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Lagomorph Ladders

Assessing a Multi-Host Community and Potential for Spillover of Rabbit Hemorrhagic Disease at Great Sand Dunes National Park and Preserve

Images from Great Sand Dunes National Park and Preserve (clockwise from left): A fall-line transect in the lagomorph ladders study (photo by Samuel Rode), a collection of lagomorph and other scat (photo by Airy Peralta), and an American pika.

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Lagomorph ladders: Assessing a multi-host community and potential for spillover of rabbit hemorrhagic disease at Great Sand Dunes National Park and Preserve

Science Report NPS/SR—2024/126

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Abstract

Rabbit hemorrhagic disease virus type 2 (RHDV2) has caused dramatic declines in rabbits and hares on several continents, with cascading effects on local ecology. Recent mortalities have been reported for several rabbit and hare species in the United States, suggesting broad susceptibility of lagomorphs. If this susceptibility extends to the American pika (*Ochotona princeps*), the most cold-adapted lagomorph, it could compound climate-mediated threats to this species. Due to climate change, American pikas are predicted to experience significant upslope range retraction during this century. Using an analogy borrowed from wildfire scenarios, other lagomorph species occurring at lower and mid-elevations could act as "ladder fuels" to wick RHDV2 into high-elevation pika populations. To address this concern, we investigated spatial patterns of habitat use by pikas and other lagomorphs in Great Sand Dunes National Park and Preserve (GRSA), which borders several counties that have reported RHDV2.

In 2022, we surveyed 115 plots from a spatially balanced sample of pika habitats in the park, including 48 legacy plots from a pika survey conducted in 2010-2012. Pika detections at the plot level were paired with topographic and environmental indices to estimate minimum habitat occupancy and determine its covariates. Leporid (rabbit and hare) detections at these same plots were used to model presence using similar covariates and correcting for imperfect detection. Our best-supported models of pika and leporid presence were then used to estimate the probability of contact between these taxa within the park.

Our mean estimate of pika habitat occupancy was at least 95% during 2022 in GRSA, slightly higher than in 2010-2012, and effects of elevation and precipitation on pika occupancy were as expected from the previous study. Leporid presence at these same plots was 48% after correcting for imperfect detection. The best model of leporid presence supported a negative effect of elevation, in agreement with other studies of these taxa. The best pika and leporid models also included a positive effect of incoming solar radiation.

Finally, we used our best models of pika habitat occupancy and leporid presence within the park to map the potential for areas of contact and RHDV2 transmission between these taxa. Our results indicate some potential for contact within subalpine forests, Specifically in the northern half of the park near the lower reach of the Sand Creek Trail and in the far south just north of California Peak.

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Introduction

"The link between climate change and infectious disease should raise a call to action for scientists and governments to evaluate the risks of inevitable effects of climate change on epidemics and pandemics" — Oliveira and Tegally (2023). This advice, offered in reference to human disease management, is also relevant to disease management in wildlife. Many human diseases have a zoonotic origin, and even those restricted to wildlife can affect humans indirectly through the impairment of ecological services (Monterroso et al. 2016, Paseka et al. 2020).

Currently, the United States is experiencing the rapid spread of a pathogen that affects the Lagomorph community. Rabbit hemorrhagic disease (RHD) is an exotic viral disease little known in the US before 2020 (USDA 2020a). RHDV, the viral agent of RHD, was first reported in China in 1983, and affects primarily the European rabbit (*Oryctolagus cuniculus*), causing such high rates of mortality that it has been used effectively as a biocontrol agent for invasive rabbits in Australia (Mutze et al. 1998). By the late 1990s, RHD had reached enzootic status in many of the countries where domestic and wild European rabbits commonly occur (Mahar et. al 2018). In 2010, a new viral serotype (RHDV2) was reported from France that has proven lethal to multiple lagomorph species and, unlike RHDV, also infects young lagomorphs. RHDV2 has spread rapidly, apparently replacing or coexisting with RHDV in many areas (Mahar et al. 2018, Ramsey et al. 2019). Where RHDV2 has become established, lagomorph populations have declined dramatically, with cascading effects on the larger community (Bruce et al. 2004, Calvete et al. 2004, Calvete et al. 2006, Sarmento et al. 2012, Pedler et al. 2016, Ramsey et al. 2019). Due to its higher pathogenicity, RHDV2 is a biosecurity concern worldwide (Le Gall-Reculé et al. 2013, Capucci et al. 2017).

RHD viruses can survive for long periods in carcasses or on vegetation or other surfaces contacted by infectious hosts. Susceptible hosts can contract the virus directly through contact with infectious hosts or their secretions/excretions, indirectly through contact with shared resources (forage, water, bedding), or through the action of vectors, including blood parasites and flies (McColl et al. 2002, Abrantes et al. 2012, Eden et al. 2015).

RHDV2 arrived in North America in approximately 2016 and spread from Canada to the US within the next two years (Wainwright 2019, Ambagala et al. 2021). Early cases of RHDV2 in the US appeared in domestic rabbits (Wainwright 2019) and were estimated to have cost the American rabbit industry well over two billion dollars (USDA APHIS 2018). The first confirmed detection of RHDV2 in wild lagomorphs occurred in New Mexico; since then, RHDV2 has affected a wide range of lagomorph species native to North America (Cole 2020, Spickler 2020). The ecological costs of this invasion could be dramatic. In Portugal, for example, the high mortality of rabbits caused by RHDV2 disrupted the trophic network hosting the Iberian lynx and the Spanish imperial eagle, two endangered predators that have been the subject of costly reintroduction and conservation efforts (Monterroso et al. 2016).

A potential parallel involves the Canada lynx, which is protected under the US Endangered Species Act and was reintroduced to Colorado in the 1990s (Colorado Parks and Wildlife 2023). Although 250 lynx now roam Colorado's subalpine forests, the success of this reintroduction will ultimately

depend on healthy populations of *Lepus americanus*, the snowshoe hare, which comprises 70% of this predator's diet (Saunders 1963, O'Donoghue et al. 1998). Species in the genus Lepus have been affected by RHDV2 in Colorado, where multiple cases have been reported in wild jackrabbits (Colorado Department of Agriculture 2023). Nevertheless, the impact of RHDV2 on leporid (rabbit and hare) populations is unknown, especially in montane settings like those preferred by snowshoe hares in Colorado (Berg et al. 2012). Identification of sick animals is made primarily through passive sampling of carcasses, and finding carcasses near well-traveled routes within these settings is unlikely (Shapiro et al. 2022). A preference for montane habitats might help to isolate some lagomorphs from highly transmissible diseases like RHD, or might simply delay the introduction of disease and our ability to detect its prevalence and distribution. In this respect, the American pika would be the lagomorph most likely to be isolated by its preference for high-elevation habitats.

The American pika (*Ochotona princeps*), hereafter pika, is a small mammal found in rocky habitats like talus slopes and lava beds from New Mexico to British Columbia. In Colorado, pikas are typically found in alpine habitats (Hafner 1994). The pika is a species of concern due to projections that climate change will cause further range retraction in at least two of Colorado's National Parks. Pikas in Great Sand Dunes National Park and Preserve are predicted to experience a range retraction by mid-century, and pikas in Rocky Mountain National Park could be completely eliminated by the end of the century, given the current climate trajectory (Schwalm et al. 2016).

Climatic threats might soon be compounded by impacts of disease, if RHDV2 can spill over from leporids to pikas. By mid-2021, mortalities attributed to RHDV2 had been reported in several rabbit and hare species of the western US, including black-tailed jackrabbits (*Lepus californicus*), desert cottontails (*Sylvilagus audubonii*), eastern cottontails (*Sylvilagus floridanus*) and mountain cottontails (*Sylvilagus nuttallii*) (USGS 2021). Pikas in Great Sand Dunes National Park and Preserve (GRSA) are surrounded by several counties reporting RHDV2 in leporids (https://ag.colorado.gov/animals/reportable-diseases/rabbit-hemorrhagic-disease-virus-rhdv2). Using an analogy borrowed from wildfire scenarios, other lagomorph species occurring along an elevational gradient might act as "ladder fuels" to wick RHDV2 into pika populations at higher elevations in these landscapes. Losing pikas from these settings would not only reduce the prey available for predators in the alpine, but also alter the available vegetation. The pika is considered an allogenic engineer that regulates nutrient availability by caching food among the rocks, which seeds and fertilizes growth in what otherwise would be a more barren landscape (Aho et al. 1998). Fortunately, these "haypiles" as well as their characteristic scat and frequent vocalizations make pikas relatively easy to detect (Grinnell 1917, Nichols 2010, Jeffress et al. 2013a,b), allowing many studies of range dynamics based on habitat occupancy surveys (Beever et al. 2003, Wilkening et al. 2011, Schwalm et al. 2016, Stewart et al. 2017, Smith et al. 2020).

The purpose of this study was to determine the current distribution of lagomorph populations in alpine and subalpine habitats of GRSA, and to suggest the potential for spillover of RHDV2 among lagomorph populations along an elevational gradient. Therefore, we quantified the use of pika habitats (taluses) by both pikas and leporids that might act as a source of RHDV2, to characterize the spatial overlap of these taxa in the park. This study also presented an opportunity to update estimates

of GRSA pika habitat occupancy developed by Jeffress et al. (2013b), and to provide an early evaluation of trends in occupancy predicted by Schwalm et al. (2016). The Jeffress et al. (2013b) and Schwalm et al. (2016) studies were part of the "Pikas in Peril" project funded by the National Park Service in 2010 (https://www.nps.gov/articles/pikas-in-peril.htm), hereafter referred to as the PIP study. We expanded the PIP study by adding a large number of pika survey plots and by extending each plot into surrounding habitats to determine whether or where habitats occupied by pikas were immediately adjacent to habitats used by other lagomorphs within the park.

Methods

Plot Selection

To expand and improve the spatial balance of the PIP survey in GRSA, we first identified survey plots vetted as suitable pika habitat during that study, and then included those legacy plots in a new draw of plot centers using a Generalized Random Tessellation-Stratified (GRTS) algorithm (Stevens and Olsen, 2004). Our sampling frame included all potential pika habitat throughout GRSA, where pika habitat was defined as taluses and boulder-fields containing at least some individual rocks larger than 50 cm in diameter (longest axis). Because no maps of talus and boulder-fields were available for the park, we used Google Earth imagery to estimate rock sizes and delineate pika habitat polygons (hereafter, talus polygons) throughout the park.

To provide a basis for evaluating the draw in terms of its representation of the variety of pika habitats available, the apparent habitat quality represented by each talus polygon was classified as good, fair, or poor based on professional opinion incorporating the following considerations, in this approximate order: apparent size of the larger rocks in the polygon (bigger was better), area of the polygon (bigger was better), proximity to surrounding polygons (closer was better), surrounding vegetation amount (more was better), surrounding vegetation height (shorter was better), slope (less steep was better), aspect (north-facing was better) and elevation (higher was better). For example, relatively small polygons that were surrounded by forest and filled mostly with rocks smaller than 50 cm were classified as poor, while those comprised of bigger rocks in larger or more closely clustered polygons intermixed with more short vegetation were classified as good. Slope, aspect and elevation were considered but carried least weight in our classifications.

Talus occurred only in the preserve portion of the park (Figure 1), and tended to cluster around the higher peaks in the northern half of the preserve, where most habitat appeared to be good or fair (Figure 1a). Gaps between polygon clusters often represented low-lying drainages, which were relatively devoid of talus. These gaps resulted in apparent clusters of pika habitat that might serve as natural management units, especially if population connectivity and the potential for disease transmission are higher within than between clusters. We designated five spatially distinct clusters of talus polygons (Figure 1b), including two large clusters (Cluster 1 in the northern end of the preserve and Cluster 2 lying largely between Sand Creek and Medano Creek) and four smaller clusters (Cluster 3 near Blueberry Peak one-quarter of the way down the eastern boundary, Cluster 4 just south of Medano Creek, Cluster 5 more than halfway down the eastern boundary, and Cluster 6 at the southern end of the preserve). Within each cluster, the distances between neighboring talus polygons appeared unlikely to pose a serious barrier to pika dispersal, while the distances between most taluses in separate clusters appeared likely to limit population connectivity to some extent. Clusters 5 and 6 were especially isolated from the larger clusters in the northern half of the preserve.

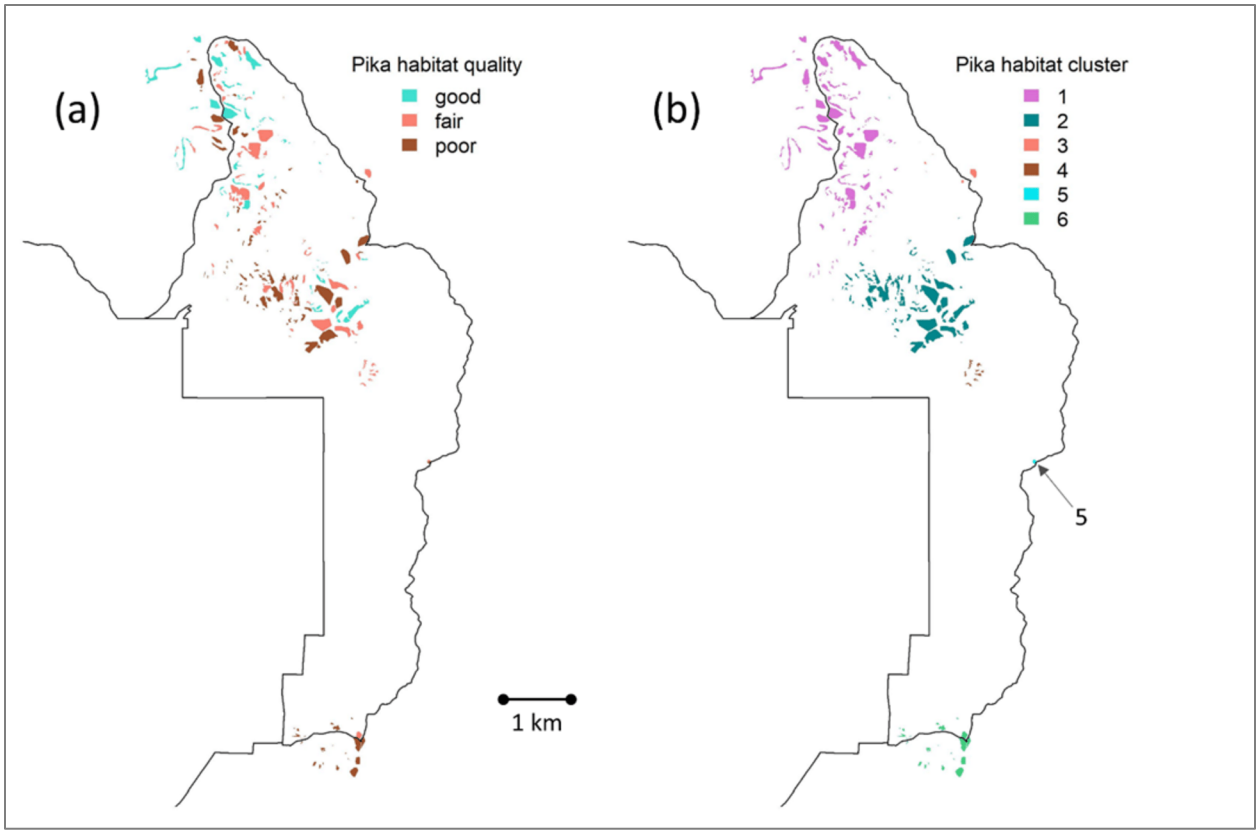

Figure 1. Talus polygons (American pika habitat) within the preserve portion (continuous black boundary) of Great Sand Dunes National Park and Preserve (GRSA), classified by apparent habitat quality (a) and organized into clusters with potentially high internal connectivity (b). Cluster 5 consists of a single, fair-quality polygon on the eastern border of the preserve (see arrow). Talus polygons outside the preserve boundary (top left and bottom center) do not lie within GRSA and were not included in this analysis.

