparian and non-vascular plant species.
4. Ecosystem Function: We hypothesized that pika persistence and occupancy may be positively associated with metrics of ecosystem function, such as species richness, species evenness, and negatively associated with relative cover of invasive plant species. Species richness and species evenness are indices of local biodiversity, and higher values may suggest a stable and relatively resilient ecosystem (Stirling and Wilsey 2001)—perhaps especially important in the extreme and dynamic alpine habitat of Great Basin pikas. Relative cover of invasive plant species may negatively index ecosystem function, given that an ecosystem unbalanced by the expansion of non-native plant species can become less diverse and less stable (Hejda et al. 2009).
5. Synergistic Effects: Pika persistence and occupancy may be substantially driven by the combined effects of two or more of the above hypothesis categories, potentially implicating the interactive influences of multiple pathways as the overarching mechanism.

Logistic mixed-effects models

All statistical analyses were conducted using R 3.0.1 (R Development Core Team 2016), and significance was assessed at $\alpha = 0.05$. Competing models were constructed a priori using understanding from existing literature and a quarter-century of our work on pikas in this region, evaluated in an information–theoretic framework, and fitted using the R package lme4 (Bates et al. 2012). Relative support for each of the 26 candidate models and for each predictor was compared using AIC (Burnham and Anderson 2002). Mixed-effects logistic regression models were used to account for sampling across years (2005–2006) at the same locations (Buckley et al. 2003). Year and site were treated in every model as random effects on model intercept and slope and vegetation-based predictors as fixed effects. Highly correlated predictors (Spearman's $r > 0.50$) were not used together in the same model. Because only fixed effects differed among models, maximum likelihood (rather than restricted maximum likelihood) was used to estimate coefficients and compare nested models. Interaction terms were omitted if not significant (P-value > 0.10). We ranked the overall importance of vegetation predictors by dividing the variable weight of each individual predictor by the number of models it appeared in, following Beever et al. (2011).

Results

Site-level analysis (extirpated vs. extant sites)

Among predictor variables, species richness (SpecRich) was positively correlated with species evenness (SpecEven; Spearman's $r = 0.92$), and these two variables were accordingly not used together in the same model. Similarly, cover of riparian-associated plants (CovRiparian) was

positively correlated with cover of non-vascular plants (CovNonVasPlant; 0.55), and RatioGramToChem was positively correlated with RatioGramToForb (0.58).

The four best models (ΔAIC ≤ 2) within this model set included one or several of the following vegetation predictors: cover of invasive plants (CovInvasives), RatioGramToChem, cover of pinyon and juniper trees (CovPinyonPlusJuniper), species evenness (SpecEven), and relative cover of rabbitbrush (*Ericameria nauseosa* and, more commonly, *Chrysothamnus viscidiflorus*) and sagebrush (*Artemisia tridentata*) (CovRabbitPlusSage). Two of the top four models included the same interaction term (CovInvasives * RatioGramToChem). The signs of the coefficients of predictors were all as we hypothesized a priori, except that relative cover of non-vascular plants negatively (rather than positively) predicted persistence (Table 3). Furthermore, signs of coefficients did not differ across models, for any predictor. Model results appeared to provide the most support for interacting effects of multiple classes of mechanisms, as most top-ranking models were part of the group of hypotheses implicating synergistic effects (Tables 3, 4). Among predictors of persistence, CovInvasives (0.64) garnered the most support, followed by RatioGramToChem (0.61, Table 4).

Within-site-level analysis (occupied vs. unoccupied patches, within transitional sites)

Among vegetation predictors, SpecRich was positively correlated with SpecEven (Spearman's $r = 0.89$) and negatively correlated with RatioGramToForb (−0.52). SpecEven was also positively correlated with CovNonVasPlant (0.51) and RatioGramToForb (−0.50). CovNonVasPlant was also positively correlated with CovRiparian (0.55). RatioGramPlusForbToChem was positively correlated with RatioGramToChem (0.59) and negatively correlated with RatioGramToForb (Spearman's $r = -0.60$); therefore, these predictors were not used in combination in any models. Invasive species cover was not included as a vegetation predictor in this much-smaller dataset, because only 1 survey recorded any cover of invasive plant species, within transitional sites.

