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Research article

Combining past and contemporary species occurrences with ordinal species distribution modeling to investigate responses to climate change

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Many organisms leave evidence of their former occurrence, such as scat, abandoned burrows, middens, ancient eDNA or fossils, which indicate areas from which a species has since disappeared. However, combining this evidence with contemporary occurrences within a single modeling framework remains challenging. Traditional binary species-distribution modeling reduces occurrence to two temporally coarse states (present/absent), so thus cannot leverage the information inherent in temporal sequences of evidence of past occurrence. In contrast, ordinal modeling can use the natural time-varying order of states (e.g. never occupied versus previously occupied versus currently occupied) to provide greater insights into range shifts. We demonstrate the power of ordinal modeling for identifying the major influences of biogeographic and climatic variables on current and past occupancy of the American pika *Ochotona princeps*, a climate-sensitive mammal. Sampling over five years across the species' southernmost, warm-edge range limit, we tested the effects of these variables at 570 habitat patches where occurrence was classified either as binary or ordinal. The two analyses produced different top models and predictors – ordinal modeling highlighted chronic cold as the most-important predictor of occurrence, whereas binary modeling indicated primacy of average summer-long temperatures. Colder wintertime temperatures were associated in ordinal models with higher likelihood of occurrence, which we hypothesize reflect longer retention of insulative and meltwater-provisioning snowpacks. Our binary results mirrored those of other past pika investigations employing binary analysis, wherein warmer temperatures decrease likelihood of occurrence. Because both ordinal- and binary-analysis top models included climatic and biogeographic factors, results constitute important considerations for climate-adaptation planning. Cross-time evidences of species occurrences remain underutilized for assessing responses to climate change. Compared to multi-state occupancy modeling, which presumes all

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states occur in the same time period, ordinal models enable use of historical evidence of species' occurrence to identify factors driving species' distributions more finely across time.

Keywords: Distributional declines, geographic range retraction, logistic regression, ordinal regression, ordinal response, temporal interpretation

Introduction

Species distributions shift in response to changes in the biotic and abiotic environment, and due to variability in species' intrinsic characteristics (Maclean and Early 2023, Rubenstein et al. 2023). Many species leave traces of past occurrence across landscapes they once inhabited (e.g. fecal pellets, pollen grains, tree stumps, middens, fossils, owl pellets, environmental or ancient DNA, biogenic habitat modifications), though these traces vary in their antiquity. These evidences attest to past conditions that may have once been suitable but may now no longer be – for example, indicating landscapes or regions from which a species has recently disappeared. Combined with contemporary occurrences, past evidences provide rich documentation of present and past range dynamics and may highlight factors that present-day data alone cannot (Smith et al. 2009). Nevertheless, most analyses of species distributions concatenate evidence categories down to two site states – 1) currently occupied (present), and 2) unoccupied, assumed absent (pseudo-absence), or 'background' (Guisan et al. 2017).

Beyond binary characterizations of species status as occupied versus unoccupied (or extant versus extirpated), there are often other categories that are of biological relevance in distributional and metapopulation hypotheses (MacKenzie et al. 2009). For example, multi-state occupancy models with three or more response types can discriminate among the environmental factors that influence occupancy, in addition to other biological states such as breeding status (Nichols et al. 2007, Martin et al. 2009). Using multi-state models can also provide deeper temporal insights into ecological processes that may play out over timescales beyond the reach of contemporary sampling feasibility. Paleoecological studies, for example, have often used three or four evidence or occurrence states when examining historical shifts in species distributions over centuries to millennia: present currently but not in the past, only present historically, always present, and complete absence of the species from all time periods (Smith et al. 2009). However, studies using contemporary data typically exclude the 'extirpated' or 'never-present' categories, or combine the two categories into 'not present,' when modeling the factors limiting distributions (but see the dynamic-distribution model of Bennie et al. 2013). Thus, only analyzing present-day distributions as binary typically reduces the amount of information presented to the model, and thereby potentially biases interpretations of which factors actually shape species' distributions and range shifts, and how these factors may change over various time scales. Additionally, the ability to include historical occurrences that may or may not be able to be assigned to a particular time period overcomes the hurdle of matching these occurrences to past environmental conditions, which may or may not be available at the same level of coverage (resolution, temporal extent, types of variables) as contemporary environmental data.

Here, we highlight an approach that categorizes species occurrence with multiple conditions in an ordered fashion: currently occupied, formerly occupied, and no evidence of occupancy. Ordinal occurrence differs from binary occurrence 1) by utilizing a third occurrence category that separates previously occupied sites from sites with no evidence whatsoever, and 2) because the occurrence categories, as listed above, are explicitly treated as having an order. This approach allows investigation of distributional controls from contemporary to multiple retrospective time periods. Ordinal modeling is similar to, yet fundamentally different from, classical multi-state occupancy modeling that estimates a state conditional on observations and probabilities of other, lesser or simpler states (Nichols et al. 2008, MacKenzie et al. 2009). For example, multi-state occupancy modeling would allow for estimating the probability a site was occupied by gravid females, conditional on the site being occupied (Nichols et al. 2008), but it cannot be used for modeling a temporally ordered sequence of occupancy states. Likewise, dynamic occupancy models allow for estimating site-specific occupancy states through time (MacKenzie et al. 2003), but require occupancy-type data for each time period and cannot use data from time periods of indeterminate length.

The structure of an ordinal model is similar to that of a binary (logistic) generalized linear model, and assumes that J possible states of sites can be ordered as never present, recently occupied, or currently occupied with index $j = 1, 2, 3, \ldots, J - 1$ such that for each j,

$$\ln\left(\frac{p_{\leq j}}{p_{>j}}\right) = \beta_j - \vec{\beta}X \quad (1)$$

where $p_{\leq j}$ is the probability of observing a site in state 1 through j, and $p_{>j}$ is the probability of observing a site in a state that is greater than j. β_j is an intercept, $\vec{\beta}$ a vector of coefficients, and $\boldsymbol{X}$ a model matrix of predictor values. Ordinal models thus estimate the log-odds of a site being in states up to j versus the site being in states 'higher' than j. The minus sign here is included because as j increases, it allows intuitive interpretation of $\vec{\beta}$, which will take positive values if the predictor is associated with a higher probability of obtaining a higher state indexed by j (note also that 'higher' states of j are in the denominator on the left-hand-side). Although each state has its own intercept, the model form assumes the odds of changing between any two adjacent

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states is constant (Agresti 2010, ch. 6, Tutz 2012, ch. 9). Alternative formulations

of ordinal models exist for relaxing this assumption, but these variants can also allow violation of the assumption of order among responses, so may not be amenable to cases where predictor variables span a substantial range (Agresti 2010, ch. 3.6). Ordinal modeling is also called cumulative-odds modeling or proportional-odds modeling (Tutz 2012).