We retained 64 legacy plots and added 122 new plots to improve spatial balance across the park. To ensure representation of all clusters in the current study, separate draws were completed for each cluster (Table 1). Legacy plots occurred only in Clusters 1, 2 and 3, due to logistical constraints on plot access during the PIP study.

The number of plot centers drawn from a cluster was selected based roughly on the total area of its talus polygons. We drew 70 plot centers from each of the two larger clusters and 6-20 from each of the four smaller clusters (Table 1). For each plot center in the draw, two nearby points were drawn that could serve as a replacement in case the original center was not in pika habitat or could not be accessed safely. An oversample was also provided for each cluster to retain spatial balance in the survey design in case neither the original nor replacement centers could be used in certain situations. We also included a 50-m limit on the proximity of any two plots. We did not stratify draws by apparent habitat quality, in part because we were not confident about this metric based on available imagery. However, we used apparent habitat quality to evaluate whether each draw included a representative range of the three habitat quality classes (cf. Figure 1a and Table 1).

Table 1. Number of plots by cluster, type, talus polygon size and talus habitat quality. Legacy plots were retained from the Pikas in Peril study of 2010-2012. Clusters 3-6 contained only 'small' polygons (<5 ha), and Cluster 4 contained only taluses of 'fair' quality.

Cluster	Number of legacy plots [A]	Number of new plots	Plots (%) in small talus polygons	Plots (%) in large talus polygons	Plots (%) in good talus polygons	Plots (%) in fair talus polygons	Plots (%) in poor talus polygons
1	29	41	84	16	39	41	20
2	33	37	60	40	19	24	57
3	2	6	100	0	33	17	50
4	–	20	100	0	0	100	0
5	–	6	100	0	0	50	50
6	–	12	100	0	0	33	67
Totals	**64**	**122**	**–**	**–**	**–**	**–**	**–**

[A] The original PIP identification numbers for legacy plots retained in this study were 0002, 0003, 0005, 0007, 0008, 0014, 0016, 0017, 0018, 0019, 0021, 0028, 0030, 0037, 0040, 0041, 0044, 0046, 0051, 0053, 0057, 0058, 0060, 0062, 0065, 0066, 0067, 0069, 0071, 0072, 0073, 0075, 0076, 0077, 0078, 0081, 0083, 0085, 0092, 0094, 0098, 0101, 0105, 0110, 0115, 0121, 0125, 0130, 0131, 0135, 0137, 0139, 0141, 0142, 0147, 0158, 0165, 0169, 0181, 0185, 0200, 0213, 0241 and 0661.

Talus polygons with smaller areas generally have larger perimeter-to-area ratios, which could enhance pika contact with the non-talus habitats used by leporids. To ensure sampling of these smaller polygons, we stratified draws by polygon area (small versus large) for the two largest clusters, which were dominated by large polygons (Figure 2). For Cluster 1, which contained the largest polygons, small polygons were defined as <10 ha (<100,000 m2); for Cluster 2, <5 ha (<50,000 m2).

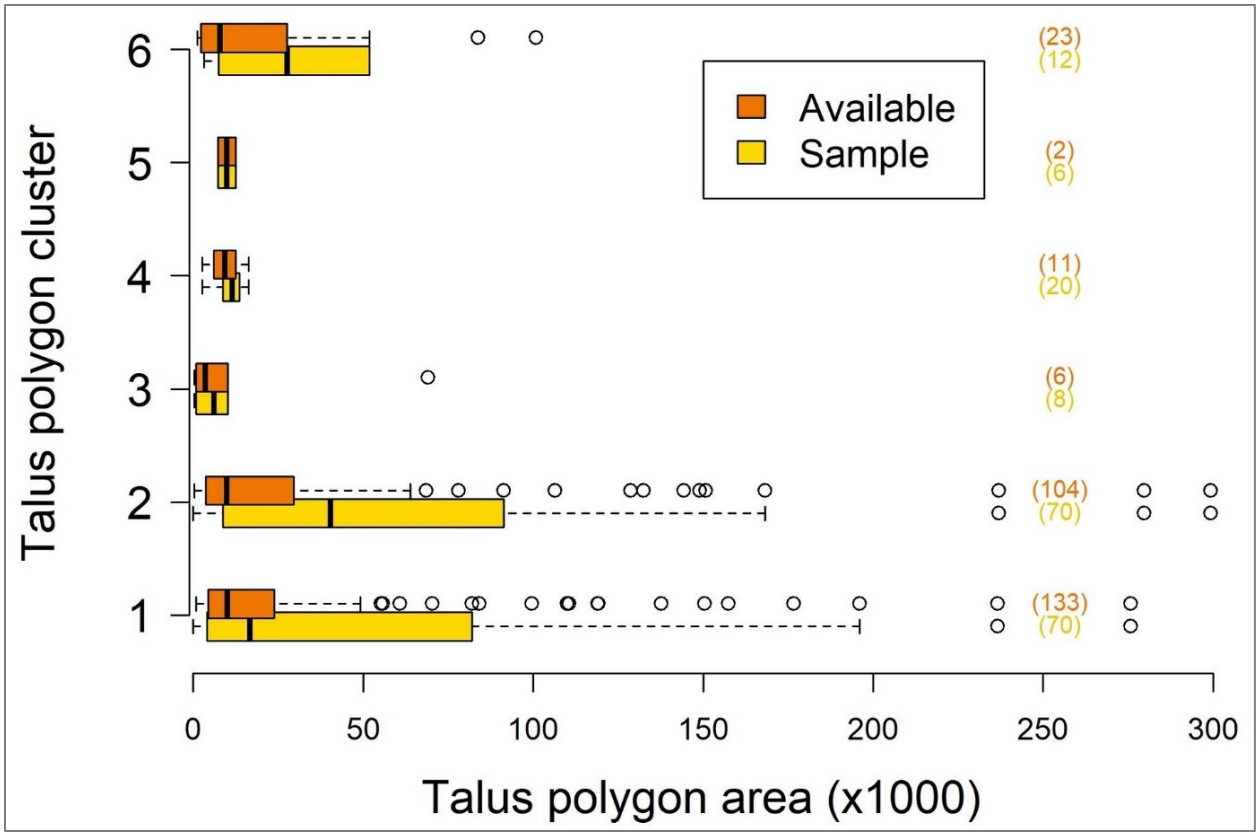

Figure 2. Talus polygon areas sampled by each plot in the GRTS draw (lighter bars) as compared to polygon areas available in the sampling frame (darker bars). Numbers in parentheses on the right represent the number of samples (plots, lighter font) and the number of polygons available (darker font).

Plot Surveys

Our lagomorph survey protocol was designed to support investigation of taxon-specific habitat quality and range dynamics in an occupancy modeling framework (Rodhouse et al. 2010, Jeffress et al. 2013a, Ray et al. 2016), accounting for habitat and community covariates that might affect occupancy as well as survey covariates that might affect detection. To allow estimation of detection probability and to account for imperfect detection in models of pika and leporid occupancy, it would be ideal to conduct repeated surveys at each plot. However, plots were often located in steep and remote locations, requiring long access times and early departures (to avoid lightning), limiting the time available for repeated surveys. For this reason, we targeted a subset (approximately 20%) of plots for double surveys, and we conducted these efficiently by surveying twice during a single visit to each double-survey plot (GRSA Lagomorph Survey Manual 2022).

To standardize pika survey results for comparison with the PIP study, surveys were conducted in summer following protocols (GRSA Lagomorph Survey Manual 2022) based on the well-published pika survey protocol used for the PIP study (Rodhouse et al. 2010; Jeffress et al. 2011, 2013b; Ray et al. 2016). To accommodate surveys for both pikas and leporids, we extended the pika-specific PIP plots described in Jeffress et al. (2013). Each full plot consisted of a circular pika survey plot, extending 12 m in radius from the plot center, plus a pair of leporid survey transects extending

outward an additional 50 m (Figure 3). The crew was trained on site by Chris Ray, who covered all aspects of the survey protocol, including classification of pika sign (haypiles and scat) and leporid sign (scat) as fresh or old. Surveyors were further guided through protocols during data entry using the ArcGIS Survey123 platform (ESRI 2023a).

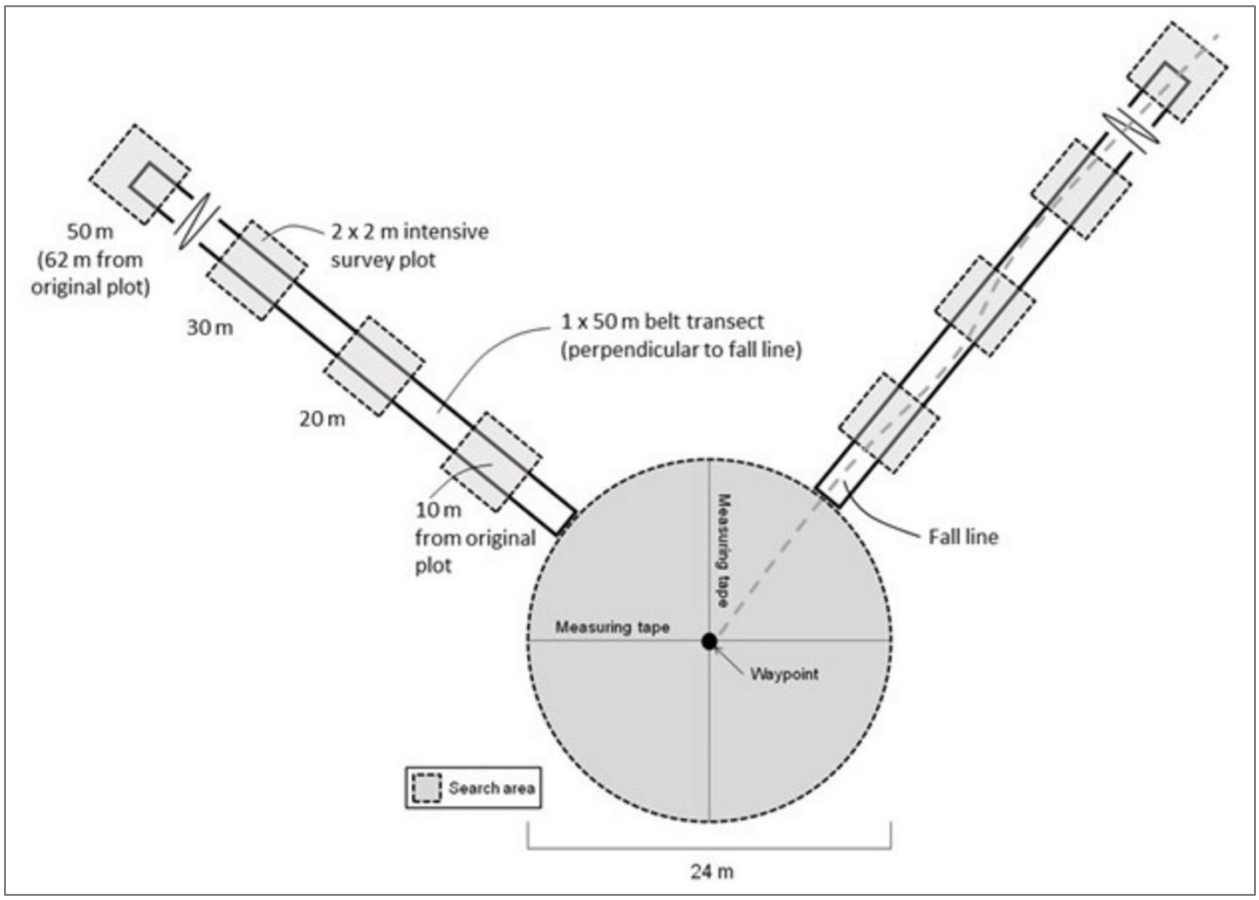

Figure 3. Lagomorph survey plot, including plot center (waypoint), circular pika survey sub-plot and two leporid survey transects (extending along the fall line of the terrain (dashed path) and the other perpendicular to the fall line). Leporid survey transects are shortened here for ease of presentation.

Typically, each plot survey was conducted during morning hours by a crew of two. Following a five-minute (stationary) observation period in which the crew recorded focal species detections by sight or sound, the circular pika plot was systematically surveyed for focal species scat and talus characteristics (depth and clast size) for a period of 20-30 minutes (depending on habitat complexity), while the other crew member recorded habitat characteristics and environmental conditions during the survey as detailed in the GRSA Lagomorph Survey Manual 2022. Each plot record included standardized photographs and data on location, temperature, wind, skies, vegetation (percentage of broad land-cover classes within the plot, including graminoids, forbs, shrubs, trees, talus and barren areas), and standardized evidence of water features in the plot vicinity. Focal species included pikas, marmots, woodrats, weasels, and leporids detected directly (e.g., animal sightings) or indirectly (e.g., through scat or tracks). If the plot was designated for double survey, the two crew

members would reverse roles and repeat the circular sub-plot survey without exchanging information on any survey results.