Within this model set, all of the top-ranked models (AIC ≤ 2) included CovRabbitPlusSage, either alone or in combination with one of the following predictors: CovPinyonPlusJuniper, RatioGramToChem, or CovOceanPlusFern. Interaction terms were not significant for any models

Table 3. Relative support for models related to vegetation communities and pika persistence at the site level (N = 148) and pika occupancy at the within-site level (N = 34) in the hydrographic Great Basin.

Level of analysis	Model with predictor(s) and effect sign	AIC	ΔAIC	Akaike weight	Evidence ratio^{-1}
Site level	CovInvasives(−), RatioGramToChem(−)	167.1	0	0.2614	1
Site level	CovInvasives(−), CovPinyonPlusJuniper(−)	167.2	0.1	0.2486	0.9510
Site level	SpecEven(+), RatioGramToChem(−)	167.4	0.3	0.2250	0.8607
Site level	CovInvasives(−), CovRabbitPlusSage(−), RatioGramToChem(−)	169	1.9	0.1011	0.3868
Site level	CovRiparian(+), CovPinyonPlusJuniper(−)	169.2	2.1	0.0914	0.3497
Site level	Null	194.6	27.5	0	0
Within-site level	CovRabbitPlusSage(−)	34.8	0	0.3170	1
Within-site level	CovRabbitPlusSage(−), CovPinyonPlusJuniper(−)	35.9	1.1	0.1829	0.5770
Within-site level	CovRabbitPlusSage(−), RatioGramToChem(+)	36	1.2	0.1740	0.5489
Within-site level	CovOceanPlusFern(+), CovRabbitPlusSage(−)	36.8	2.0	0.1166	0.3678
Within-site level	CovRabbitPlusSage(−), CovPinyonPlusJuniper(−), RatioGramToChem(+)	36.9	2.1	0.1109	0.3498
Within-site level	CovOceanPlusFern(+), CovRabbitPlusSage(−), RatioGramToChem(+)	37.9	3.1	0.0672	0.2120
Within-site level	Null	46.8	12.0	0.0008	0.0025

Notes: Models are ranked in order of increasing Akaike's information criterion (AIC) values and ΔAIC is the difference between the indicated model and the best model. Models with ΔAIC > 4 are not shown, except for the null model. Significance was assessed at $\alpha = 0.05$. The Akaike weight (w_i) ranges from 0 to 1 and indicates the strength of evidence in support of each model, given the model set. The evidence ratio is calculated by w_o/w_i, where w_o is the Akaike weight of the model with the lowest AIC. Because the evidence ratio is inverted, smaller numbers indicate relatively less support.

Table 4. Relative support for vegetation-related predictors of pika persistence and occupancy in the hydrographic Great Basin, western United States.

Level of analysis	Predictor	Akaike weight	Mean Akaike weight/model	Sign of coefficient
Site level	CovInvasives	0.6428	0.0918	−(7)
Site level	SpecEven	0.2489	0.0829	+(3)
Site level	RatioGramToChem	0.6140	0.0682	−(9)
Site level	CovPinyonPlusJuniper	0.3801	0.0633	−(6)
Site level	CovRiparian	0.0915	0.0457	+(2)
Site level	CovRabbitPlusSage	0.1309	0.0145	−(9)
Site level	SpecRich	0.0080	0.0040	+(2)
Site level	CovNonVasPlant	0.0048	0.0023	−(2)
Site level	RatioGramToForb	0.0001	0.0000	−(1)
Site level	CovOceanPlusFern	0.0001	0.0000	+(4)
Site level	RatioGramPlusForbToChem	0.0000	0.0000	+(1)
Within-site level	CovRabbitPlusSage	0.9689	0.1615	−(6)
Within-site level	CovPinyonPlusJuniper	0.3011	0.0602	−(5)
Within-site level	RatioGramToChem	0.3564	0.0594	+(6)
Within-site level	CovOceanPlusFern	0.1851	0.0463	+(3), −(1)
Within-site level	RatioGramPlusForbToChem	0.0104	0.0105	+(1)
Within-site level	RatioGramToForb	0.0042	0.0043	−(1)
Within-site level	CovNonVasPlant	0.0022	0.0011	+(2)
Within-site level	CovRiparian	0.0020	0.0010	−(2)
Within-site level	SpecEven	0.0011	0.0006	+(1), −(1)
Within-site level	SpecRich	0.0002	0.0002	−(1)