Within the context in which ordinal modeling is used here, we assume observed site states represent a 'snapshot' in time of the outcome of a relatively long time-series in which sites can transition from occupied to recently extirpated to no evidence of occupancy. Transitions do not necessarily need to be in this order, however, as a site could have – prior to observation – transitioned from one with no past evidence to occupied, then to recently extirpated. Whatever the site history, site states are matched to environmental conditions at the time of observation, not any of the times of past transitions. Thus, the model answers the question, 'Given present-day environmental conditions, what are the odds of a site belonging to a particular state that is the outcome of (unobserved) past conditions inducing (unobserved) site transitions?'

To illustrate this technique's utility, we compare results using traditional binary-response data versus trinary, ordinal data using a five-year, ecoregional-scale dataset of a climate-sensitive species, the American pika *Ochotona princeps*, a small mountain-dwelling lagomorph of western North America. Because pika haypiles (caches of vegetation) and fecal pellets can persist for decades or longer (Millar et al. 2014), surveys for pikas provide an opportunity to identify not only where the species currently exists, but also where it previously existed – even without prior surveys or historical records. Thus, this study system provides an outstanding opportunity to address our main objective: compare both distributional controls and bioclimatic niche space between binary (currently occupied versus unoccupied) and ordinal (currently occupied > previously occupied > no evidence detected) regression. This latter approach has rarely, if ever, been used for investigating distributional controls. We conducted surveys for pikas across the southern terminus of the Rocky Mountains (USA) during 2016 through 2020, and recorded evidence that allowed us to classify sites as presently occupied, past-occurrence, and no-pika-evidence alternatives. As a null assumption, we predicted that the two modeling approaches would identify the same bioclimatic factors as being most important. The results of such investigations have implications for predicting where future distributional and abundance changes are likely to be most pronounced, identification of locations where and which conservation-management interventions may be most effective, and prioritization of limited conservation resources.

Methods

Study domain

Our study domain contains four geographic sub-regions of mountainous habitat in the southern Rocky Mountains in New Mexico, USA – the Jemez Mountains (southwest, or SW), the San Juan Mountains (northwest, or NW), and the northern (northeast, or NE) and southern Sangre de Cristo Mountains (southeast, or SE). These are each separated from all other sub-regions by > 50–100 km and lower-elevation habitats, such as arid valleys and canyons, that are inhospitable to pikas (Fig. 1) and can act as barriers to dispersal for typically high-elevation species (Alexander et al. 2018). The domain spans marked climatic diversity over sharp physiographic gradients. Mean temperatures at our sites ranged from 9.0–19.0°C in the summer (June–September), and from −6.7 to 1.9°C in the winter (November–March), and snow can persist at highest elevations for up to 5–8.5 months of the year. Annual precipitation at study sites ranged from 33–115 cm (PRISM AN81d data, 2006–2021; Daly et al. 2002), of which approximately one-third to one-half is received as snow, on average (https://wrcc.dri.edu/summary/Climsmnm.html). Summer-monsoon rains and thunderstorms are characteristic of our study sites and usually occur from July through mid-September, but may vary in exact timing and duration.

Field surveys

During 2016–2020, we surveyed 570 independent patches of talus (i.e. each separated from all other patches by > 25 m of non-talus habitat, which is 1 meter greater than mean nearest-neighbor distances published for our focal species; Smith and Weston 1990) across our study domain (Fig. 1). Patches were primarily identified by intensive manual searches for talus using high-resolution imagery in www.CalTopo.com, prior to field surveys. Surveyed-patch elevations spanned 2280–3884 m (Supporting information).

Field methods reflected our focal species' life-history characteristics and iterative refinements to our sampling approach developed over three decades (Beever et al. 2003, Billman et al. 2023, also see the supporting information). Pikas are philopatric (Tapper 1973, Smith and Ivins 1983), most active crepuscularly in warmer regions and seasons (Smith 1974), and obligately associated with broken-rock (talus) habitats (Smith and Weston 1990), where they are easily detected (detectability is often between 0.93 and 1.00 in typical talus habitats like those herein; Beever et al. 2010, Ray et al. 2016, Thompson 2017). These dietary-generalist herbivores are central-place foragers that produce unique, peppercorn-like fecal pellets that can persist for years to centuries in sheltered rock interstices (Millar et al. 2014). Pika distributional shifts and declines, occupancy, abundance, genetics, and behavior have all been strongly predicted by climatic variables at multiple temporal scales (Galbreath et al. 2009, Beever et al. 2013, Stewart et al. 2017, Smith et al. 2019, Billman et al. 2023, summarized in Beever et al. 2023). Consequently, pikas constitute an excellent model system to investigate patterns and drivers of occupancy at multiple timescales (Supporting information).

We primarily performed surveys at patches from 0.5 hours before sunrise until 12:15 p.m. and from 4:00 p.m. until 0.5 hours after sundown during May–October of 2016–2020.