Following the pika plot survey, each crew member conducted an independent belt-transect survey for lagomorph sign (Figure 3), in keeping with general protocols recommended for rabbit surveys (Lenard et al. 2005, Calvete et al. 2006, Roy Nielsen et al. 2008), as detailed in the GRSA Lagomorph Survey Manual 2022. One belt transect extended 50 m from the pika plot edge along the down-slope fall line, and the other extended 50 m from the pika plot edge perpendicular to the fall-line transect in the direction of highest apparent abundance of shrubs or similar vegetation, offering potential cover for lagomorphs. Each crew member walked outbound along a transect, focusing within ½-meter of the transect centerline (to survey a belt one meter wide by 50 m long), recording the GPS location of each lagomorph sign observed, including taxon (leporid or pika) and sign characteristics, as follow: 1) latrine type as caecal and/or fecal pellets, 2) latrine size as the number (by tens) of pellets separated by 1 m from other latrines, 3) latrine age as a modification of Lenard et al. (2005), where fresh latrines exhibited fecal pellets with at least some greenish-brown coloring, intermediate latrines exhibited tan or grey intact pellets, and old latrines exhibited all pellets with a light-gray coloring and a crumbling consistency.

If neither the circular sub-plot survey nor the outbound belt transect resulted in sign of leporids, then the density of leporid sign along that transect was recorded as negligible, and a more thorough survey was conducted to bolster evidence of presence/absence. The crew member, in this case, conducted a 5-minute survey of a 2x2-m sub-plot centered at the end of the 50-m transect (Figure 3), followed by similar 5-minute surveys of sub-plots centered at 40, 30, 20 and 10 m along the belt transect. These inbound surveys continued toward the plot center until leporid sign was detected or until all 5 square sub-plots were surveyed, whichever came first. Regardless of leporid survey results, vegetation was recorded in each square sub-plot (as for the circular sub-plot) during inbound transit along the belt transect. If the plot was designated for double survey, the two crew members reversed roles and repeated the belt-transect portion of the lagomorph and vegetation survey (outbound and inbound).

Scat Collection

Fecal pellets of both pikas and leporids were collected opportunistically when fresh pellets could be found in quantities suitable for future analyses of species identity or epidemiology. Our scat collection protocol (GRSA Lagomorph Survey Manual 2022) included standard precautions to ensure that each sample contained only pellets that were likely to have been deposited by a single individual (Castillo et al. 2016, Mahar et al. 2018). At double-survey plots, a sample of any fresh pellets encountered was collected after all surveys were complete, using current guidelines for minimizing risk of RHDV2 transfer among plots (e.g., USDA 2020a). At all other plots, fresh pellets were collected as encountered during surveys. Crew members were also encouraged to collect fresh pellets when encountered while in transit to or from plots. Each sample was sealed in a coin envelope, labeled by taxon (pika or leporid) and sampling location (plot ID or GPS coordinates), and transferred to cold storage at the University of Colorado Boulder.

Covariates Selection and Estimation

During each plot survey, we recorded survey covariates such as observer, date, time and conditions (temperature, wind and skies as defined in Table 5 in Appendix A) and plot covariates such as land cover, talus characteristics (rock size and crevice depth), evidence of subsurface ice, and distance to forage. Additional covariates relating to climatic indices and topography were estimated *ex-situ* using digital resources (Table 6 in Appendix A). Briefly, we used a 10-m resolution Digital Elevation Model (USGS 2020b) to calculate slope, aspect, and solar radiation (Table 7 in Appendix A) using ArcGIS Pro (ESRI 2023b). Average solar radiation was calculated both at the plot scale using a 12-m buffer around the plot center, and at the scale of a typical pika genetic neighborhood within GRSA (Castillo et al. 2016) using a 1100-m buffer around the plot center. These two scales were selected to address different ecological processes: solar radiation at the plot scale should influence microclimatic conditions (temperature and snowmelt) that might control the suitability of the plot as part of an individual pika's territory, while solar radiation at the scale of a genetic neighborhood should influence growing-season length and primary production that might control the quality of foraging habitat for a larger population of pikas.

Especially in mountainous terrain, exposure to solar radiation and wind affects the distribution of snow and microclimate, with cascading effects on vegetation structure. Beers et al. (1966) proposed an effect of aspect in mountainous landscapes of western North America that scales from relatively cool and mesic on northeast aspects to warm and arid on southwest aspects. We transformed aspect according to Beers et al. (1966) as one potential covariate of pika and leporid presence, expecting positive covariation with pika presence and negative covariation with the presence of some leporid taxa, such as the mountain cottontail, which prefers xeric, shrubland habitats (Herdman et al. 2017). However, we also considered the potential for processes with less coupled north-south and east-west components, in part because prevailing winds in Colorado come from the west (Doesken et al. 2003). We estimated northern exposure separately from eastern exposure as in Dial (2023):

$$aspect_{radians} = \frac{(aspect_{degrees} \times \pi)}{180}$$

$$slope_{radians} = \frac{(slope_{degrees} \times \pi)}{180}$$

$$northness = \cos(aspect_{radians})$$

$$eastness = \sin(aspect_{radiants})$$

$$northern_exposure = \sin(slope_{radians}) \times northness$$

$$eastern_exposure = \sin(slope_{radians}) \times eastness$$

Downscaled climatic covariates were downloaded from ClimateNA (Wang et al. 2016) using the DEM and the 'Raster to ASCII' tool in ArcGIS Pro to produce the required ASCII file of plot coordinates and elevations. We focused on monthly climate indices from 2021-2022 and normals from 1991-2020 to model single-season presence as a function of climatic conditions at different time scales. Monthly climate indices and other predictors suggested in the literature (Table 6 in

Appendix A) were later used to calculate bioclimatic predictors of occupancy across the park as described in O'Donnell and Ignizio (2012).

Occupancy Modeling

We modeled pikas and leporids separately, based on separate detection histories for each taxon at each plot. The detection history for each plot consisted of one or two values, depending on whether the plot received one or two surveys during 2022. Detection of pikas during a given survey was determined by any of several observations: detection=1 was assigned if the crew observed fresh pika fecal pellets (scat) or fresh hay within the plot, or detected any pika (by sight or sound) within 100 m of the plot center. The 100-m cutoff for pika detection by sight or sound was adopted following Ray et al. (2016), because pikas can quickly move 100 m to forage for preferred vegetation or to access mates or nursery sites, and because it is difficult to detect or estimate the distance to pikas that show themselves or call from more than 100 m away. For leporids, detection=1 was assigned if the crew observed fresh scat or scat of intermediate freshness (hereafter, "fresh scat") along either leporid transect. Other signs of leporid presence (e.g., sightings of live leporids or tracks) were not observed during our plot surveys. We did not attempt to distinguish among leporid taxa, because the specific origin of leporid pellets could not be distinguished reliably in the field. For either taxon, detection=0 was recorded if the crew observed no sign or only old sign (as defined the GRSA Lagomorph Survey Manual 2022) during the plot survey.

We used these detection histories to model detection and occupancy in a single-season framework assuming a closed population for each taxon, facilitated by a short survey season and same-day re-surveys. Occupancy at the plot level was modeled as a logistic response to random and/or fixed effects suggested by our study design and previous lagomorph studies, including PIP analyses of GRSA pika data (Jeffress et al. 2013, Schwalm et al. 2016). We adopted an information-theoretic approach to construct and evaluate the relative support for our candidate models. Given our sample size, we limited each candidate model to a small subset of the potential covariates listed in Appendices' Tables 5 and 6 in Appendix A, and we did not consider interaction effects.

We took several precautions to reduce potential effects of leverage and multicollinearity among our proposed covariates of occupancy. Exploratory data analysis included inspection of the distribution of each potential covariate and its correlation with other covariates that might occur in the same model. Covariates with conspicuous skew were transformed to reduce leverage using the `bestNormalize` (Peterson 2021) in the R platform for statistical computing (R Core Team 2022). Among the normalized covariates were slope12m, rockCover, bareCover, grassCover, forbCover, shrubCover, treeCover, and distance2veg (Table 6 in Appendix A). Multicollinearity largely involved elevation effects on other covariates. For this reason, any covariate x that was highly correlated with elevation (such as climate metrics in Table 5 in Appendix A) was regressed on elevation to obtain residuals that were then used in any models designed to represent effects of both elevation and x (Graham 2003). All covariates were also standardized using the `scale()` function in base R prior to model-fitting procedures, to facilitate the convergence of parameter estimates and the comparison of effect sizes among covariates. After fitting each model, variance inflation factors

(VIF) were inspected using the vif() function in the R package car (Fox 2019) and models were accepted only when the 95% CI of each VIF was below 5.

We accounted for imperfect detection where possible using hierarchical models fitted in maximum likelihood and Bayesian frameworks using several R packages, including unmarked (Kellner et al. 2023), ubms (Kellner et al. 2022), rstanarm (Goodrich et al. 2023), and lme4 (Bates et al. 2015). Our hierarchical models were coupled logistic regressions of the form

$$z_i \sim \text{Bernoulli}(\psi_i)$$
$$y_{ij} \sim \text{Bernoulli}(z_i \times p_{ij})$$
$$\text{logit}(\psi_i) = \alpha_\psi + \Sigma_x (\beta_{\psi x} \times x_i)$$
$$\text{logit}(p_{ij}) = \alpha_p + \Sigma_x (\beta_{px} \times x_{ij}) \ ,$$

where the state variable z_i represents the true occupancy (0 or 1) at plot i, and y_{ij} represents our observed detection of sign (0 or 1) at plot i during survey j (the first or second survey of 2023). In this model, occupancy z_i is modeled as the result of a single-trial binomial process controlled by ψ_i, the expected probability of occupancy at plot i, which in turn is modeled as a logistic function of plot i covariates x_i. Detection y_{ij} is modeled as the result of a single-trial binomial process controlled by p_{ij}, the expected probability of detection at plot i in survey j, which in turn is modeled as a logistic function of plot and/or survey covariates x_{ij}.

Hierarchical models were developed in two steps, beginning with selection of the most parsimonious model of detection probability, $\text{logit}(p_{ij}) = \alpha_p + \Sigma_x (\beta_{px} \times x_{ij})$, with expected occupancy held constant as $\text{logit}(\psi_i) = \alpha_\psi$. Candidate models of detection were based on plot and/or survey covariates such as metrics of vegetative cover that might reduce the visibility of animal sign, and a random effect of observer (Table 5 in Appendix A). To rank these candidate models, we used Akaike's information criterion corrected for sample size (AIC_c; Burnham and Anderson 2002), calculated via the R package aiccmodavg (Mazerolle 2023). We then coupled the best model of p_i to every candidate model of ψ_i, and used AIC_c to select the best overall model. Finally, we used the mb.gof.test() function in the aiccmodavg package to apply MacKenzie and Bailey's goodness-of-fit test for single season occupancy models, which indicates lack of fit for $p < 0.05$ (Mazerolle 2023).

When hierarchical models were not supported, we used the stats package in base R and data from the first survey of 2022 to construct Generalized Linear Models of the form

$$y_i \sim \text{Bernoulli}(\psi_i)$$
$$\text{logit}(\psi_i) = \alpha + \Sigma_x (\beta_x \times x_i) \ ,$$

where symbols are as defined above. This approach can be justified when naïve estimates of occupancy are high and/or the focal species is highly detectable. Regardless, high occupancy and high detection probability result in low statistical power for determining the covariates of detection and/or occupancy, especially when both processes appear in the same model. For these reasons, our GLMs are unlikely to perform well if occupancy declines.

Estimating Occupancy and Co-occurrence of Pikas and Leporids

The best model of pika occupancy in our spatially balanced sample of pika habitat was used to map pika occupancy in taluses throughout the park, based on the spatial pattern of supported covariates and talus. Specifically, we produced rasters representing the spatially varying values of each covariate in the best pika occupancy model, and generated spatially varying predictions of pika occupancy across the park using these rasters and the predict() function from the R package raster (Hijmans 2023). Pika occupancy predictions were then restricted to taluses within the park by applying the mask() function from the raster package to assign zero probability of pika occurrence outside of our talus polygons. The best model of leporid occupancy was projected throughout the park in a similar manner, except that we placed no restrictions on where leporids might occur within the preserve.

Finally, we calculated the joint probability of pika and leporid occupancy in each raster cell of the park as $\psi_{\text{pika+leporid}} = \psi_{\text{pika}} \times \psi_{\text{leporid}}$, which assumes complete independence between pika and leporid distributions. To test this assumption, we added ψ_{leporid} as a covariate in our candidate models of ψ_{pika}, and compared AIC_c values between models with and without a dependence of ψ_{pika} on ψ_{leporid}. We also mapped $\psi_{\text{pika+leporid}}$ across the park, to display any areas of potential contact between these taxa that might have been revealed by our surveys.

Datasets

Field data were collected using a customized Survey123 application (ESRI 2023a) to standardize and (in some cases) automate the data entered, with the goal of reducing errors of omission and commission, by programming each question's appearance and associated response options, constraints and calculations. Inputs were then harvested to populate a flat table of all data described in the GRSA Lagomorph Survey Manual 2022. These data were reviewed and cleaned via custom R scripts. Clean data were exported in delimited format, with metadata in Ecological Metadata Language (EML) format, using a standard template (National Park Service Inventory and Monitoring Division 2023). This archive included plot-level evidence of detection and non-detection of pikas and other focal taxa, habitat conditions including the relative abundance of broad land-cover classes in pika habitats and adjacent areas, and variables used in determining effective survey effort and detection probability of the focal taxa. Spatial data layers were prepared as .tif files documenting talus polygons and occupancy predictions for both pikas and leporids.