Notes: The Akaike weight of each predictor indicates the sum of model weights across all models containing that predictor and indicates the strength of evidence for that predictor calculated across all candidate models. The mean Akaike weight is the sum of the weights from all the models which contained the predictor, divided by the number of models which contained the predictor. The sign associated with each predictor indicates that predictor's effect, and the number of models where this was positive or negative is given. Site-level analyses were performed across all extant and extirpated sites, whereas within-site analyses used occupied vs. unoccupied locations, within each transitional site.

within this set. CovRabbitPlusSage and CovPinyonPlusJuniper were consistently negatively correlated with pika occupancy, whereas RatioGramToChem and cover of ocean spray plus cover of fernbush (CovOceanPlusFern) were positively correlated (Table 3). Support appeared to be split equally among hypotheses that reflected nutritional ecology or a patch's aridity. Among predictors of occupancy, CovRabbitPlusSage garnered the most support (variable weight = 0.97), followed by RatioGramToChem (0.36) and CoverPinyonPlusJuniper (0.30, Table 4).

Discussion

As is true for most species, herbivore niches may be limited primarily by three classes of constraints—the physical, predatory, and competitive environments. Whereas the physical environment includes a menagerie of climatic aspects that herbivore species must cope with, obtaining sufficient energy via foraging can involve considerations of both the predatory and competitive environments. Specifically, optimal foraging theory, competition theory, and "landscapes of fear" (i.e., minimizing risk of predation; sensu Brown et al. 1999) make different predictions about how herbivores should forage. In another melding of two such environments, distributions of herbivores may correspond to distribution of one or more plant species, not because of the nutrition or the visual protection from predators that the plants provide, but rather because distributions of both the plant and herbivore species co-vary with the same climatic aspects at finer spatial resolutions.

More broadly, the specific life-history strategy of pikas differs somewhat from other animals that may undergo hibernation or torpor, undergo seasonal or long-distance migrations, have larger home ranges, or not rely on vegetative food caches. Consequently, we acknowledge that our identification and assessment of hypothesis groups, as well as interpretation of the

importance of various mechanisms, may differ for species that utilize these other life-history strategies to cope with seasonal and inter-annual variability in conditions. For example, mule deer (Aikens et al. 2017), moose, and bighorn sheep (Jesmer et al. 2018) typically synchronize their migratory movements to track forage availability across the landscape, as phenology advances in spring. In Sierra Nevada bighorn sheep, most populations are partially migratory (i.e., they display both migrant and resident behaviors). Across 14 subpopulations tracked between 2005 and 2016, migratory tactics varied among subpopulations, and individuals switched migratory status on average every 4 yr, contingent upon conditions (Spitz et al. 2018). Similarly, animals such as wolverines or grizzly bears that range more widely can be opportunistic and flexible in both their diet and movements, because they are not place-based foragers like pikas that always return to their haypile. Whereas pikas in northern Wyoming selected more strongly for higher-nitrogen and low-fiber vegetation when exposed to higher daytime temperatures (Hall and Chalfoun 2018), dietary-generalist species may not necessarily be equally selective. Similarly, whereas pikas are active year-round and thus have an exceedingly high annual caloric requirement per unit body mass, other species such as marmots, bears, squirrels, and herpetofauna either use torpor, hibernation, or estivation to conserve energy and avoid stressful climatic conditions.

Synergistic-effects hypothesis group

The group of hypotheses implicating synergistic effects included all of the four most-predictive models of pika persistence at the site level (i.e., among extant and extirpated sites), which collectively accounted for 83.6% of the total model weight. Climate, forage quality, and foraging behavior are tightly linked; for example, pikas are more selective for nitrogen when surrounded by low-quality vegetation and at sites with higher average summer temperatures (Smith and Erb 2013). Pikas balance the energetic costs of haying by increasing selectivity for higher-quality food and reducing exposure to heat stress by spending less time foraging (Stafl and O'Connor 2015). A synergistic relationship has been demonstrated previously between high mean summer temperature and low relative forb cover to predict pika absence (Wilkening et al. 2011). Selectivity for plants with high water content decreases with increasing elevation, though metabolic water content does not correlate across the same elevation gradient, indicating that pikas are likely responding to differences in climate and free water availability at different elevations (Smith and Erb 2013). Plant communities that both reflect mesic microclimates, while also providing adequate nutritional value, offer considerable advantages for pikas.