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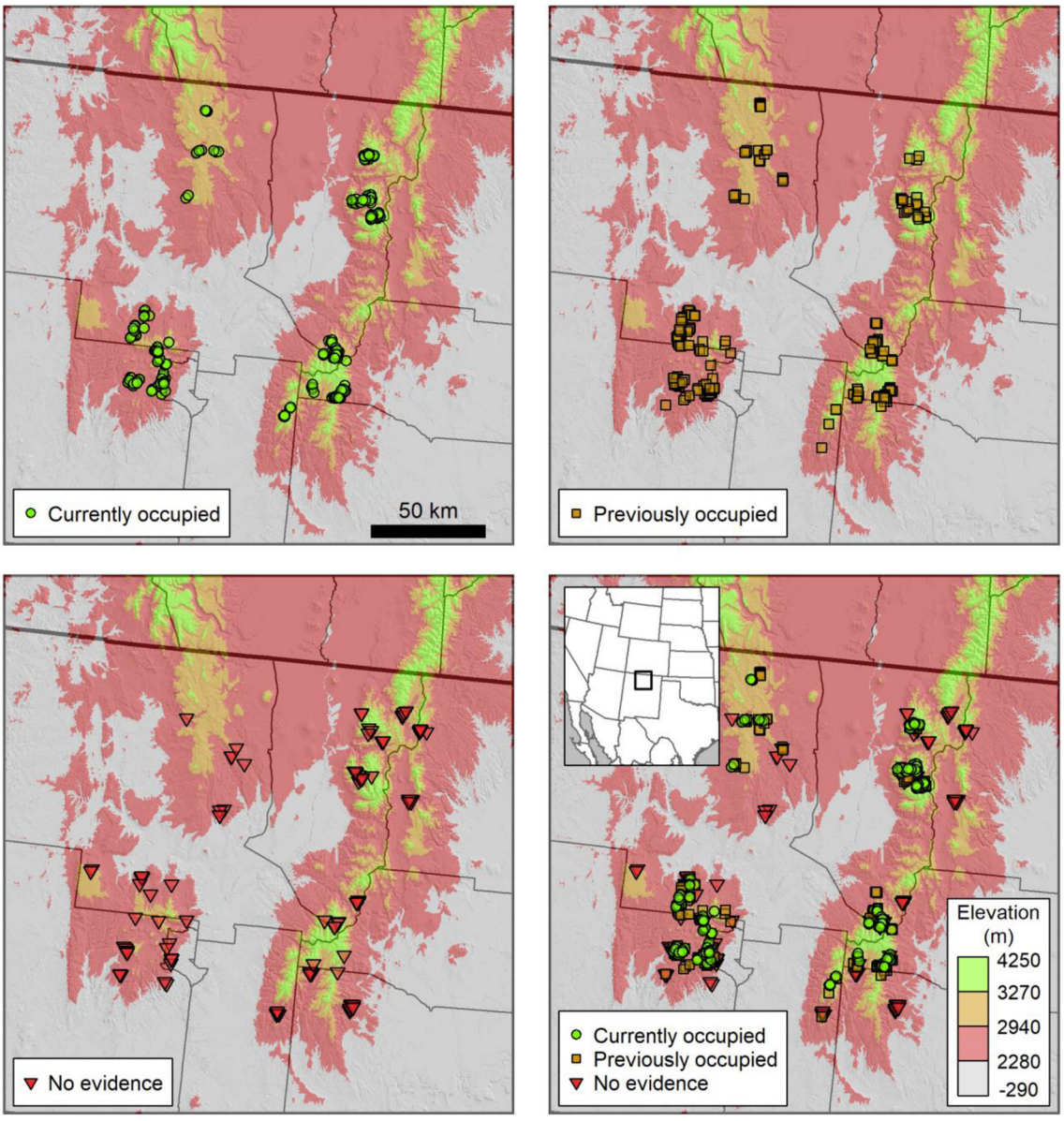

Figure 1. Study domain and survey sites, across the southern terminus of the Rocky Mountains, North America. Sites were classified into 'currently (pika-)occupied,' 'previously occupied' (in past years), and 'no evidence detected.' Each panel clearly depicts the four sub-regions we used in modeling to address numerous questions – NW, NE, SE and SW. For visual clarity, the ordinal-occurrence states are shown separately, and in the lower-right panel, all together. Points are colored by their ordinal occurrence state, but the background elevation map is broken into classes: the lowest 'no-evidence' site occurred at 2280 m, the median elevation of 'previously occupied' sites at 2940 m, and the median elevation of 'occupied' sites at 3270 m. Maps are in Albers conic equal-area projection.

We searched for evidence of current or past pika occupancy by walking a path of continuously linked 50-m transects along the lower-elevation margin of the patch and along elevational contours (approximately 15 m apart elevationally) spanning the entire patch. Particularly close attention was paid to large boulders, which often serve as centers of pika activity. At each patch, we also recorded spatial extent of talus with rock diameters 0.2–1.0 m to calculate the number of 20 × 20 m potential pika home ranges in the patch. Whereas data associated with each detection use a 24-m diameter circle because that is the midpoint of nearest-neighbor distances reported in Smith and Weston (1990), estimating home ranges in the field (to accurately ascertain the proportion of the patch that has pika-appropriate rock diameters) is: 1) more repeatable when dimensions are smaller; and 2) easier to calculate patch-level home-range totals when length and width are accurately measured with a laser rangefinder (wherein patch-shape deviations from a perfect rectangle can be quantified and accordingly modifying the total). Importantly, the 400 m^2 area closely approximates the 454 m^2 area of the circle. Current occurrence was indicated when we saw pika(s), heard pika(s), or detected a fresh haypile (i.e. >10 sprigs of green vegetation;

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Billman et al. 2021). Old haypiles and/or old fecal pellets indicated previous pika occupancy (Table 3 of Beever et al. 2016). We used several criteria to maximize likelihood of detecting past or current occupancy (Supporting information). Given these numerous precautions, we use naïve occurrence herein, and acknowledge that we may have failed to detect current or especially past occupancy at a few sites.

Analyses

We evaluated binary and ordinal occurrence using several weather-related variables reflecting resource availability, extreme conditions, and water and heat balance (Supporting information). The model set included univariate models of each predictor, plus models with other predictors in additive and/or multiplicative terms, selected to obviate high pairwise collinearity between predictors ($|\rho| \leq 0.7$; Supporting information), and reflect specific hypotheses about how pikas respond to environmental stressors (e.g. Supporting information in Billman et al. 2021) across this domain. Daily weather data were obtained from PRISM version AN81d (Daly et al. 2002) at 30 arcsec (~ 750 m) resolution. Depending on the variable, the mean value or number of days above/below a threshold was calculated for each variable-specific date window (Supporting information). All climate variables and numeric covariates were centered by their mean values and divided by their SD prior to modeling. Lastly, we used the four mountain sub-regions as categorical predictors in some models to account for potential differences in responses among sub-regions (Fig. 1, Supporting information).

We used an information-theoretic framework that competed a priori models using AIC_c to assess which climate and biogeographic predictor(s) best explained observed patterns of occupancy. To analyze occurrence, we used the exact same model suite for each of two types of models: 1) ordinal models, which assume that occurrence states can be ordered naturally from low-to-high (from 'no evidence,' to 'previously occupied,' to 'currently occupied') along continuous climate predictors, and a logistic error distribution (function *plor* in package 'MASS' ver. 7.3-60.2 for R, Venables and Ripley 2002, R ver. 4.3.0; www.r-project.org); and 2) binary models, which used currently occupied sites as presences and amalgamated unoccupied (both 'no-evidence' and 'previously-occupied') patches as absences, assuming a binomial error distribution (function *glm* within R-package 'stats', www.r-project.org). For each model type (ordinal or binary), we constructed 66 models with combinations of climate variable(s) depicting particular mechanisms of climatic influence, each crossed with all possible combinations of including versus not including three biogeographic covariates (patch size, sub-region and patch isolation; 8 models per set of climate variable(s)); an intercept-only model; and models including only all subsets of the three non-climatic variables (Supporting information).

For binary and ordinal models, variable importance was assessed by calculating the average AIC_c-based weight of each model in which the variable appeared (Kittle et al. 2008, Billman et al. 2021; i.e. [summed variable weight / no. of models]). This differs slightly from the traditional method of simply summing AIC_c weights ('variable weight' of Burnham and Anderson 2002), which we also report, by correcting for the fact that the apparent importance of less-influential predictors tends to be upwardly biased when they appear in otherwise well-supported models (Giam and Olden 2016).