Results

In late summer of 2022, we conducted pika and leporid surveys at 115 plots out of 186 plots targeted for survey across GRSA. Steep slopes and trees downed by wildfire slowed survey progress and limited the number of plots that could be accessed given project resources. Survey dates ranged from July 30 to September 3, and all but three surveys occurred during August 2-14. Ninety of the 115 plots were surveyed once and 25 (22%) were surveyed twice, for a total of 140 surveys of 115 plots. Double surveys were conducted during the same plot visit by independent observers.

Detections

Pikas or fresh pika sign were detected during the first (or only) survey in 99 of 115 plots (Figure 4a; Table 8 in Appendix B), resulting in a naïve estimate of 86% occupancy. Conversely, fresh leporid sign was detected during the first survey in 35 of 115 plots (Figure 4b; Table 9 in Appendix C), resulting in a naïve estimate of 30% occupancy for leporids in these habitats (in or immediately adjacent to taluses). At each double-survey plot, detection results were generally similar during the first and second surveys, especially for pika sign. Pika detection differed between the first and second surveys in only one (4%) of 25 re-surveyed plots, while leporid detection differed in six (24%).

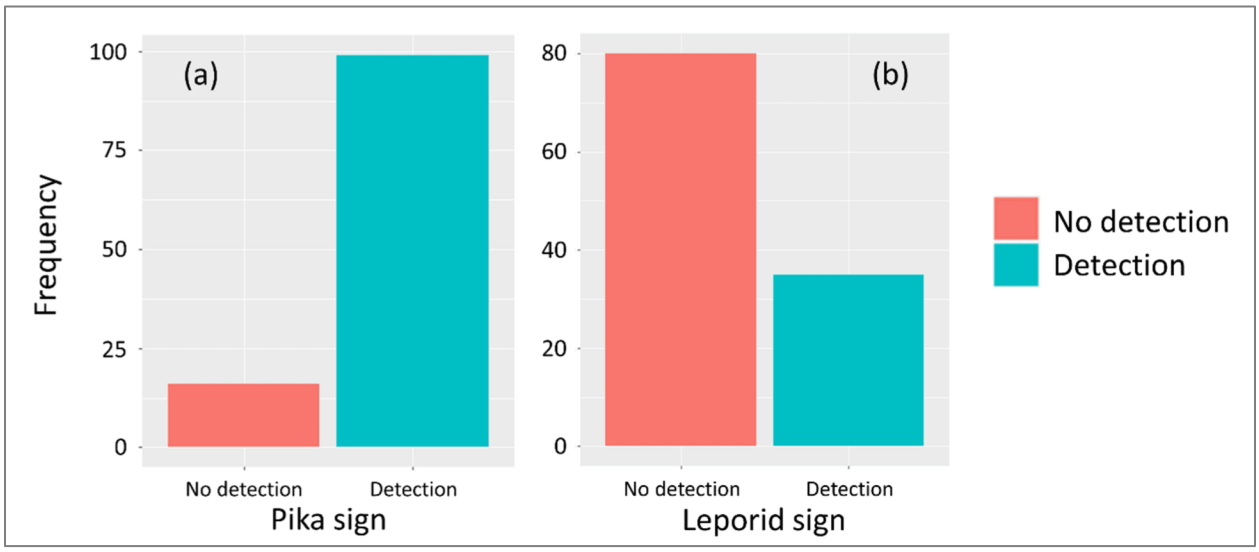

Figure 4. Detection frequencies for pika sign (a) and leporid sign (b) across n=115 pika habitat plots surveyed during late summer of 2022 in Great Sand Dunes National Park and Preserve. Note the change in scale between (a) and (b).

In plots where no fresh sign was detected, we tended to detect no sign at all. In 14 of the 16 plots where survey crews detected no fresh pika sign, they also detected no old pika sign, and in 74 of 80 plots where survey crews detected no fresh leporid sign, they also detected no old leporid sign. Because pika pellets are relatively resistant to decay (Nichols 2010, Millar et al. 2014), an absence of old pika sign might indicate absence of the target habitat (talus); if so, these plots should be omitted from further analyses. However, our *in-situ* plot photos indicated that each plot contained talus apparently suitable for pikas; therefore, all 115 plots were used in subsequent analyses. Because all

plots were centered on talus, it is certainly possible that the 74 plots lacking detection of any leporid sign also lacked suitable leporid habitat. We did not omit these 74 plots from further analyses because our goal was to determine leporid occupancy of pika habitats, whether or not they were leporid habitats. We note also that these apparent absences of leporid sign cannot be due to mistaking scat age, because no leporid scat of any age was found in these 74 plots.

Scat Collection

Fecal pellets were collected on 72 occasions, including 50 pika samples and 22 leporid samples. In 63 cases, samples were collected from surveyed plots; 9 others were collected opportunistically by crew members in transit to or from plots. The number of samples collected from plots scaled roughly with cluster size: 22 from plots in cluster 1, 21 from cluster 2, 3 from cluster 3, 7 from cluster 4, 4 from cluster 5, and 6 from cluster 6. Pellets from each taxon were usually sampled no more than once per plot, but we obtained 2 samples of pika pellets from each of 3 plots (Site1-025, Site1-027 and Site5-005) and 2 samples of leporid pellets from each of 3 plots (Site3-005, Site4-014 and Site6-002). Samples from the same plot and taxon might derive from the same individual, so a more conservative estimate of sample sizes would be 47 pika and 19 leporid samples available for genetic or epidemiological analyses.

The distribution of detections across the park suggested that the distribution of pikas was nearly a mirror image of the distribution of leporids during our survey (Figure 5). These taxa appeared to separate along elevational gradients throughout the park.

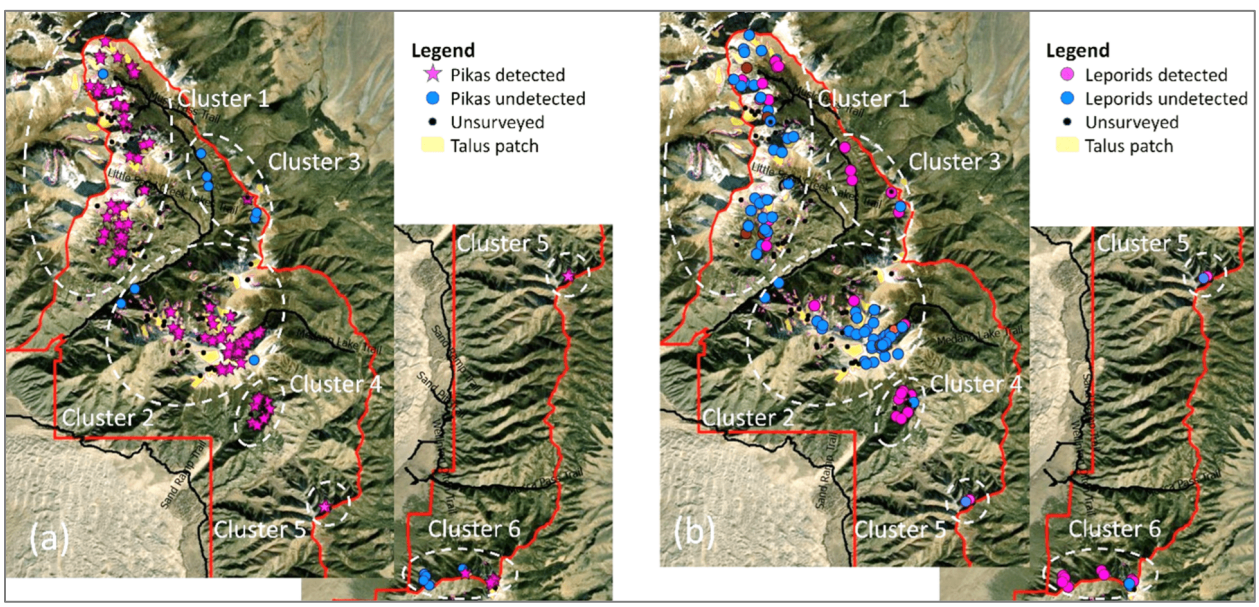

Figure 5. Distributions of pika (a) and leporid (b) detection throughout Great Sand Dunes National Park and Preserve in late summer of 2022. Each map was split near pika habitat cluster 5 to create a more compact figure, so cluster 5 appears twice in each panel for reference.

Exploratory Analyses

Visual summaries relating detections to plot covariate values verified that many of the covariates suggested in the literature might be useful in modeling the occupancy of these taxa. Covariates that clearly differed between detection and non-detection plots are presented in Figures 11 to14 in Appendix D (pika summaries), and Figures 15 to 17 in Appendix E (leporid summaries). Pika detections generally occurred in plots at higher elevations (above about 3375 m) with lower temperatures, higher precipitation throughout the year, and less seasonality in precipitation (Figures 11 to 14 in Appendix D, panels a, c, and e). Plots where only old pika sign was found were rare (n = 2) but might be of intermediate quality, so we summarized them separately (Figures 11 to 14 in Appendix D, panels b, d and f); these old-sign plots were more similar to fresh-sign plots than no-sign plots with respect to elevation, temperature and precipitation, but more similar to no-sign plots with respect to seasonality in precipitation. In contrast with pika detections, leporid detections generally occurred in plots at lower elevations (below about 3550 m) with lower precipitation, higher temperatures and more seasonality in precipitation than those where no leporid sign was found (Figures 15-17 in Appendix E). Leporid sign was also found more often where there was more tree cover (Figure 15b in Appendix E).

Pika Occupancy

Given our realized sample size (n = 115), we limited each candidate model to no more than eight fitted parameters, allowing for intercepts of detection and occupancy plus up to six fixed and random effects, including potential random effects of plot and/or observer and fixed effects of plot and/or survey covariates. However, we could not fit hierarchical models to the pika data, regardless of model structure or fitting procedure (described in *Occupancy modeling* above). The high number of detections in our dataset, combined with a low number of double surveys, gave our models little power to distinguish between the separate processes of detection and occupancy.

In previous studies, pika detection probabilities have regularly exceeded 90% (Beever et al. 2010, Erb et al. 2011, Jeffress et al. 2013, Ray et al. 2016) due to their territorial vocalizations, haypiling activity and conspicuous latrines. This pattern, combined with our current finding of high minimum occupancy (86%), suggests that relatively unbiased estimates of pika occupancy can be obtained for this study without accounting for imperfect detection. Therefore, we used a set of logistic regressions, each based on up to six fixed effects from Table 6 in Appendix A, to model pika occupancy during our survey. A random effect of observer (Table 5 in Appendix A) was also considered, but was not supported by the data, resulting in (singular/boundary effect) estimates of zero observer effect. All models of pika occupancy with support equal to or higher than the null model are presented in Table 10 in Appendix F.

Our best model of pika occupancy included effects of elevation, precipitation and insolation (Table 2). With each covariate held at its mean value, this model produced a naïve occupancy estimate of 95%, with CI_{95} = (0.88,0.98) being the 95% confidence interval on the probability scale. The top nine models of pika occupancy included a positive effect of elevation, and 99% of the weight of evidence went to models that included elevation as a covariate (Table 10 in Appendix F). The top nine models ($\Delta AIC_c \leq 5.17$) also included positive effects of precipitation. However, we focus here on the best

model (with lowest AIC_c), which was highly supported (Akaike weight = 0.31) relative to all other models (Akaike weight ≤ 0.16). In the best model, the fitted coefficients of our standardized covariates suggest that the effect of elevation (mean estimate ± SE = 1.82 ± 0.47) was almost ten times stronger than the effect of precipitation (0.19 ± 0.40) and three times stronger than the effect of insolation (0.61 ± 0.39). The precipitation covariate was based on total precipitation during June-August of the previous year (precipTotalWarmQtrLag1, Table 6 in Appendix A; hereafter, lagged summer precipitation); specifically, precipTotalWarmQtrLag1 was the residual of lagged summer precipitation regressed on elevation, to eliminate collinearity in this model. The insolation covariate was incoming solar radiation at the scale of the genetic neighborhood (solRad1100m, Table 6 in Appendix A).

The sign of precipitation effects varied among top models. A positive effect of lagged summer precipitation appeared in two of the three top models ($\Delta AIC_c > 2$), and 72% of the weight of evidence went to models that included lagged summer precipitation as a covariate (Table 10 in Appendix F). However, the second-best model included not a positive effect of lagged summer precipitation but an opposing, negative effect of a seemingly similar covariate, the normal (1990-2020 average) total precipitation during the warmest quarter (precipTotalWarmQtrNormal, Table 6 in Appendix A; hereafter, normal summer precipitation). Overall, only 18% of the weight went to models that included normal summer precipitation, so the apparently positive effect of summer precipitation in 2021 on pika occupancy in 2022 had much greater support than the apparently negative effect of long-term average summer precipitation.

The sign of insolation effects varied between spatial scales. The top two models included a positive effect of insolation at the scale of the genetic neighborhood, and 59% of the weight of evidence went to models that included this effect. However, 27% of the weight went to models that included an opposing, negative effect of insolation at the plot scale (solRad12m, Table 6 in Appendix A), including three models with some support ($\Delta AIC_c < 4$).

The remaining effects in top models were a (combined) negative linear and positive quadratic effect of slope at the plot scale (slope12m, Table 6 in Appendix A), and a negative effect of northeast-facing aspects within the plot (northeastness, Table 6 in Appendix A). The combination of negative linear and positive quadratic slope effects suggests that (apparent) occupancy fell with increasing slope until it reached a relatively static minimum at higher slope angles. The weight of evidence for all models containing linear and quadratic effects of slope at the plot scale was 27%. Northeastness appeared in only one model with any support, having a weight of 15%, so this (counterintuitive) negative effect was the least supported among effects in the top models.

Table 2. Supported models of pika occupancy (*y*, uncorrected for imperfect detection) based on single surveys of 115 plots conducted in late summer of 2022 at Great Sand Dunes National Park and Preserve. Each model represents a logistic regression of pika detection (0 or 1) as a function of covariates described in Tables 5 and 6 in Appendix A.