That the synergistic models outperformed the other hypothesis groups at the site level may reflect the idiosyncrasies of alpine ecosystems and the adaptive capacity of pikas (sensu Nicotra et al. 2015). Influences of contemporary climate change on pikas have been shown to be place-based and thus heterogeneous across the pika's range (Beever et al. 2016, Rodhouse et al. 2018) Climatic variables can interact synergistically to mediate pika occupancy (e.g., heat stress has a greater effect in areas with low precipitation), mirroring the dynamic ecological feedbacks suggested by our top-ranking models. Pikas have been noted to exist seemingly outside of their bioclimatic niche in many areas, attributed to factors of dietary plasticity and habitat refugia. In such locations, there exists substantial decoupling of macro- and meso-climate from the microclimates that pikas actually experience (Varner and Dearing 2014, Varner et al. 2016) indicating the contextually subjective importance of macroclimate and forage quality to pika persistence.

Similar relationships among climate, forage quality, and foraging behavior have been established for other mammalian herbivores living in comparably harsh environments, such as caribou (*Rangifer tarandus)*. Summer forage quality affects physical condition and ultimately reproduction (Gerhart et al. 1996), and female caribou rely upon abundant summer vegetation to improve body condition and replenish depleted nitrogen reserves (Cameron et al. 1993). Experiments designed to mimic the predicted future climatic conditions of the region (specifically, cloudier summer days) found that adding shade over vegetated areas led to higher-nitrogen concentrations in plant species, but lower overall biomass in vegetation (Lenart et al. 2002). However, cloudy, cooler summers can also lead to reduced

abundance of insects, which would decrease insect harassment (Helle and Kojola 1994) and allow more time for foraging, thus potentially counteracting negative effects associated with reduced plant biomass (Lenart et al. 2002). Climate change could thus result in overall positive benefits for caribou, especially in locations where forage amounts are high (Lenart et al. 2002).

Conversely, research related to caribou and winter forage has concluded that consequences of climate change will be mostly negative. Benefits from increased plant abundance in the summer would most likely be outweighed by negative impacts associated with distributional shifts in preferred winter forage (lichens), and diminished access to winter foraging plants with increased amounts of snow and ice (Heggberget et al. 2002). Alpine and arctic ungulates such as ibex (*Capra ibex)* and moose (*Alces alces*) are known to reduce foraging time in response to hotter temperatures, and these species may also be dealing with a climate-change trade-off, as any increases in summer plant biomass may be offset by reduced foraging opportunities and/or increased ectoparasite loads (Renecker and Hudson 1986, Aublet et al. 2009). Our results, along with these examples, underscore the importance of examining interacting effects, such as behavioral responses or changing interactions with predators or conspecifics, when considering climate-change impacts in mountain communities. Future research investigating relationships among climate, forage quality, and foraging behavior specific to small mammals in arid regions could provide additional insight into patterns described here.

Nutritional ecology hypothesis group

Models related to nutritional ecology were least predictive of pika persistence at the site level (i.e., among extant and extirpated sites) but the most predictive of occupancy at the within-site level (i.e., within transitional sites), suggesting that forage quality may be more variable and limiting at finer spatial scales. The nutritional value and phenology of available vegetation within a site can buffer pikas from atypical climatic conditions (Rodhouse et al. 2010, Varner and Dearing 2014, Yandow et al. 2015), whereas abiotic environmental factors appear to drive broader patterns of persistence at macroscales (Beever et al. 2010, 2011, Erb et al. 2011, Stewart et al. 2015). Specifically, the relative cover of rabbitbrush plus sagebrush outperformed all other models and was present in each of the top six models at the within-site level; however, its negative coefficient disagrees with a previous study demonstrating a positive relationship between pikas and sagebrush (Ray et al. 2016). This latter result may have been indicative of a positive association with increased overall vegetation cover, as sagebrush is the most common shrub across that landscape. Sagebrush and rabbitbrush may serve as high-quality forage via significant protein and secondary metabolite content (Buttkus et al. 1977, Bhat et al. 1990, Halls et al. 1994), but these advantages could be overshadowed by the negative effects of the warm, xeric conditions generally associated with these plants (Scheinost et al. 2010). Cover of ocean spray and fernbush also appeared in two of our top nutritional ecology models at the within-site level, supporting previous evidence showing a positive correlation between pika site-use intensity and the number of fernbushes (Ray et al. 2016). Further research into the chemical makeup and nutritional characteristics of ocean spray and fernbush could elucidate the mechanism underlying this apparent relationship.