All analyses described above were repeated using site-level weighting to account for cases where multiple sites occurred in the same environmental cell (Supporting information). We also evaluated model accuracy using cross-validation using two-thirds of the data for calibration and one-third for evaluation data, where sites were selected for each set in a random manner stratified by region and the three site states. For this exercise, we used the best binary and ordinal model, and repeated the folds 100 times. For each fold, we calculated the area under the receiver operating characteristic curve (AUC) and the continuous Boyce index (CBI), comparing binary model predictions at presence sites to ordinal model predictions at presence sites, and binary model predictions at absence sites to ordinal model predictions at 'no-evidence' and 'previously occupied' sites.

All code for the analysis is archived at https://github.com/adamlilith/pika_newMexico_2016through2020.

Results

Distributional extent

Each category of occurrence (currently occupied, previously occupied, no evidence) occurred in all four sub-regions (Fig. 1). The low-elevation perimeter of each sub-region was dominated by patches with no evidence of pikas, except for the northern edge of the northwestern sub-region, which is connected to larger massifs in Colorado (Fig. 1). The northeastern sub-region also extends northward into Colorado, but connectivity may be limited by low-elevation corridors that bisect the Cordillera. Out of the 570 surveyed patches, 226 patches (39.6%) were currently-pika-occupied in the most-recent survey, 233 patches had only old evidence ('previously occupied'; 40.9%), and 111 (19.5%) had no evidence of pikas (Supporting information). Depending on how many of our no-evidence patches were previously occupied by pikas at timescales beyond the persistence of fecal pellets and haypiles, between 50.8% (if none; [233/(233 + 226)]) and 60.4% (if all; [(233 + 111)/(233 + 111 + 226)]) of previously occupied patches suffered apparent extirpation. Among the 142 patches in the lowest quartile of elevation, only 12.7% (n = 18) patches were currently pika-occupied, and 78.8% (n = 67) of all 85 patches with pika evidence were previously (but not currently) occupied. Among all 428 remaining (i.e. the higher-elevation 75% of) patches surveyed, 48.6% (n = 208) were currently occupied and 44.4% (n = 166) of those 374 patches with pika evidence were previously (but not currently) occupied. The frequency histograms of most climatic predictors showed our hypothesized pattern that 1) no-evidence sites were climatically,

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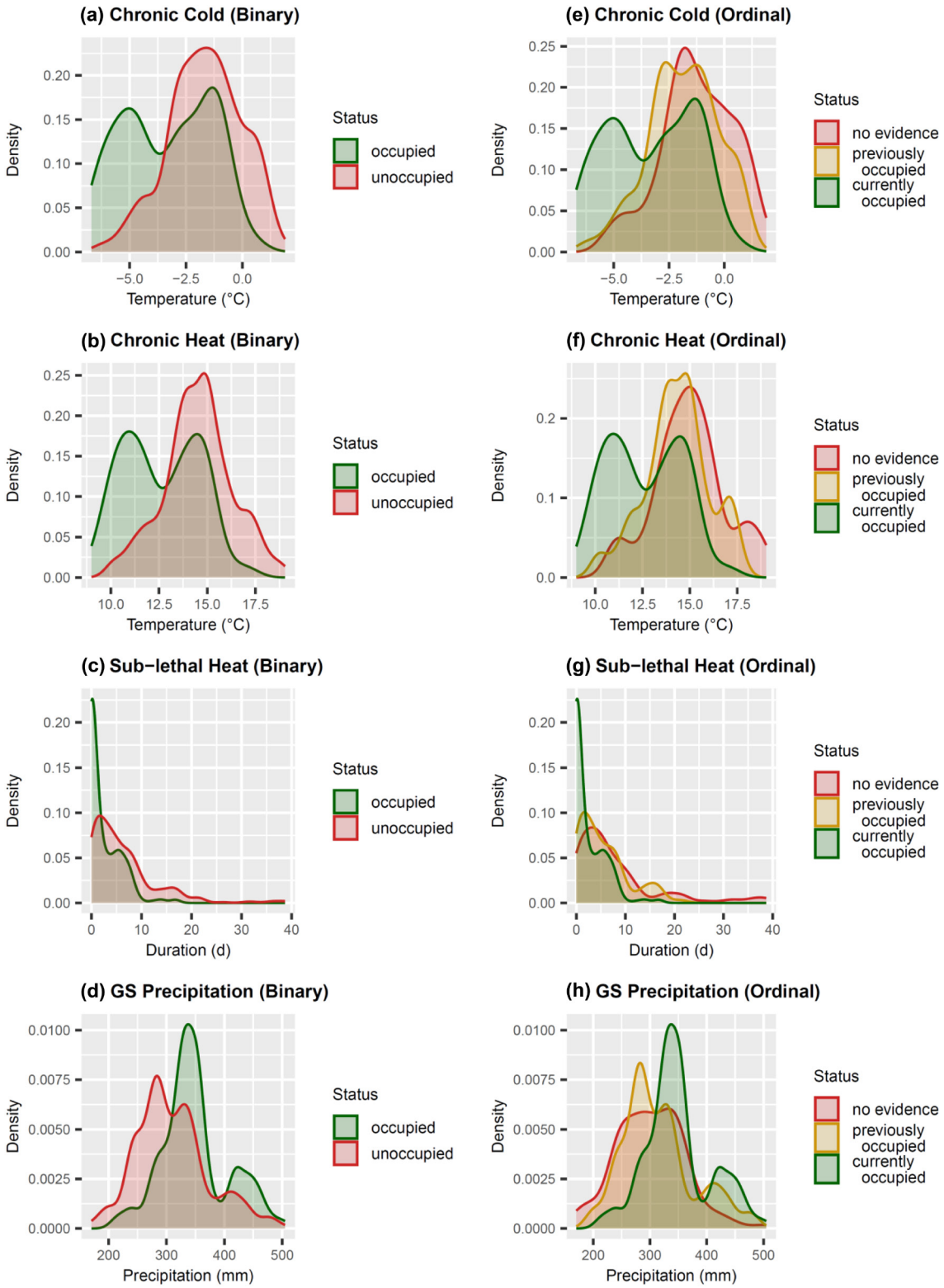

Figure 2. Distributions of values of climatic variables at n = 570 sampled patches used to predict occurrence, split by ordinal state (right column) or binary state (left column). (a–d) Green = pikas detected as currently present on the focal patch; red = pikas not detected on focal patch; (e–h) green = currently pika-occupied, yellow = previously pika-occupied, and red = no evidence of occupancy detected.