Pika occupancy model	**DF [A]**	**AIC_c [B]**	**ΔAIC_c [C]**	**Akaike wt [D]**
logit(*y*) ~ elevation + precipTotalWarmQtrLag1 + solRad1100m	4	57.16	0.00	0.31
logit(*y*) ~ elevation + precipTotalWarmQtrNormal + solRad1100m + slope12m + slope12m^2	6	58.45	1.29	0.16
logit(*y*) ~ elevation + precipTotalWarmQtrLag1 + northeastness	4	58.69	1.53	0.15
logit(*y*) ~ elevation + precipTotalWarmQtrLag1 + solRad1100m + slope12m + slope12m^2	6	59.28	2.12	0.11
logit(*y*) ~ elevation + precipTotalWarmQtrLag1 + solRad12m	4	59.50	2.34	0.10
logit(*y*) ~ elevation + precipTotalColdQtrLag1 + tempColdQtrLag1 + solRad12m	5	60.24	3.08	0.07
logit(*y*) ~ elevation + precipTotalWarmQtrLag1 + tempWarmQtrLag1 + solRad12m	5	60.94	3.78	0.05

[A] Degrees of freedom used in model fit.

[B] Akaike's information criterion corrected for small sample size.

[C] Difference in AIC_c values between a given model and the best model (with lowest AIC_c).

[D] Weight of evidence in support of a given model (a function of ΔAIC_c).

Leporid Occupancy

As for pika occupancy models, we limited each candidate model of leporid occupancy to no more than eight fitted parameters, allowing for intercepts of detection and occupancy plus up to six fixed and random effects, including potential random effects of plot and/or observer and fixed effects of plot and/or survey covariates. We were able to fit hierarchical models to the leporid data, despite the low number of double surveys, perhaps partly due to the more equitable numbers of detections and non-detections of this taxon.

During surveys, crew members noticed that leporid scat was easier to locate in plots with lower cover of graminoids and forbs, and these areas often supported sparse shrubs with a canopy high enough to allow increased visibility of fecal pellets on the ground or in the duff under the canopy. For this reason, vegetative cover variables (Table 6 in Appendix A) were included in candidate models of leporid detection, along with other survey variables that might affect detection (Table 5 in Appendix A). All candidate models of leporid detection are listed by rank in Table 11 in Appendix F, where each model includes a mean, intercept-only model of occupancy.

All top models of leporid detection included a positive effect of shrub cover (shrubCover, Table 6 in Appendix A), and 84% of the weight of evidence went to models containing shrubCover, while other covariates garnered much less weight: grassCover, 51%; forbCover, 18%; temperature, 17%; temperature2, 17%; surveyTime, 1%; bareCover, 1%; rockLargest, 1%; rock10thLargest, 1%; and <0.5% for skies, (Tables 5 and 6 in Appendix A). The best model of leporid detection included a positive effect of shrub cover, a negative effect of graminoid cover (grassCover, Table 6 in Appendix A), and a random effect of observer (Table 5 in Appendix A). Both shrub and graminoid cover tended to be low across our surveyed plots (Figure 6 a and b), so their effects were likely due to results from just a few plots. Leverage might be more important in the effect of shrub cover than in the effect of graminoid cover, because our attempts to reduce the skew in these data (by applying a normalizing transformation) were less successful for shrub cover (Figure 6c) than for graminoid cover (Figure 6d). The random effect of observer was supported by all the models. The models suggest that different observers have different levels of variability in their ability to detect pika sign. However, the difference between AIC_c of the mean model (~ 1 ~1 in Table 11 in Appendix F, AIC_c = 167.16) and a model based solely on the observer effect (AIC_c = 165.14) differ by only two units, suggesting that models based on the observer effect were just as well-supported as the mean model. We also considered a random effect of plot on detection, but that effect explained no variance and led to the highest AIC_c (Table 11 in Appendix F).

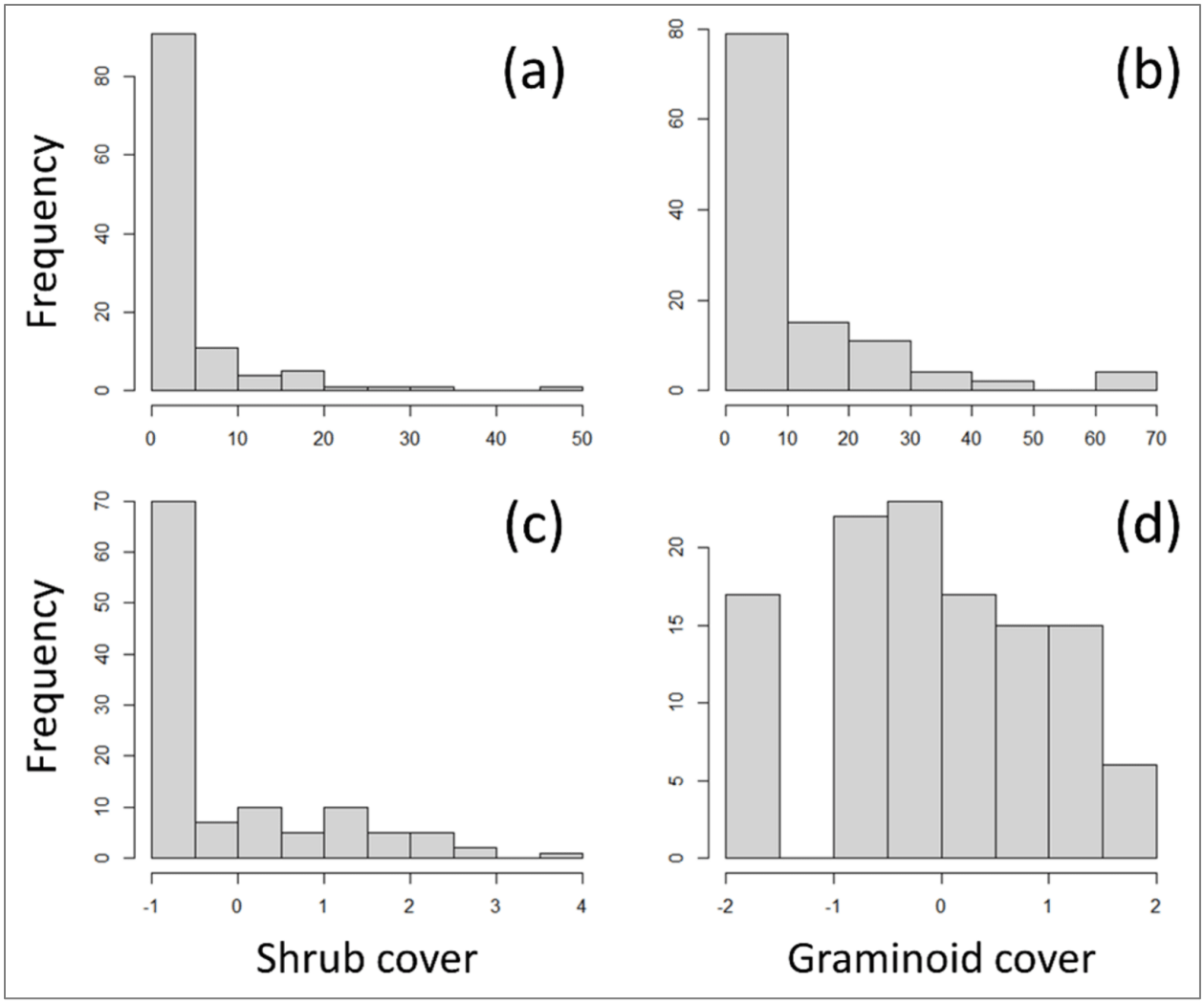

Figure 6. Histograms of shrub and graminoid cover estimates from late summer of 2022 for 115 plots in Great Sand Dunes National Park and Preserve. Raw estimates of percent cover appear in (a) and (b). Values in (c) and (d) were transformed to reduce skew.

We considered models of leporid occupancy based on up to three covariates, so as not to exceed a total of eight fitted parameters per hierarchical model, including three covariates in the detection model (shrubCover, grassCover and observer) and intercepts of detection and occupancy. All models of leporid occupancy with support equal to or higher than the null model are presented in Table 11 in Appendix F, and every supported model ($\Delta AIC_c < 4$) is presented in Table 3. Every supported model included a negative effect of elevation on leporid occupancy, and 100% of the weight of evidence went to models containing elevation. Other covariates (defined in Table 6 in Appendix A) garnered no more than 10% of the weight: solRad12m, 10%; precipTotalAnnualLag1, 8%; northern_exposure, 8%; tempColdQtrLag1, 8%; potsnowLag1, 8%; tempWarmQtrLag1, 7%; potsnowNormal, 6%; eastern_exposure, 6%; precipSeasonalityLag1, 5%; grassCover, 5%; forbCover, 4%; shrubCover, 4%; northeastness, 4%; precipTotalWarmQtrLag1, 4%; slope12m, 3%; and slope12m^2, 3%. The best model of leporid occupancy included a negative effect of elevation and a positive effect of

solRad12m, although 13 models with similar support included elevation by itself or elevation and one of the following: a positive effect of precipTotalAnnualLag1, potsnowLag1, potsnowNormal, eastern_exposure, shrubCover, or forbCover, or a negative effect of northern_exposure, tempColdQtrLag1, precipSeasonalityLag1, tempWarmQtrLag1, northeastness, precipTotalWarmQtrLag1, grassCover, or (linear and quadratic) slope12m (the negative effect of slope angle was stronger for steeper slopes).

Table 3. Supported hierarchical models of pika plot occupancy by leporids, based on single surveys of 90 plots and double surveys of 25 plots conducted in late summer of 2022 at Great Sand Dunes National Park and Preserve. Each model represents a logistic regression of the probability of occupancy (ψ) conditional on detection, where the probability of detection (p) was modeled as logit(p) ~ shrubCover + grassCover + (1|observer), and covariates of both ψ and p are as defined in Tables 5 and 6 in Appendix A.

Leporid occupancy model	**DF** [A]	**AIC$_c$** [B]	**ΔAIC$_c$** [C]	**Akaike wt** [D]
logit(ψ) ~ elevation + solRad12m	7	130.21	0.00	0.10
logit(ψ) ~ elevation	6	130.26	0.05	0.10
logit(ψ) ~ elevation + northern_exposure	7	130.53	0.32	0.08
logit(ψ) ~ elevation + precipTotalAnnualLag1	7	130.56	0.34	0.08
logit(ψ) ~ elevation + potsnowLag1	7	130.74	0.53	0.08
logit(ψ) ~ elevation + tempColdQtrLag1	7	130.75	0.54	0.08
logit(ψ) ~ elevation + tempWarmQtrLag1	7	130.94	0.73	0.07
logit(ψ) ~ elevation + potsnowNormal	7	131.08	0.87	0.06
logit(ψ) ~ elevation + eastern_exposure	7	131.36	1.15	0.06
logit(ψ) ~ elevation + precipSeasonalityLag1	7	131.48	1.27	0.05
logit(ψ) ~ elevation + grassCover	7	131.72	1.51	0.05
logit(ψ) ~ elevation + forbCover	7	131.98	1.77	0.04
logit(ψ) ~ elevation + northeastness	7	131.99	1.78	0.04
logit(ψ) ~ elevation + shrubCover	7	132.04	1.83	0.04
logit(ψ) ~ elevation + precipTotalWarmQtrLag1	7	132.07	1.86	0.04
logit(ψ) ~ elevation + slope12m + I(slope12m^2)	8	132.42	2.21	0.03

[A] Degrees of freedom used in model fit.

[B] Akaike's information criterion corrected for small sample size.

[C] Difference in AIC$_c$ values between a given model and the best model (with lowest AIC$_c$).

[D] Weight of evidence in support of a given model (a function of ΔAIC$_c$).

The best model of leporid occupancy (Table 4) indicated no lack of fit according to MacKenzie and Bailey's goodness-of-fit test (p = 0.20). Using this model, mean detection probability (p) was estimated as 0.55, with SE = 0.19 and CI_{95} = (0.21,0.85), while mean occupancy probability (ψ) was estimated as 0.48, with SE = 0.04 and CI_{95} = (0.38,0.73).

Table 4. Parameter estimates in the top-ranked hierarchical model of leporid occupancy.

Model	Parameter	Estimate	Standard Error	Z-Value	P(>|z|)	Variance	Standard Deviation
Occupancy	Intercept	0.88	0.70	1.25	0.21	–	–
	Elevation	-5.19	1.69	-3.06	0.00	–	–
	solRad12m	0.69	0.51	1.34	0.18	–	–
Detection – fixed effects	Intercept	0.28	0.41	0.67	0.50	–	–
	shrubCover	0.22	0.30	0.76	0.45	–	–
	grassCover	-0.54	0.37	-1.48	0.14	–	–
Detection – random effect	Observer (Intercept)	–	–	–	–	0.55	0.74

Overlap In Habitat Use by Leporids and Pikas

Given the opposing effects of elevation on occupancy of these taxa, there might also be an inverse relationship between pika and leporid occupancy—a pattern that could be caused by direct competition for resources or apparent competition due to shared predators or disease. We tested for this pattern by replacing elevation with ψ_{leporid} as a covariate in univariate and multivariate models of ψ_{pika}; however, none of these models were supported (all $\Delta AIC_c > 4$). Therefore, we proceeded to predict joint occupancy under the assumption that pika and leporid occupancy were independent events.

We predicted leporid occupancy across the preserve by applying the predict() function from the unmarked package on our best model of leporid occupancy, which was based only on elevation, and a mean-centered version of the 10-m DEM clipped to the preserve boundary within GRSA. Although this approach produced a spatially complete prediction of leporid occupancy across the preserve (Figure 7), these predictions might be biased at locations outside our sampling frame, which was restricted to within about 60 m of each talus patch within the preserve. We predicted pika occupancy in a similar manner by applying the predict() function from the raster package on 10-m rasters of elevation, precipitation and insolation clipped to the preserve boundary. As in the best model of pika occupancy, precipitation entered this model as the residuals of lagged summer precipitation regressed on elevation, to eliminate collinearity with elevation, and insolation was defined as incoming solar radiation at the scale of the genetic neighborhood. This approach produced a complete raster of pika occupancy predictions across the preserve, with 10-m resolution, which we masked using our talus polygons, assigning zero probability of occupancy to any non-talus raster cell (Figure 8).