Pika density appears limited by forage availability in at least some locations (Erb et al. 2014, Yandow et al. 2015), a limitation that may be exacerbated at local scales as many plant species travel upslope in response to contemporary climate change (Kelly and Goulden 2008). In the hydrographic Great Basin, minimum elevation of plant species occurrence has risen markedly since time of historic field collecting (Beever et al. 2016). Many plant species at higher elevations have narrower elevation tolerances when compared to plant species at lower elevations within the same range, putting them at greater risk of localized extinction (Guisan and Theurillat 2000). As species shift upward, habitat area becomes restricted due to the conic shape of mountains (Elsen and Tingley 2015), establishing a negative feedback loop. In the western United States, some high-elevation plant communities have already experienced significant compositional transformations in response to climate change, including fewer forbs and more graminoids and shrubs (Zorio et al. 2016). Forbs may be

particularly vulnerable to continued warming (Franklin et al. 2016), which could affect winter dietary requirements of pikas. Such effects reflect the facts that (1) pikas are known to preferentially cache forbs and other plants high in secondary metabolites (Huntly et al. 1986, Dearing 1997), and (2) metrics of forb cover, height, and diversity have been shown to positively predict pika persistence (Rodhouse et al. 2010, Erb et al. 2014, Moyer-Horner et al. 2016, Ray et al. 2016). Further research into the exact nutritional and secondary chemical factors that promote pika persistence could inform targeted conservation and restoration strategies for this species and other mountain-dwelling herbivores.

Climate hypothesis group

The group of hypotheses related to climate comprised the second-most-predictive set of models at both the across-site (i.e., among extant and extirpated sites) and within-site (i.e., within transitional sites) levels. Both pikas and plants exhibit distributional patterns that co-vary with one or more climatic aspects (Kelly and Goulden 2008, Beever et al. 2010), which may account for this relatively strong, consistent relationship across spatial levels. Paleo-historic climate-change-driven species extinction on a global scale has occurred only a handful of times, but localized extinctions (i.e., extirpations) resulting from range contractions at the warm edge have occurred in hundreds of species (Cahill et al. 2013). Many of these local extinctions may be the result of individuals dispersing out of unsuitable habitats or declines in recruitment, rather than individuals dying. Climate change could be negatively affecting individuals directly, as pikas are known to perish when exposed to high temperatures (Smith 1974), in addition to indirect effects associated with altered vegetation communities.

Climate appears to have been a primary driver of past range fluctuations of the American pika, as well as of nearby plant communities that co-evolved with pikas. During the late Pleistocene interval (~12,000 radiocarbon years ago), a sub-epoch characterized by a cooler climate, pikas existed at much lower elevations compared to the present day and may not have exclusively utilized talus habitat (Grayson 2006, Galbreath et al. 2009). Across the Great Basin, the average elevation of pika populations has increased by 783 m since the last glacial maximum of the late Wisconsinan (~40,000–10,000 radiocarbon years ago), corresponding with a rise in global temperatures (Grayson 2005, Beever et al. 2011). Similarly, the shift from C3-dominated plant communities to C4-dominated plant communities 4–8 million years ago contributed to wide-scale extinctions and range contractions of ochotonids, resulting in the persistence of only a single genus, *Ochotona*, until the present (Ge et al. 2013). Pikas prefer to consume C3 plants over C4 plants; the latter are largely characterized by a high carbon: nitrogen ratio and low protein content (Ge et al. 2012, 2013). The relationship between carbon dioxide levels and C3 and C4 plant-community dynamics is complicated, and it is still uncertain whether C4 plants may lose their competitive advantage in response to elevated carbon dioxide levels (Wand et al. 1999). Furthermore, it remains unknown whether a potential shift toward C3-dominated plant communities will benefit pikas nutritionally, or if the associated rise in temperature might negate any nutritional benefits via direct (i.e., physiological) climatic stress on pikas.