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(a) Top ordinal models (ΔAIC_c <4)	Pseudo-R^2	ΔAIC_c	Model weight (ω_i)
-1.80 chronic cold +0.80 GS precip. +0.56 HRs -0.39 isolation +region	0.458	0	0.760
-2.22 chronic heat +0.45 sub-lethal heat +0.54 GS precip. +0.56 HRs -0.37 isolation +region	0.446	3.923	0.107
intercept-only		1202.3	

(b) Top binary models (ΔAIC_c <4)	Pseudo-R^2	ΔAIC_c	Model weight (ω_i)
-1.79 chronic heat +0.71 monsoon precip. +0.75 HRs -0.31 isolation +region	0.370	0	0.427
-1.69 chronic heat +0.75 GS precip. +0.75 HRs -0.30 isolation +region	0.370	0.894	0.272
-1.79 chronic heat +0.14 sub-lethal heat +0.75 GS precip. +0.75 HRs -0.29 isolation +region	0.369	2.820	0.104
intercept-only	0	249.1	0

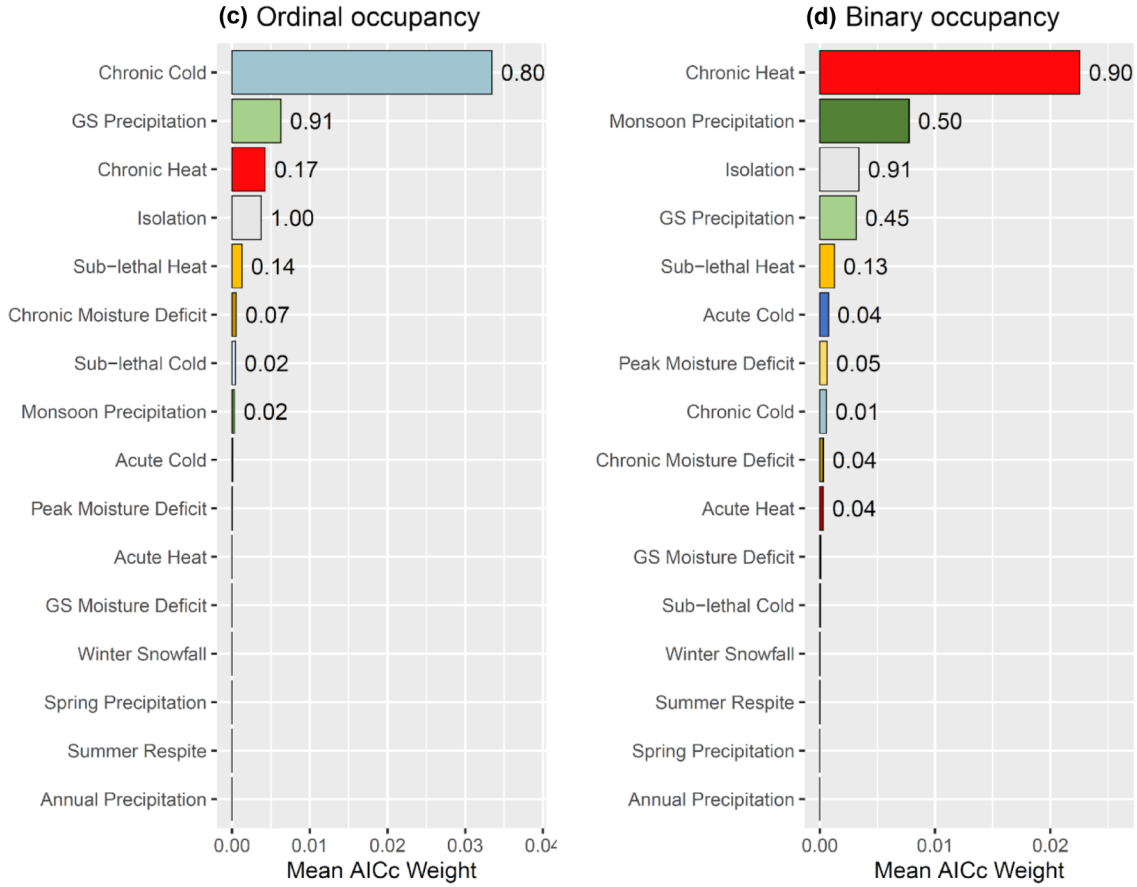

Figure 3. Top-ranked models and relative variable importance. Top-ranked models (ΔAIC_c<4) for (a) ordinal occupancy, and (b) binary occupancy. 'HRs' denotes patch size or spatial extent, measured in situ as the number of potential pika home ranges in the patch. 'GS' is growing-season. Inclusion of the variable 'region' indicates that occupancy differed significantly among sub-regions in a given model; it appeared in all top models. 'Isolation' reflects mean distance to the nearest four patches from each focal patch. Values of coefficients represent $\vec{\beta}$ (not $-\vec{\beta}$) in Eq. 1 in the Introduction. We used Nagelkerke's R^2 to calculate pseudo-R^2 (Nagelkerke 1991). R^2 values can only be meaningfully compared within the same model structure. 'Model weight' is AIC_c-based model weight. Variable importance in information-theoretic analyses of (c) ordinal occupancy, and (d) binary occupancy. Width of each horizontal bar represents average AIC_c (model) weight for the models in which each variable appears (i.e. summed variable weight/no. of models). Values on the right of each bar represent that predictor's variable weight (i.e. the sum of the weight of all models in which the predictor appears).

and presumably physiologically, harshest, 2) sites with only old pika evidence were intermediate, and 3) currently occupied patches were least stressful for this cold-adapted species (Fig. 2e–h, Supporting information). The bimodal distribution of climatic conditions at currently occupied sites reflected non-overlapping climatic niches along several climatic axes across the four sub-regions, using either two or three occurrence categories (see green lines in Fig. 2, Supporting information).

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Table 1. (a) Mean ± 1 SE isolation distance, averaged across patches, of the average distance from the focal patch to each of the four closest patches, when stratified by sub-region. Given private and sovereign lands (and overlap of our sampling with the pandemic), the NW sub-region was incompletely sampled; that region's distances are thus over-estimates. Only the right-most two columns in the SE sub-region strayed from biogeographic predictions. (b) Mean ± 1 SE isolation distance of the average of the four closest patches (as in a), domain-wide. Sample size for each class of occurrence appears in brackets. (c) Mean ± 1 SE isolation distance from the single closest patch, averaged domain-wide. Sample sizes for each class are as in (b. These distances less accurately reflect the networked nature of metapopulation dynamics in *O. princeps* than those in (b), and except in strongholds of current pika occupancy (e.g. at highest elevations), typically underestimate the distance to the nearest source of colonists.