Figures 7 and 8 display the plot-specific expected probabilities of leporid and pika occupancy, respectively. Using these estimates of ψ_{leporid} and ψ_{pika}, we calculated the joint probability of these presumably independent events as $\psi_{\text{leporid}} \times \psi_{\text{pika}}$, to find the areas of highest potential overlap between these taxa. The maximum probability of overlap was 0.46, and there were just two areas with probability > 0.05 of supporting both pikas (in taluses) and leporids (adjacent to taluses): 1) in the northern half of the preserve near the southern portion of the Sand Creek trail, and 2) near the southern border of the preserve just north of California Peak (Figure 9).

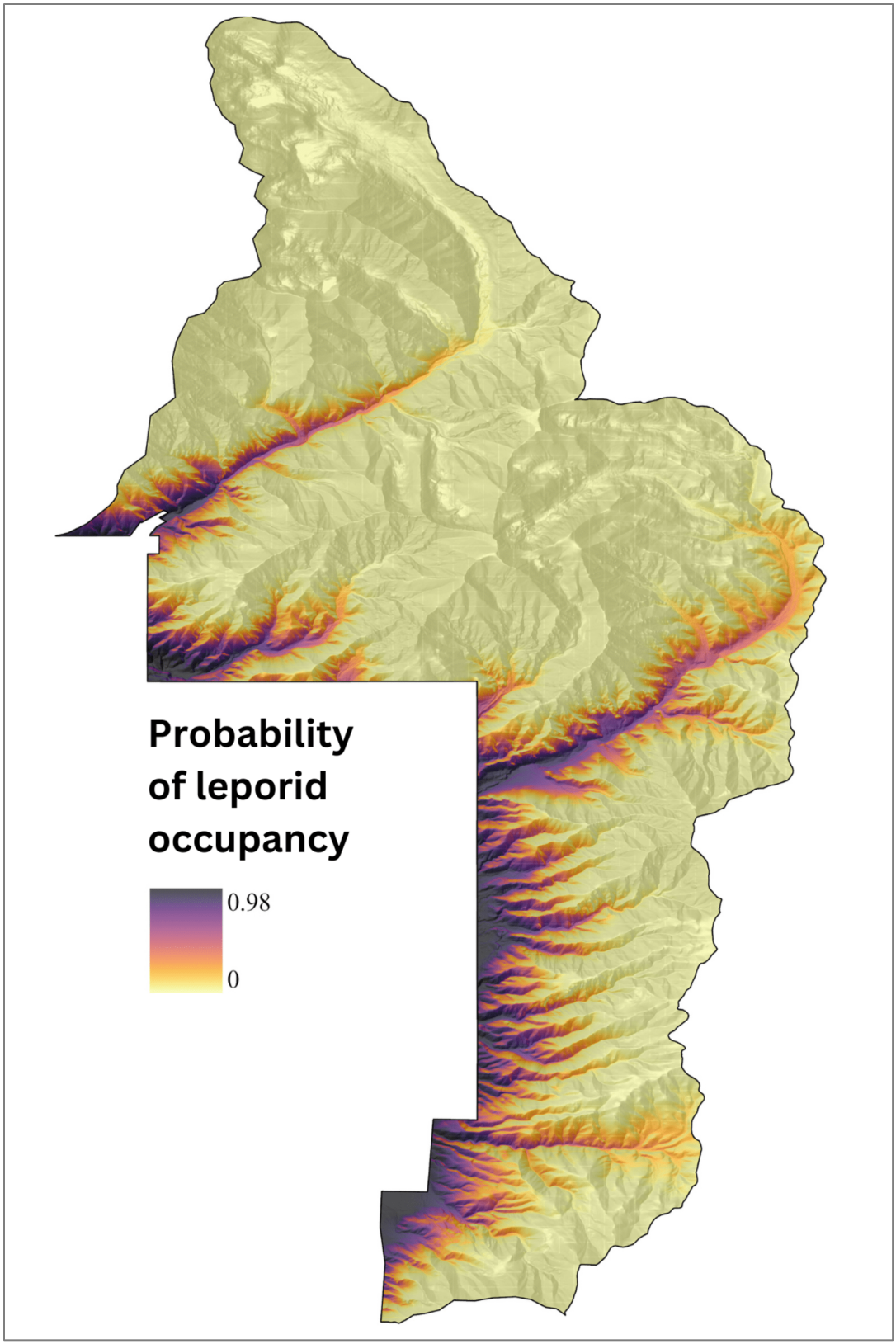

Figure 7. Predictions of 2022 leporid occupancy within the preserve boundary of Great Sand Dunes National Park and Preserve, based on the model in Table 4.

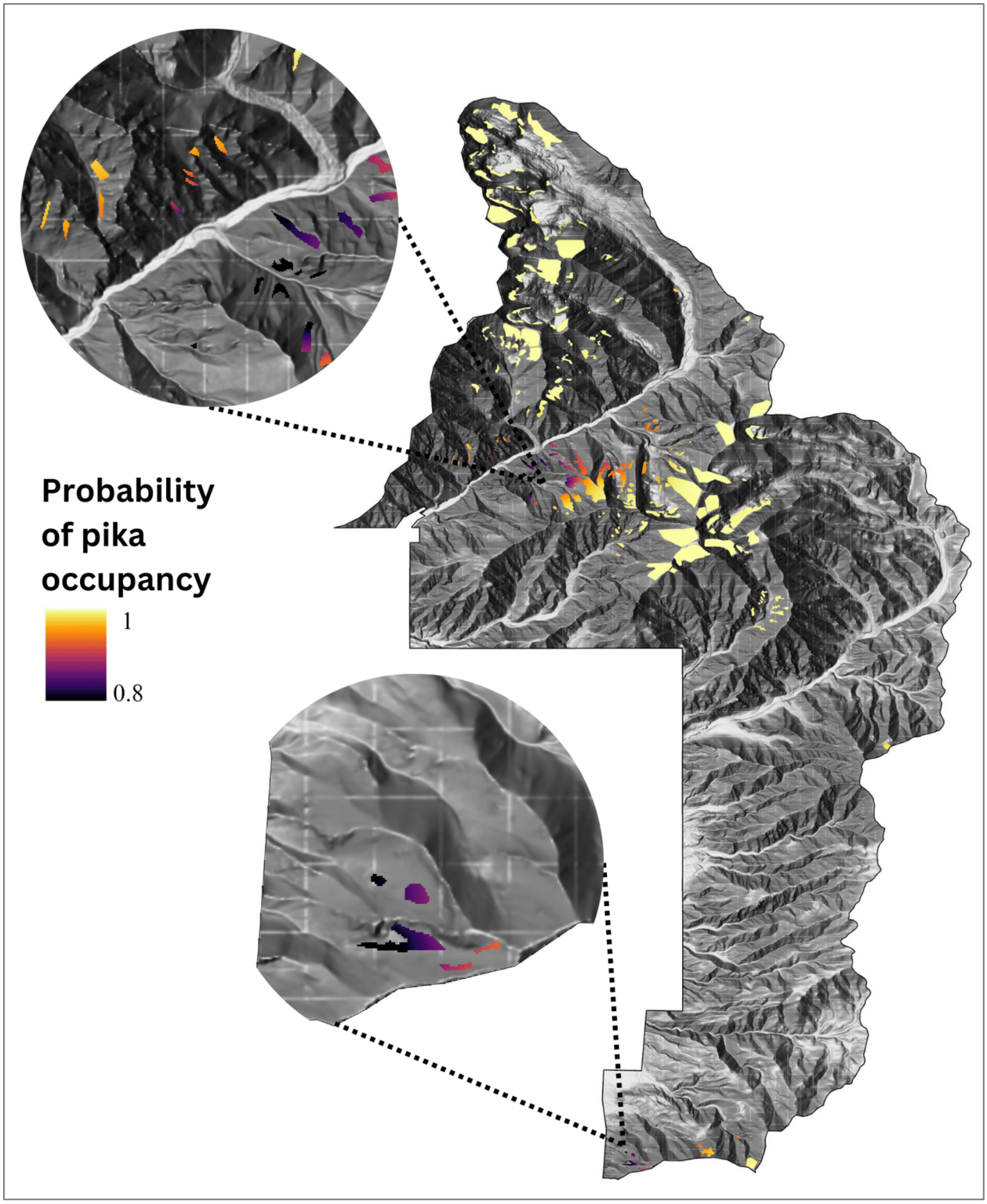

Figure 8. Predictions of 2022 pika occupancy within the preserve boundary of Great Sand Dunes National Park and Preserve, based on the top model in Table 2.

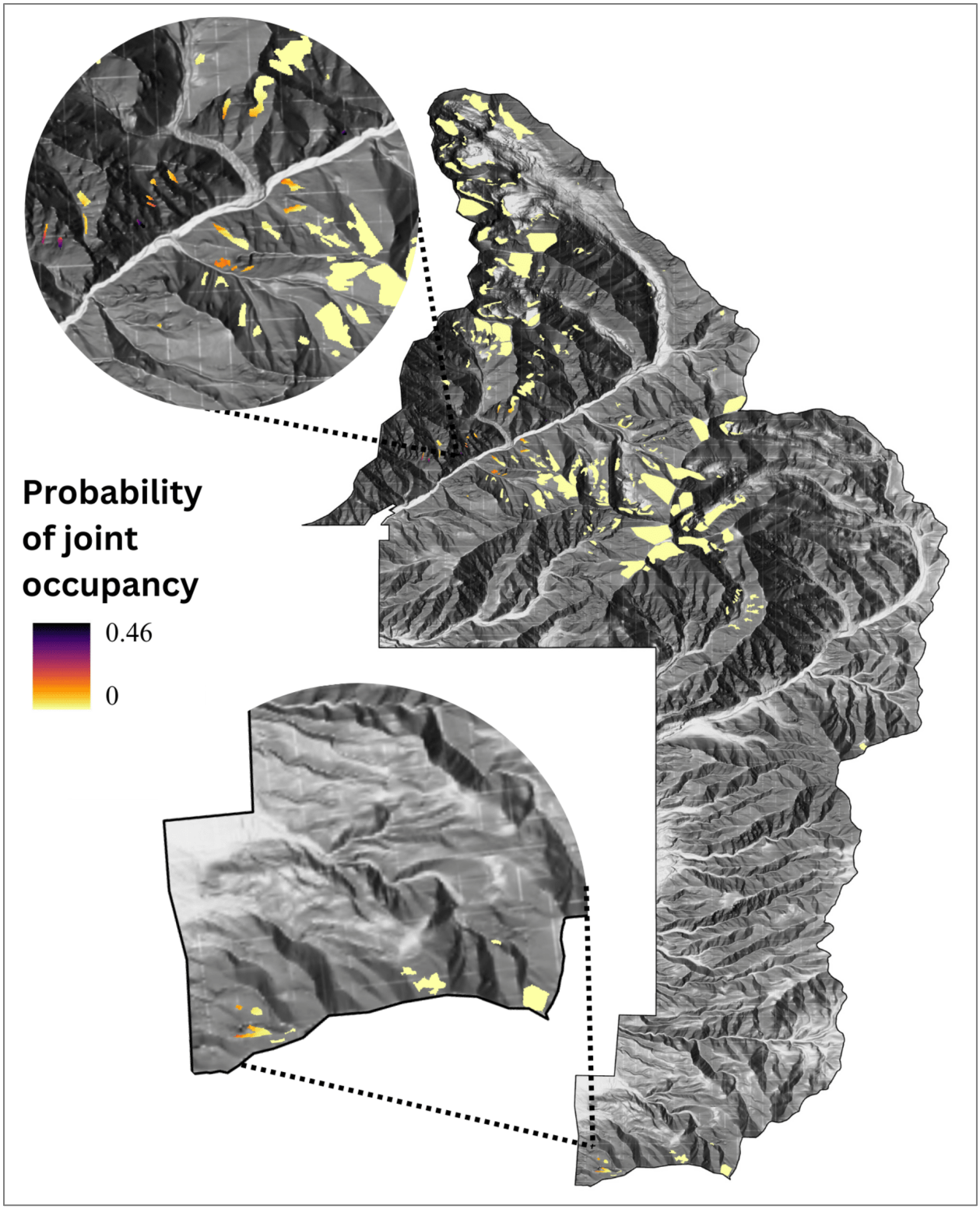

Figure 9. Predictions of 2022 occupancy of both pikas and leporids within the preserve boundary of Great Sand Dunes National Park and Preserve, based on the top models in Tables 2 and 3, emphasizing the only two areas with probability > 0.05 of supporting both pikas in taluses and leporids in habitats immediately adjacent to taluses.

Discussion

The primary goal of this study was to assess whether there have been recent declines in pika habitat occupancy within GRSA that might be explained by disease spillover within the lagomorph community based on the spatial configuration of pika losses and habitat shared with other lagomorphs. We did not find evidence of recent pika decline, or of dependence between pika occupancy and leporid occupancy. Even our naïve estimates of pika habitat occupancy in 2022 trended higher than similar estimates from the 2010-2012 PIP study. We also found limited evidence of potential contact between pikas occupying taluses and leporids in the immediate vicinity of those taluses. These taxa separated largely along the strong elevational gradient within the preserve, with pikas occurring at higher elevations and all other lagomorphs limited to lower elevations. Although it appeared during our surveys that this pattern might be related to canopy cover, with leporids occurring below and pikas occurring above treeline, elevation rather than treeline (biome) was the primary predictor of occupancy for both taxa.

Context and Interpretation of Current Results

Our estimate of pika habitat occupancy was high (95%), and the best-supported covariate of pika occupancy was elevation, a covariate supported in previous studies of pika occupancy in this park and in other parks where annual precipitation is low (Jeffress et al. 2013b). The top model of pika occupancy suggested effects of elevation combined with lagged summer precipitation and average solar radiation measured at the scale of the genetic neighborhood. Although effects of precipitation and insolation received low relative support, each has been supported in previous studies. Lagged summer precipitation was supported in the PIP model of pika vulnerability to climate change in GRSA, where it was proposed as a driver of forage availability and quality (Schwalm et al. 2016). Also, climatology tells us that precipitation has a cooling effect, especially during the warm season (Geiger et al. 1995), so summer precipitation might reduce exposure of pikas to extreme heat.