Ecosystem or plant-community function hypothesis group

Hypotheses in this group included predictors such as plant species richness, plant species evenness, and relative cover of invasive plant species. Species richness and species evenness serve as metrics of biodiversity and are associated with enhanced ecosystem and plant-community productivity and function (Wilsey and Potvin 2000, Allan et al. 2011). Invasive species have been shown to reduce species richness and evenness, disrupting ecosystem and plant-community function (Hejda et al. 2009). Arguably, the most-pervasive and transformative invasive species across the Great Basin is cheatgrass (*Bromus tectorum*). Cheatgrass comprised nearly all of the invasive plant cover measured by our surveys and has degraded ecosystem function and negatively impacted small-mammal communities across the ecoregion (Freeman et al. 2014). Cheatgrass sprouts early in the spring and early after fires, thus co-opting resources before native plants can benefit from those resources; native grasses and shrubs typically decline after cheatgrass invasion. In addition to these effects, cheatgrass primarily affects herbivores by (1) markedly increasing the fire

frequency in a given community (D'Antonio and Vitousek 1992); and (2) senescing early in the summer-fall season and becoming mechanically and chemically poor in forage quality (Young and Allen 1997). For animals inhabiting high-elevation habitats, forecasts of cheatgrass distribution expanding upslope (Bradley et al. 2016) may not bode well, but our paper is the first to have empirical results suggesting that such expansions may (directly or indirectly) contribute to animal declines. This hypothesis group performed poorly at both the site (i.e., among extant and extirpated sites) and within-site (i.e., within transitional sites) levels. However, at both levels, species evenness improved significantly when combined with the ratio gram: chem, even becoming the third-ranked model at the site level. Plant communities with a high ratio of graminoids and low overall species evenness may represent an unstable, poor-quality source of nutrition, especially detrimental for late-season foraging and haypile production (Jakopak et al. 2017). Relative cover of invasive species appeared in the top two model combinations at the site level, potentially reflecting the pervasiveness of invasive cheatgrass within individual sites.

Our findings convey several important implications related to the management and conservation of vegetation and animal communities in mountainous areas under changing climates. First, synergistic effects should be considered thoughtfully when assessing potential ecological response to climate change for a single species or ecological community. Our results suggest that vegetation communities may respond in a variety of ways and that a particular mechanism of climate-change influence should not be assessed in isolation (Watson 2005). Many natural-resource managers recognize this need and are increasingly examining interactive effects of multiple climate stressors (Heller and Zavaleta 2009). Collaboration with scientists from other disciplines is also essential for the creation of climate-change-integrated conservation strategies (CCS: Hannah et al. 2002), which can greatly improve the development and implementation of management actions designed to respond to changing conditions.

Second, our results underscore the importance of forage quality in addition to forage quantity. Reductions in nutritional quality of forage may affect other herbivore species and could have cascading effects for predators. Many mountain herbivores preferentially select for plants higher in nitrogen, which is typically limited in high-elevation ecosystems (Bowman et al. 2012); pikas are considered allogenic engineers because they locally enrich environmental nitrogen via the construction of hay piles (Aho et al. 1998). The loss of pikas in an area may signify unsuitable vegetation for other herbivore species or result in predator species abandoning these areas in favor of regions with more-abundant prey. Similar climate-change-driven losses in biodiversity have been documented in other mountainous regions, such as the Tibetan plateau and the Arctic (Klein et al. 2004, Gilg et al. 2009).

Finally, although climate change is now recognized as a substantial threat to biodiversity and is projected to be a major contributor to species extinctions, the underlying causes of these extinctions remain largely unexplored. There is a growing body of evidence documenting climate-driven population decline and extinctions, but very few studies identify specific causes of projected extinctions. Furthermore, when mechanisms are identified, they rarely pinpoint straightforward relationships between temperature tolerances and extinctions, but instead reveal more-convoluted relationships such as those deriving from species interactions (Cahill et al. 2013). Results from our study corroborate these findings and emphasize the need to prioritize research investigating the underlying mechanisms behind climate-induced range shifts or population loss, because such research can inform management and aid in successful species conservation.

Acknowledgments

We thank A. Bies, R. Delano, B. Eversull, L. Niell, S. Leslie, and S. Weber for assistance with fieldwork and data collection. We also thank C. Malone and J. Tiehm at the University of Nevada, Reno herbarium for assistance with plant identification. B. Smithers provided insightful, constructively critical review of an earlier draft. We thank Constance I. Millar, Donelle Schwalm, and an anonymous reviewer for their insightful comments that considerably strengthened the manuscript. The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U. S. Fish and Wildlife Service. Any use of trade, firm, or product names is for descriptive

purposes only and does not imply endorsement by the U.S. Government. Author Contributions: JLW and EAB formulated the idea and conducted fieldwork; JLW and EJC performed data analyses; JLW, EJC, and EAB wrote the manuscript.

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