Sub-region	n (no. of patches)	Currently pika-occupied patches (m)	Previously pika-occupied patches (m)	No-pika-evidence patches (m)
(a)				
Northeast	125	525.3 ± 31.2	742.5 ± 87.5	916.3 ± 159.9
Northwest	53	657.3 ± 109.6	1318.5 ± 251.8	2724.5 ± 614.1
Southeast	169	410.9 ± 25.3	722.1 ± 101.2	661.1 ± 54.7
Southwest	223	666.0 ± 45.3	838.5 ± 95.2	3580.9 ± 1146.0
(b)				
		384.2 ± 15.5 [n = 226]	556.0 ± 42.6 [n=233]	961.2 ± 153.4 [n=111]
(c)				
		201.2 ± 10.5	253.3 ± 25.5	320.3 ± 39.7

Ordinal occurrence

Among the climate variables, chronic cold (mean winter temperature) appeared in the top model (ω_i=0.744; Fig. 3a), and was the variable with greatest average AIC_c weight per model in which it appeared (Fig. 3c). Growing-season precipitation had the second-highest weight per model, and appeared in both of the top-ranked models (Fig. 3a, c). The likelihood of pika occurrence increased with colder winter temperatures (i.e. chronic cold) and wetter growing seasons. Signs of climatic predictors' coefficients were all as we had hypothesized (Supporting information), except for 3 of our 15 climatic variables. We provide more details of these exceptions in the Supporting information. Each of the top four models included one temperature and one precipitation variable. Ordinal regressions explained up to 45.8% of variation (pseudo-R^2) in ordinal occupancy status (Supporting information).

Regarding biogeographic factors, levels of patch-scale ordinal occupancy differed markedly across sub-regions (see 'region' in Fig. 3a). Additionally, patch size positively affected the likelihood of a patch being in a higher category of occupancy (see 'HRs' [i.e. 'HomeRanges'] in Fig. 3a). Conversely, greater patch isolation consistently reduced the likelihood of a 'higher' occupancy status (AIC_c-weighted coefficient for $\log_{10}$ of isolation distance: -0.39).

Binary occurrence

Several findings were similar between binary and ordinal models. First, levels of patch-scale binary occupancy differed notably across sub-regions (see 'region' in Fig. 3b). Second, an aspect of both temperature and precipitation (monsoon or growing-season) occurred in the 6 highest-ranked models (Supporting information). Third, directionality of all other predictors was again consistent with our a priori predictions (Supporting information), with only three exceptions. Fourth, larger patch size again significantly improved the likelihood of current pika occupancy (see 'HRs' [i.e. 'HomeRanges'] in Fig. 3b). The mean AIC_c-weighted coefficient for patch size across all models was 0.57 for ordinal and 0.75 for binary occupancy. Finally, across models, greater isolation of a patch reduced its probability of being pika-occupied (see 'isolation' in Fig. 3b; also Table 1). Regressions explained up to 37.0% of variation (pseudo-R^2) in binary occupancy status (Supporting information), though the underlying data type is different from that of the ordinal models, so the pseudo-R^2 values cannot be meaningfully compared.

In contrast, several results differed between analyses of binary versus ordinal models. Most prominently, chronic cold predicted binary occupancy much less strongly than ordinal occupancy. Instead, chronic heat most strongly predicted binary occupancy, and monsoon precipitation was the second-most-important predictor (whereas the latter was sixth-most-important in ordinal analyses; Fig. 3d).

For ordinal models, weighting sites by the inverse of the number sites in each environmental cell had minor effects on variable importance (mean absolute rank difference 1.25), and all top-six-ranked variables were the same (Supporting information). Binary models were more sensitive to weighting (mean absolute rank difference 2.5), and the top-ranked variables were not always the same.

Model accuracy and predictions

Cross-validation results suggested that, compared to ordinal models, binary models more accurately differentiated presences from absences (mean AUC for binary models across 100 folds: 0.865, ordinal models: 0.772) and were better calibrated (continuous Boyce index for binary models: 0.917, ordinal models: 0.805).

Spatially, predictions from binary and ordinal models were largely similar (Fig. 4). For the ordinal model, areas predicted to be likely 'previously occupied' were located between areas predicted to be most likely 'no evidence' or 'occupied.'

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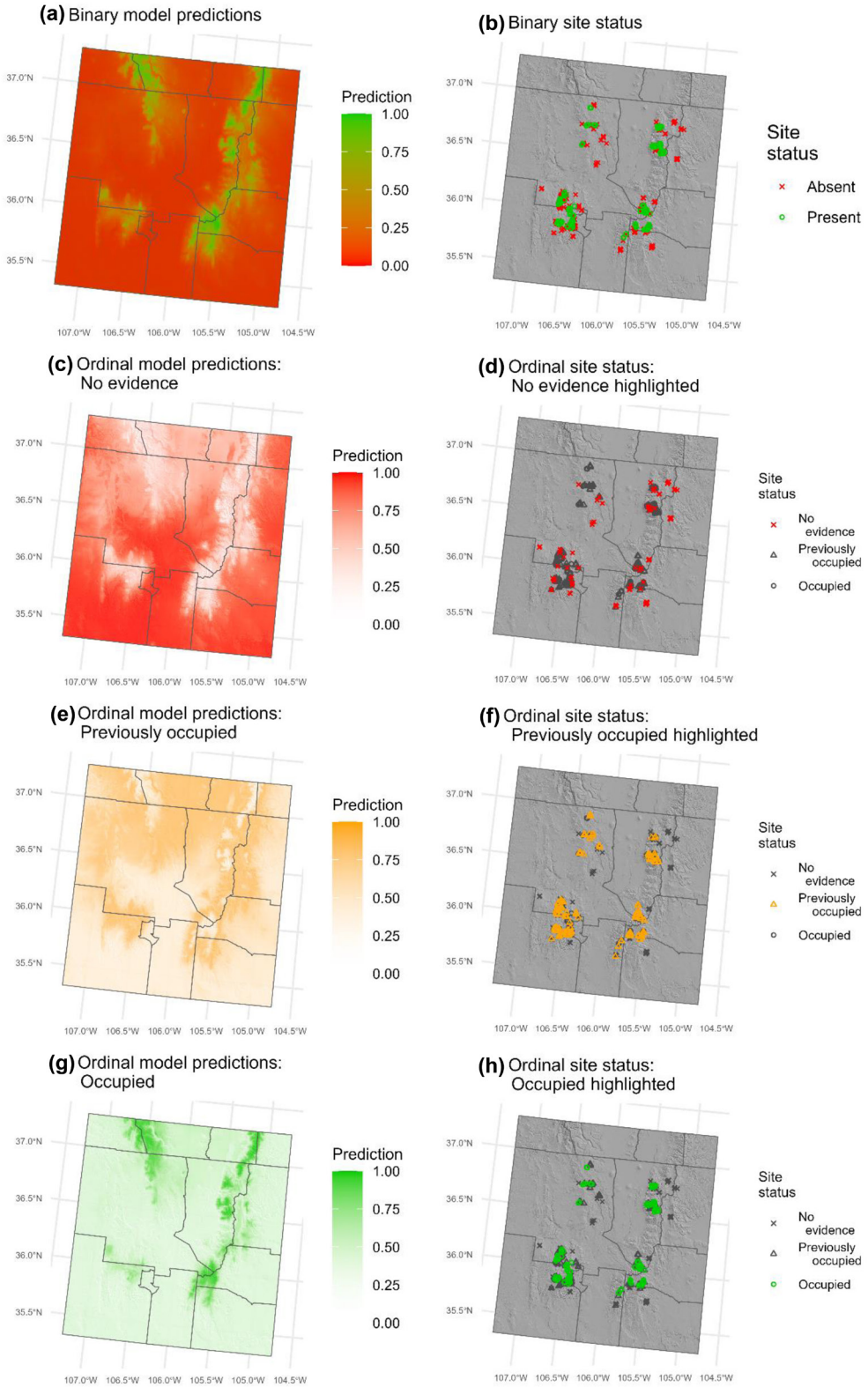