The relationship between pika occupancy and insolation might be more complex. Jeffress et al. (2013) assessed the effect of total incoming solar radiation using the northeastness covariate at the plot scale and found a negative relationship with pika occupancy at that scale, suggesting that northeast-facing slopes allow pikas to escape summer heat stress. While our third-ranked model is in agreement with that study, models ranked 1, 2, and 4 suggest that the effect of insolation is also positive at the larger scale of a pika's genetic neighborhood in GRSA. This result might not necessarily mean that pikas are more suited to southern slopes in the preserve; rather, we suggest that slopes receiving a higher amount of indirect and direct solar radiation at large scales might provide more food for pikas due to increased net primary productivity (NPP) and early snowmelt (Morrison et al. 2009). A study in pika habitat on the Tibetan Plateau (Zheng et al. 2020), which is located near the same latitude as GRSA, found that solar radiation is the main factor affecting NPP at the seasonal scale, and suggested that photosynthesis could be promoted by prolonged incidence of sunshine. We suggest that individual pikas require immediate access—within each territory—to cool microclimates that might be more prevalent on northeast-facing slopes, but they also benefit from productive habitats at the larger scale over which they can forage. In GRSA, this larger-scale effect of insolation was dominant in our study, perhaps due to our small sample size or the availability of surprisingly

cool microclimates even at some of the lowest-elevation taluses in the preserve. For example, at one occupied, low-elevation talus in cluster 4, we observed moss that brought to mind pika habitats in the generally more mesic areas of the Pacific Northwest (Figure 10).

Our analysis suggests that leporid detection was often imperfect in our sampling frame. We detected leporid sign in only 30% of plots, but our detection-corrected estimate of leporid occupancy was 48%, suggesting that leporids occurred in almost half of the areas adjacent to talus in the preserve. In the field, we experienced that leporid scat was harder to detect where dense, short vegetation (like grasses and forbs) was present, whereas increased shrub cover (like willows) allowed for better detection. Under the canopies of the shrubs, there were often fewer grasses or forbs, allowing an unobstructed view of scat. Our top detection models supported these findings, suggesting a negative effect of grass and forb cover, as well as a positive effect of shrub cover. This is not the only study where similar barriers to scat detection have been noted. Berg et al. (2012) mentioned these constraints in a study where snowshoe hare scat was the response unit, although those types of cover were very sparse in that particular study. In other species where scat surveys are implemented, grass and forb cover also seem to play a role in detection, such as in Keither et al. (2016), who found that increased ground cover affected the detection of *Sus scrofa* fecal pellets; their models also noted that the effect was amplified with smaller pellet sizes from juveniles.

Although there is no historical information on leporid occupancy at GRSA, at other places elevation has been found to affect the occupancy of some lagomorph species that are known to occupy this park. For example, elevation has been related to occupancy for snowshoe hares (*Lepus americanus*), white-tailed jack rabbits (*Lepus townsendii*), and Nuttall's cottontails (*Sylvilagus nuttallii*; Berg et al. 2012, Goad et al. 2014, National Park Service 2020). Goad et al. (2014) built models of occupancy based on camera trap data for a small mammal community that included *S. nuttallii* in Larimer County, CO, and found a negative relationship with elevation attributed to the species' association with the edges of forested plant communities. Berg et al. (2012) also found a negative relationship between elevation and snowshoe hare fecal pellets; in their study, they argue for the importance of high-density horizontal vegetation cover and the presence of fir and spruce trees as predictors of a high density of snowshoe hares in Wyoming, supporting similar findings in the northern Rockies (Holbrook et al. 2017).

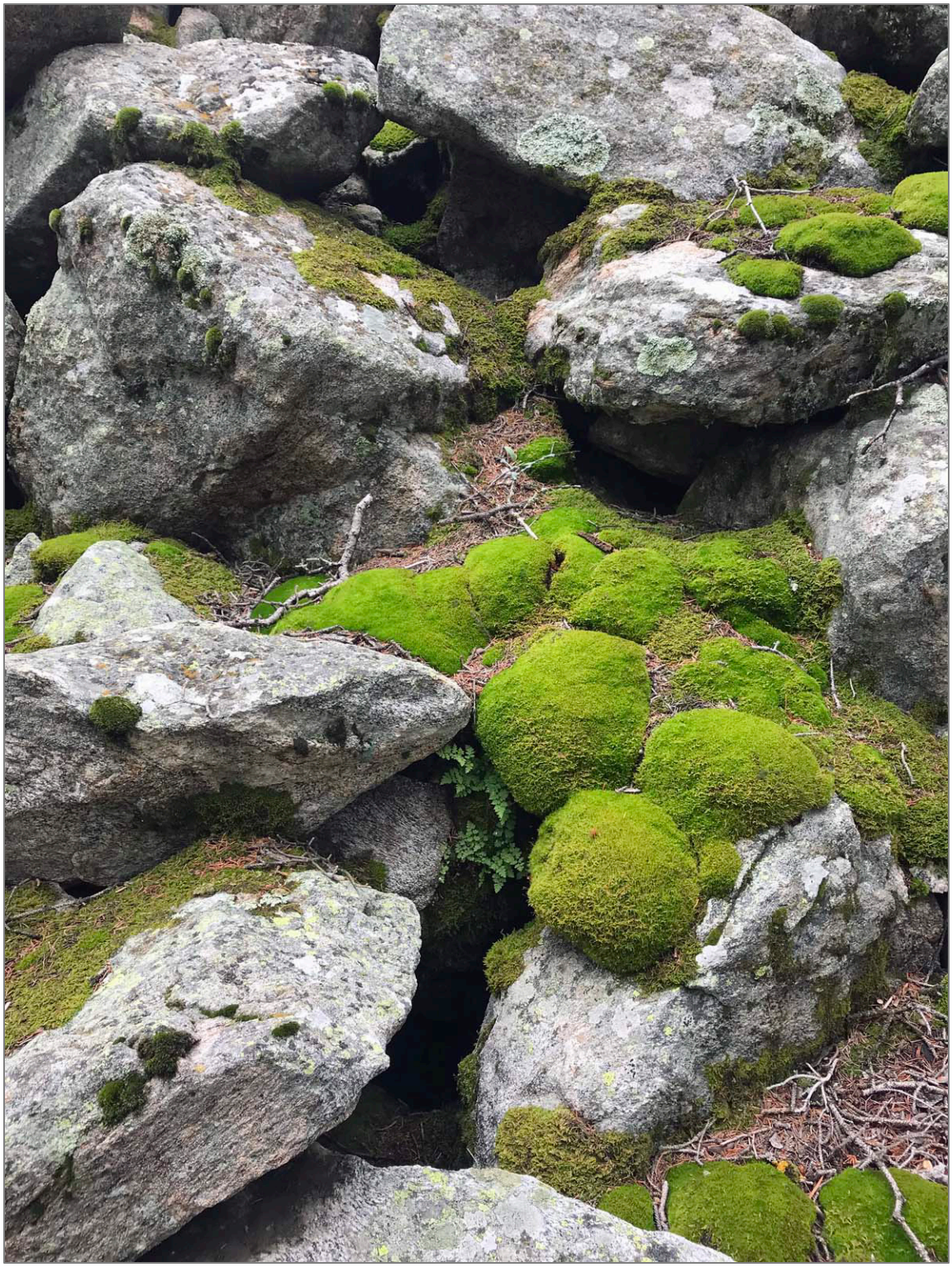

Figure 10. A surprisingly mesic habitat occupied by pikas at relatively low elevation in Great Sand Dunes National Park and Preserve: Site4-002 at latitude 37.82902656, longitude -105.4800967 (decimal degrees).

The positive relationship between leporid occupancy and covariates indicating a preference for sites with higher solar radiation at the plot scale (solRad12m or eastern_exposure) was dominant and contrary to our expectations. We expected a negative relationship because lower solar radiation at smaller scales might relate to colder climates and higher soil moisture, which provides the necessary climates for a higher density of tree cover, like those observed on north-facing slopes. Tree cover has been suggested as important for leporids that usually inhabit the subalpine forest, like the snowshoe hare (Malaney & Frey 2006, Berg et al. 2012). However, the positive effect of solar radiation in the leporid model might be attributed partially to our sampling frame, which might be biased towards a certain species of leporid as opposed to the general family-level taxon, because taluses tend to be free of tree cover; for example, open canopies are less suitable for snowshoe hares than for Nuttall's cottontail (Frey & Malaney 2006, Malaney & Frey 2006). In fact, the apparently recent invasion of the San Juan Mountains by Nuttall's cottontail might be due to anthropogenic habitat alteration, including fires, logging, and road construction that result in more of the fine-scale open canopy, higher herbaceous cover and warmer microclimates preferred by this species (Malaney & Frey 2006). If our leporid sampling was biased toward Nuttall's cottontail, the probability of RHDV2 spillover to pikas from leporids might be more substantial than indicated in this report, because this leporid might be able to disperse long distances and commonly occupies foothill habitats (Frey & Malaney 2006, Malaney & Frey 2006) like the ones where RHDV2 has been reported in counties surrounding GRSA.

Finally, our estimates of the joint probability of pika and leporid occupancy tell us that if there is any likelihood of these two taxa coming in contact, that would occur at the lowest elevations of pika habitat use, at occupied talus in the subalpine forest. However, given the nature of this study design, it is important to point out that those probabilities mainly apply to adult pikas who have already established a territory, because our sampling focused on talus polygons, which is where territorial adults reside. However, juvenile pikas could be more likely to come in contact with other leporids during their natal dispersal event, which often involves traversing non-talus habitats and which overlaps in time with the breeding season of some leporid species, like the snowshoe hare, when outbreaks of disease are more likely to take place (Aldous 1937, Smith & Weston 1990, Rouco et al. 2018).

Study Limitations and Recommendations

Due to the nature of our goal in this study, and the sampling framework required to achieve our goal, the management implications of results presented in this report are at least somewhat limited. In this section, we outline these limitations and present recommendations for future studies.

Challenging in several regards, this study produced a small sample size due in part to inclement weather during the intentionally short survey period, as well as the steep topography. Over 30% of the plots targeted for survey were located where slope angles exceeded 35 degrees. We recommend that slope angles greater than 35 degrees be omitted in future survey designs to improve survey effort, which should improve safety and increase the potential to estimate all parameters originally targeted in this study. Although we suggested that field crews use the GRTS draw to replace plots that were on slope angles greater than 35 degrees, for various reasons that advice was not generally

adopted, suggesting that such slopes should be avoided during the initial draw, rather than solely by offering alternate coordinates.

Our sampling frame also limited the applicability of our estimates of leporid and pika occupancy, because it was limited to talus and areas within and immediately adjacent to taluses. This limitation arises from our research goal, which was to assess the overlap between habitat use by leporids and pikas as a proxy for the potential spillover of RHDV2 from leporids to pikas. By necessity, studies of American pika habitat occupancy and species distribution focus on the obligate habitat of this taxon: taluses and lava beds, where pikas carry out most of their activities and where several types of pika sign can be efficiently detected. However, our study has not addressed the potential for juvenile pikas to encounter RHDV2 during natal dispersal. The American pika is highly territorial and exhibits natal dispersal in which young of the year must seek out territories of their own (Smith & Weston 1990). Adults defend territories that are largely non-overlapping, so dispersing pikas are commonly forced to leave their natal patch of talus due to the naturally limited number of territories available (Peacock & Smith 1997, Peacock & Ray 2001). Thus, many dispersing juveniles are likely to move through non-talus habitats within the preserve, where they would be more likely to come into contact with rabbits and hares and the many potential sources of exposure to RHDV2 associated with these taxa. We found high pika occupancy on many small and remote talus patches surrounded by forest (e.g., clusters 4 and 5), suggesting that such dispersal might be common. For this reason, we suggest that the two areas of potential contact suggested by our study (lower Sand Creek and along the southern park border) are not the only places where pikas might be exposed to RHDV2. Fortunately, it should be possible to identify any corridors of pika movement through the preserve using the landscape resistance models developed during the PIP study (Castillo et al. 2016). A raster of PIP estimates of pika gene flow across each cell of the preserve could be interpreted as a metric of dispersing pika occupancy in non-talus habitats. Multiplying this raster by our raster of leporid occupancy estimates could produce a map of the relative risk that dispersing pikas will come in contact with potential sources of RHDV2. We are currently expanding this study to develop this metric of potential pika-leporid contact, based on our estimates of leporid occupancy and PIP estimates of genetic connectivity across the preserve. It would also be possible to improve these estimates in the future by 1) updating estimates of landscape resistance to pika gene flow through analyses of scat collected during this and subsequent studies, and 2) expanding the sampling frame for leporids to better represent non-talus habitats within the preserve.

Expanding the sampling frame for leporids could also reduce any bias regarding the taxa sampled. Our results suggest a positive relationship between insolation at the plot scale and leporid occupancy, which could mean we were sampling a species that prefers openings in the forest, such as the Nuttall's cottontail, which might preferentially use the unforested gaps associated with talus (Malaney & Frey 2006).

Finally, our failure to distinguish the taxonomic identity of the leporids we detected was a major limitation regarding the management implications of this study. Despite an occupancy estimate near 50%, no leporids were ever sighted during plot surveys in 2022. Genetic analyses of scat collected during our surveys might allow further insights regarding the makeup of the leporid community.

Unfortunately, the number of scat samples collected was much lower than the number of scats detected, due in part to the small number of fresh pellets detected in any one sample. Crews were instructed (GRSA Lagomorph Survey Manual 2022) to collect samples only if they were clearly fresh and clustered into groups of three or more pellets likely to have been deposited by a single individual, to reduce cross-contamination and ensure sufficient sample size for genetic and/or epidemiological analyses. Tools and protocols for genetic analyses have improved, however, such that even a single pellet can often be useful for determining lineage; for this reason, we recommend that single pellets be collected, both to increase sample size and to ensure that each sample contains pellets from a single individual. If a particular analysis requires multiple pellets from each individual, pellets can be pooled across any single-pellet samples collected at the same exact location.