Figure 4. Spatial predictions for the current period of binary (a) and ordinal (c, e, g) models. Predicted values should be interpreted as relative because, to make predictions, 'region' was set to 'northwest' and 'home range size' and 'isolation' set to their median values across all sites. The time period chosen for calculation of climate variables spanned September of 2009 through August of 2019 (a 10-year timespan). To aid visual comparison, survey sites and their status are displayed in the right-hand column.

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Discussion

Historical occurrence records have been underutilized in the pursuit to understand factors shaping species' niches and ranges (Fordham et al. 2020). Here, we used evidence of two unoccupied states (no evidence of prior occurrence, old evidence of occurrence), coupled with observations of present-day occurrences, to reveal otherwise hidden insights into how climate has driven distributional changes in a climate-sensitive species across time. Ordinal models are not new to ecology (Meik and Makowsky 2018, McNellie et al. 2019, Valle et al. 2019, Guisan and Harrell 2000, Cao et al. 2021), and have been used inter alia to analyze spatial patterns of species abundance (e.g. in plants, mosquitoes), population demographic patterns (e.g. fish maturity stages), and the minimum area required for population persistence (Guisan and Harrell 2000, Meik and Makowsky 2018, McNellie et al. 2019, Cao et al. 2021). However, we are unaware of any other study that utilizes these models with temporally-ordered-occurrence states.

Superficially, ordinal models appear similar to dynamic occupancy modeling in which past states (occupied/unoccupied) are accounted for when predicting present-day distributions (MacKenzie et al. 2003, 2017). However, these types of models require being able to assign past occurrences to a specific time period and environmental conditions, whereas ordinal models allow use of past occurrences across an indeterminate time span (for pikas, likely decades to centuries, according to radiocarbon-dating results across the western USA; Millar et al. 2014). Ordinal models are similar to multi-state occupancy modeling (e.g. not occupied < occupied and not breeding < occupied and breeding; MacKenzie et al. 2009), but again differ in the use of temporally ordered historical occurrences. Occupancy modeling also requires repeat visits to sites, whereas data like ours are not amenable to occupancy modeling.

Ordinal versus binary occurrence – what does it give us?

Ordinal models allow for a richer characterization of range dynamics that may be obfuscated by reducing data to a binary 'present/absent' state (Fig. 4). For our model organism, ordinal models indicated the primary importance of chronic-cold conditions (Galbreath et al. 2009), whereas binary models did not (Fig. 3c, d). The directionality of this chronic-cold effect using gridded, coarser-scale PRISM data is opposite of the direction that we have observed elsewhere based on binary analyses of sub-meter-scale (microclimate-sensor) data (Beever et al. 2010). Many other pika investigations – all of which used only binary analyses – have found chronic heat to be the strongest predictor of occupancy (Beever et al. 2010, Calkins et al. 2012, Stewart et al. 2017), mirroring our binary-occurrence results. This discrepancy suggests that coarse-scale, chronically colder conditions benefit pikas, which remain active in the subnivium throughout winter, by retaining the insulative and water-providing snowpack for longer durations (as hypothesized by Smith 1978 and tested by Beever et al. 2011, Johnston et al. 2019). In our top-ranking model, greater likelihood of ordinal occupancy occurred at sites with colder winter-long temperature and greater precipitation during the growing season (Fig. 3a). We hypothesize that these effects may synergistically influence pikas through energy balance, fecundity, and survivorship. As contemporary climate change continues, the annual number of days below freezing without snow cover is projected to increase at mid-latitudes (Zhu et al. 2019), posing an added physiological stressor on subnivean species like pikas.

The results of our analyses and from microclimate sensors across *O. princeps*' geographic range emphasize that differences in the spatial and temporal scales of climate data, as well how response (i.e. occurrence) data are categorized, may lead to divergent conclusions regarding the mechanisms underlying species responses to climate change (e.g. heat stress versus cold stress). Regarding wider context, Erb et al. (2011) re-surveyed in the vicinity of 69 historic collecting records of *O. princeps* across the southern Rocky Mountains (including at n = 6 sites in New Mexico, all of which remained pika-extant in their surveys – mirroring our study's 100% occupancy at the resolution of those sites). Given some historic collectors' tendency to go to high-elevation places where animals were easier to collect, their sites averaged > 315 m higher than our sites; their method also differed markedly from ours, in that if just one individual was found anywhere up to 3 km from the historic location, the entire site was considered pika-occupied. Choosing appropriate resolutions of organism-relevant climate data remains critical, particularly for smaller and dispersal-limited species that more strongly experience fine-scale microclimates (Nadeau et al. 2017). In addition to these data choices, we emphasize that the choice of different model structures appears to strongly affect outcomes.

Application of ordinal modeling assumes data represent a natural ordering from one stage to the next (versus unordered, categorical states; Norušis 2011). In our case, we surmised that 'no-evidence' sites are likely to be currently less suitable than 'previously-occupied' sites, which in turn are less likely to be suitable than currently occupied sites. This assumption appeared confirmed by climatic conditions at the three classes of sites, and also was reflected in the distribution of these classes from low to high elevation (i.e. warm to cold climatic conditions; Supporting information). However, site status can change many times across the period encompassing evidence of past and present occurrence. Thus – and importantly – ordinal models used in this context reflect 'net' change in site status across time along the ordered states. In our case, it is possible for 'no-evidence' sites to transition to 'occupied' if pikas were to colonize them, but very few such cases have been reported in the literature, so the temporal ordering of site status is likely a robust assumption.

Ignoring dispersal limitations can invalidate predictions from species distribution models when a species cannot occupy climatically suitable habitats (Pagel et al. 2020). Pikas, especially, are philopatric and rarely make long-distance

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movements, so we included an isolation term in the modeling. This term appeared in all top-performing models. Following biogeographic predictions, currently occupied sites were the least isolated, previously occupied sites were intermediate, and no-evidence sites were the most isolated (Table 1). This suggests pikas are unlikely to easily cross distances of an increasingly (climatically) inhospitable matrix to colonize 'no-evidence' sites, but instead may be more likely to re-colonize closer, previously-occupied sites (Peacock and Smith 1997). Indeed, all re-colonizations we have observed to date across this domain have been of previously occupied sites. Further, the no-evidence sites in our analyses have climatic conditions that are presumably the most physiologically stressful for this cold-adapted species (Supporting information). Range-wide research has additionally shown that genetic neighborhoods are more restricted and mean observed heterozygosity is lower in warmer and drier areas (Castillo et al. 2016, Schwalm et al. 2016, Supporting information of Beever et al. 2023), strongly implying that such stressful conditions directly limit dispersal distances. Thus, as global change continues apace and additional patch-level losses occur, pika occurrence at a given patch will become iteratively more challenged by a 'triple threat': 1) elevationally rising isotherms will cause patch-level conditions to become increasingly stressful; 2) rates of immigration will decline as climatic conditions in intervening matrix habitats decay relative to pikas' bioclimatic niche; and as a result, 3) distance to the nearest source habitat will tend to increase. Climate change is not uniform across the landscape, however, and extirpations do not always occur at range boundaries (i.e. at lower elevational limits, within our study domain; Oldfather et al. 2020). Identifying and prioritizing high-quality, well-connected patches that will remain macro- and micro-climatically suitable in the future is one viable strategy (Jones et al. 2023). Overall, current and future geographic isolation among patches in metapopulations will likely exacerbate the regional impacts of global change and limit species' abilities to cope with rapidly shifting conditions (Klingler et al. 2023). Although nearest-patch distance may actually decrease when populations become restricted to the areas near summits, geographic and climate-space distance traveled to reach populations on other summits would increase.

Wider applications of ordinal modeling in conservation

Although prior occupancy is much less commonly incorporated into models of species distributions than binary presence/absence data, records of prior occupancy are likely overlooked in many places where they exist. In the same way that a single survey for pikas can quickly indicate both current and former occupancy across decades or longer (Table 3 of Beever et al. 2016, Stewart et al. 2017), many other species leave distinct signatures of former occupancy across the landscape spanning various temporal scales (Jackson et al. 2005, Tingley and Beissinger 2009, Smith 2021). For other species, ordinal models could also be used effectively with historical records (e.g. field notes, museum specimens), organismal remains (including old tree stumps, bones, fossils and ancient or environmental DNA), or archaeological evidences such as human campsites, shelters or depictions in art (Smith 2021). More-recent evidence of past occupancy could also include species-specific landscape modifications including burrows and nests or feces and other excreta.

Ordinal modeling of contemporary- and past-occurrence data also addresses the problem of matching past occurrences to past environmental conditions. Methods for estimating historical dates are less precise than contemporary surveys. For example, unpublished results from radiocarbon dating of pika fecal pellets from our research have date ranges that span up to 432 years. Even if we were able to obtain more precise radiocarbon dates, we expect that many of them could not have been matched to the mechanistically-informed weather indices we used as predictors, owing to the lack of such weather datasets from the longer past (e.g. the PRISM AN81d daily weather product, used here, starts in 1981). Ordinal modeling enables use of historical records or specimens that might otherwise remain unusable.

The purpose for which models are used will determine whether binary or ordinal models are more informative. In our case, binary models had somewhat better discrimination (AUC) and calibration (CBI) accuracy than ordinal models when both were used to predict presence versus absence. Thus, for use cases where the distinction between presence and absence is critical, binary models may be more informative. The lower performance of ordinal models may be due to the increased difficulty in the requirement to simultaneously predict more than two states.

Drawing upon the deeper-time insights provided by past evidences analyzed with ordinal species distribution models can assist in conservation assessments and in designing conservation interventions. For example, our ordinal models identified chronic cold as a driving factor of distributional dynamics of the American pika in the southernmost portion of its range (Fig. 3c). The thermal insulation and snowmelt-water that longer-lasting snowpacks provide likely improve microclimatic suitability for pikas (Johnston et al. 2019, Zhu et al. 2019), so management interventions that enhance snow persistence – such as installation of snow fences – might be considered in select areas (an option not suggested by the binary models). Given that declines in elevational and geographic distribution, occupancy, and abundance have been reported widely (albeit with different magnitudes) across diverse geographies and timescales for *O. princeps* (Galbreath et al. 2009, Stewart et al. 2015, Billman et al. 2021), it remains important that conservation-planning and climate-adaptation efforts be informed by analyses that capitalize on all available information that a given survey can produce. Ordinal models allow use of past states of occurrence, and thus may provide additional insights into the processes that shape species' responses to environmental change. The demonstrated value of incorporating additional occurrence categories from deeper historical periods using ordinal models highlights such models as constituting a promising approach for further informing conservation efforts and climate-change adaptation planning.

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Author contributions

Erik A. Beever and **Marie L. Westover** contributed equally to this publication. **Erik A. Beever:** Conceptualization (equal); Data curation (equal); Funding acquisition (lead); Investigation (equal); Methodology (lead); Project administration (equal); Resources (lead); Writing - original draft (lead); Writing - review and editing (lead). **Marie L. Westover:** Conceptualization (supporting); Funding acquisition (supporting); Investigation (equal); Methodology (supporting); Project administration (supporting); Resources (supporting); Writing - original draft (supporting); Writing - review and editing (supporting). **Adam B. Smith:** Conceptualization (equal); Formal analysis (lead); Methodology (equal); Software (lead); Validation (lead); Visualization (lead); Writing - original draft (supporting); Writing - review and editing (supporting). **Francis D. Gerraty:** Data curation (equal); Investigation (supporting); Methodology (supporting); Resources (supporting); Writing - review and editing (supporting). **Peter D. Billman:** Data curation (supporting); Investigation (supporting); Methodology (supporting); Resources (supporting); Writing - review and editing (supporting). **Felisa A. Smith:** Funding acquisition (supporting); Investigation (supporting); Methodology (supporting); Resources (supporting); Writing - review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.z612jm6n0 (Beever et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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