Conclusion

The emergence and spread of new pathogens is on the rise due to direct and indirect effects of climate change, increased globalization, and increased efficiency in global transportation (Rouco et al. 2019, El-Sayed & Kamel 2020). RHDV2 provides an example of the speed with which a pathogen can reach a global distribution, highlighting the need to identify where and when diseases might disrupt the ecological systems on which we depend. Effective response to a new pathogen requires not only knowledge of the ecology of the pathogen system but also knowledge of the current status of the affected species (hosts) and other species acting as vectors. For example, the estimation of population densities can be informative regarding the odds of pathogens and hosts coming in contact with a vector. However, density can be difficult to quantify for small populations living in habitats that are challenging to access, like those where pikas live, and for species living in complex landscapes that conceal hosts and their sign, like those inhabited by rabbits and hares. This study provides insight into the current status of lagomorphs in the park through the modeling of pika and leporid occupancy as a surrogate of density, and suggests the relative risk of RHDV2 spread along an elevational gradient, from low-elevation grasslands and shrublands to the alpine tundra. Our results provide evidence that lagomorphs are still common in GRSA, despite incidents of rabbit and hare mortality due to RHDV2 reported from the counties surrounding this park, as well as evidence that pika occupancy has not declined over the past decade, contrary to what would be expected if pikas were susceptible to and infected by RHDV2. We have, however, identified potential zones of contact between pikas and other lagomorphs in the preserve that should be useful in planning for surveillance of RHDV2 or any other pathogens that might move between these taxa. We also found that the apparent drivers of pika occupancy in this park today indicate that pikas remain vulnerable to climate change. We suggest that the sampling and modeling framework we have presented could be adapted to monitor this system periodically, focusing on elevational transects in the vicinity of the identified areas of potential contact between pikas and leporids. Investment in public outreach and/or community science programs could be considered as one way to increase the feasibility of such monitoring. Finally, to better understand the risk of RHDV2 spillover from leporids to pikas, future studies could expand the sampling frame for leporids further into non-talus habitats. We also suggest further studies of genetic connectivity among pika populations in GRSA, to infer the potential for juvenile pikas to encounter RHDV2 while traversing these landscapes during their natal dispersal events. Finally, omitting or replacing sites with a slope greater than 35 degrees could improve survey effort and crew safety.

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Appendix A: Survey and plot-level covariates

This appendix lists the survey and plot-level covariates used during the model building, their justification, and the description or parameters used for calculation (Tables 5–7).

Table 5. Survey-level covariates considered in models of lagomorph detection.

Survey variable	Description	Justification
observer	Technician(s) who conducted a given survey	Random effect due to expertise, abilities, etc.
skies	Whether it was clear, partly cloudy or overcast during the survey	Might affect animal behavior or sign detection
wind	Wind speed, recorded as low (only grasses bend), medium (tree branches bend) or high (trees bend or observers are buffeted)	Might affect animal behavior or sign detection
temperature	Temperature measured during the survey or imputed from the first survey of the same plot	Might affect animal behavior or sign detection (observer discomfort)
temperature2	Temperature measured during the survey or imputed from plots in the same biome	Might affect animal behavior or sign detection (observer discomfort)
julianDate	Day of year (1-365)	Might affect animal behavior or sign detection (through a progression in observer skill)
surveyTime	Hour of day in which the survey was conducted	Might affect animal behavior

Table 6. Plot-level covariates considered in models of lagomorph occupancy. Asterisks (*) indicate variables that were also considered as covariates of detection.

Plot variable	Description	Justification
elevation	Meters above sea level	Affects temperature and precipitation
biome	Whether the plot is in subalpine forest or the alpine tundra	Associated with ecological and climatic processes
slope12m	Average slope angle at the plot scale (12-m buffer)	Affects microclimate, infiltration, erosion, vegetation [A, B, C, D]
solRad12m	Average total incoming radiation (direct + diffuse) in watt hours per square meter at the plot scale (12-m buffer)	Affects microclimate
solRad1100m	Average total incoming radiation (direct + diffuse) in watt hours per square meter at the pika genetic neighborhood scale (1100m buffer)	Affects available vegetation and length of the growing/foraging season across a population
northeastness	Average aspect at the plot scale (12-m buffer), transformed according to Beers (1966) [E]	Affects solar and wind exposure, snow accumulation, microclimate, growing season and vegetation [A, B, C, D]
northern_exposure	Continuous index of whether a plot is on a north-facing slope (1), south-facing slope (-1) or in between; 0 indicates a flat spot	Affects solar and wind exposure, snow accumulation, microclimate, growing season and vegetation [A, B, C, D]
eastern_exposure	Continuous index of whether a plot is on an east-facing (1) or west-facing slope (-1) or in between; 0 indicates a flat spot	Affects solar and wind exposure, snow accumulation, microclimate, growing season and vegetation [A, B, C, D]

[A] El Kateb H, Zhang H, Zhang P, Mosandl R. 2013. Soil erosion and surface runoff on different vegetation covers and slope gradients: A field experiment in Southern Shaanxi Province, China. CATENA. 105:1–10. doi:10.1016/j.catena.2012.12.012

[B] Morbidelli R, Corradini C, Saltalippi C, Flammini A, Dari J, Govindaraju RS. 2019. A New Conceptual Model for Slope-Infiltration. Water. 11(4):678. doi:10.3390/w11040678

[C] Lee J-K, Hwang H-S, Eum T-K, Bae H-K, Rhim S-J. 2020. Cascade effects of slope gradient on ground vegetation and small-rodent populations in a forest ecosystem. Anim Biol. 70(2):203–213. doi:10.1163/15707563-20191192

[D] Singh S. 2018. Understanding the role of slope aspect in shaping the vegetation attributes and soil properties in Montane ecosystems. Tropical Ecology. 59(3):417–430.

[E] Beers, T. W., Dress, P. E. & Wensel, L. C. Notes and Observations: Aspect Transformation in Site Productivity Research. *J. For.* **64**, 691–692 (1966).

[F] O'Donnell MS, Ignizio DA. 2012. Bioclimatic Predictors for Supporting Ecological Applications in the Conterminous United States. US Geological Survey Data Series. 691:10.

[G] Wang T, Hamann A, Spittlehouse D, Carroll C. 2016. Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America.Álvarez I, editor. PLOS ONE. 11(6):e0156720. doi:10.1371/journal.pone.0156720

[H] Schwalm D, Epps CW, Rodhouse TJ, Monahan WB, Castillo JA, Ray C, Jeffress MR. 2016. Habitat availability and gene flow influence diverging local population trajectories under scenarios of climate change: a place-based approach. Glob Change Biol. 22(4):1572–1584. doi:10.1111/gcb.13189

Table 6 (continued). Plot-level covariates considered in models of lagomorph occupancy. Asterisks (*) indicate variables that were also considered as covariates of detection.

Plot variable	Description	Justification
rockCover	Observed percent cover of loose rocks and boulders bigger than a football within the plot	Affects microclimate, cover for pikas, and sign detection
bareCover	Observed percent cover of dirt, dead "leaf litter," gravel, scree, loose rocks smaller than a football, and exposed bedrock	Affects microclimate, cover for pikas, and sign detection
grassCover*	Observed percent cover of graminoids (e.g., grasses and sedges)	Indicates microclimate, forage quality, and the potential for sign detection
forbCover*	Observed percent cover of non-graminoid flowering herbaceous plants	Indicates microclimate, forage quality, and the potential for sign detection
shrubCover*	Observed percent cover of woody plants and trees < 1 m in height	Indicates microclimate, forage quality, and the potential for sign detection
treeCover	Observed percent cover of trees > 1 m in height	Indicates microclimate, forage quality, and the potential for sign detection
distance2veg	Meters from the pika plot edge to the closest 2×2 m patch of grass/forb/shrub cover (see the GRSA Lagomorph Survey Manual 2022 for details); 0 if in plot	Affects foraging ability/risk
subIce	Plot contains (True/False) evidence of subsurface seasonal or permanent ice (see the GRSA Lagomorph Survey Manual 2022 for details)	Affects subsurface microclimate, vegetation cover/forage and water availability for animals

[A] El Kateb H, Zhang H, Zhang P, Mosandl R. 2013. Soil erosion and surface runoff on different vegetation covers and slope gradients: A field experiment in Southern Shaanxi Province, China. CATENA. 105:1–10. doi:10.1016/j.catena.2012.12.012

[B] Morbidelli R, Corradini C, Saltalippi C, Flammini A, Dari J, Govindaraju RS. 2019. A New Conceptual Model for Slope-Infiltration. Water. 11(4):678. doi:10.3390/w11040678

[C] Lee J-K, Hwang H-S, Eum T-K, Bae H-K, Rhim S-J. 2020. Cascade effects of slope gradient on ground vegetation and small-rodent populations in a forest ecosystem. Anim Biol. 70(2):203–213. doi:10.1163/15707563-20191192

[D] Singh S. 2018. Understanding the role of slope aspect in shaping the vegetation attributes and soil properties in Montane ecosystems. Tropical Ecology. 59(3):417–430.

[E] Beers, T. W., Dress, P. E. & Wensel, L. C. Notes and Observations: Aspect Transformation in Site Productivity Research. *J. For.* **64**, 691–692 (1966).

[F] O'Donnell MS, Ignizio DA. 2012. Bioclimatic Predictors for Supporting Ecological Applications in the Conterminous United States. US Geological Survey Data Series. 691:10.

[G] Wang T, Hamann A, Spittlehouse D, Carroll C. 2016. Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America.Álvarez I, editor. PLOS ONE. 11(6):e0156720. doi:10.1371/journal.pone.0156720

[H] Schwalm D, Epps CW, Rodhouse TJ, Monahan WB, Castillo JA, Ray C, Jeffress MR. 2016. Habitat availability and gene flow influence diverging local population trajectories under scenarios of climate change: a place-based approach. Glob Change Biol. 22(4):1572–1584. doi:10.1111/gcb.13189

Table 6 (continued). Plot-level covariates considered in models of lagomorph occupancy. Asterisks (*) indicate variables that were also considered as covariates of detection.

Plot variable	Description	Justification
rockLargest	Largest diameter (m) of the largest rock in the plot	Affects subsurface microclimate and cover for pikas
rock10thLargest	Largest diameter (m) of the 10th largest rock in the plot	Affects subsurface microclimate and cover for pikas
rockDiff	Size range (m) of largest 10 rocks in the plot, calculated as rockLargest – rock10thLargest	Affects subsurface microclimate and cover for pikas
creviceDepth	Depth class of deepest visible crevice observed in the plot: 1=under ½ m, 2=½ to 1 m, 3=1 to 1 ½ m, and 4=over 1 ½ m	Affects subsurface microclimate and cover for pikas
rockShade	Average shade class of all surface rocks in the plot: 1=light-colored (felsic), 2=intermediate, or 3= dark (mafic), per the shade chart in the GRSA Lagomorph Survey Manual 2022 and disregarding lichen shade	Might affect microclimate
lichenCov	Average cover class of lichen on all surface rocks in the plot: 1=under 33% cover, 2=33-67%, or 3=over 67% cover, per the cover chart in the GRSA Lagomorph Survey Manual 2022	Might affect microclimate or foraging potential
precipTotalAnnualNormal	Yearly average of total annual precipitation, calculated as in Bioclim 12 [F], but using monthly normals from 1991-2020 [G]	Affects normal water availability and vegetation type

[A] El Kateb H, Zhang H, Zhang P, Mosandl R. 2013. Soil erosion and surface runoff on different vegetation covers and slope gradients: A field experiment in Southern Shaanxi Province, China. CATENA. 105:1–10. doi:10.1016/j.catena.2012.12.012

[B] Morbidelli R, Corradini C, Saltalippi C, Flammini A, Dari J, Govindaraju RS. 2019. A New Conceptual Model for Slope-Infiltration. Water. 11(4):678. doi:10.3390/w11040678

[C] Lee J-K, Hwang H-S, Eum T-K, Bae H-K, Rhim S-J. 2020. Cascade effects of slope gradient on ground vegetation and small-rodent populations in a forest ecosystem. Anim Biol. 70(2):203–213. doi:10.1163/15707563-20191192

[D] Singh S. 2018. Understanding the role of slope aspect in shaping the vegetation attributes and soil properties in Montane ecosystems. Tropical Ecology. 59(3):417–430.

[E] Beers, T. W., Dress, P. E. & Wensel, L. C. Notes and Observations: Aspect Transformation in Site Productivity Research. *J. For.* **64**, 691–692 (1966).

[F] O'Donnell MS, Ignizio DA. 2012. Bioclimatic Predictors for Supporting Ecological Applications in the Conterminous United States. US Geological Survey Data Series. 691:10.

[G] Wang T, Hamann A, Spittlehouse D, Carroll C. 2016. Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America.Álvarez I, editor. PLOS ONE. 11(6):e0156720. doi:10.1371/journal.pone.0156720

[H] Schwalm D, Epps CW, Rodhouse TJ, Monahan WB, Castillo JA, Ray C, Jeffress MR. 2016. Habitat availability and gene flow influence diverging local population trajectories under scenarios of climate change: a place-based approach. Glob Change Biol. 22(4):1572–1584. doi:10.1111/gcb.13189

Table 6 (continued). Plot-level covariates considered in models of lagomorph occupancy. Asterisks (*) indicate variables that were also considered as covariates of detection.

Plot variable	Description	Justification
precipTotalAnnualLag1	Total precipitation during the year before the survey, calculated as in Bioclim 12 [F], but using a date range of 8/1/2021 to 7/31/2022	Affects recent water availability and vegetation health
tempWarmQtrNormal	Yearly average of mean temperature during the warmest quarter (June, July, August), calculated as in Bioclim 10, but using monthly normals from 1991-2020 [G]	Affects normal summer microclimate and the potential for chronic stress in plants and animals
tempWarmQtrLag1	Average temperature during the warmest quarter of the previous year (June, July, August of 2021)	Affects microclimate in the previous summer and the potential for recent stress in plants and animals
tempColdQtrNormal	Yearly average of mean temperature during the coldest quarter (December, January, February), calculated as in Bioclim 11, but using monthly normals from 1991-2020 [G]	Affects normal winter microclimate and the potential for chronic stress in plants and animals
tempColdQtrLag1	Average temperature during the coldest quarter of the previous year (December 2021 through February 2022)	Affects microclimate in the previous winter and the potential for recent stress in plants and animals
precipTotalWarmQtrNormal	Yearly average of total precipitation during the warmest quarter (June, July, August), calculated as in Bioclim 18, but using monthly normals from 1991-2020 [G]	Affects vegetation type and the potential for chronic stress in plants and animals

[A] El Kateb H, Zhang H, Zhang P, Mosandl R. 2013. Soil erosion and surface runoff on different vegetation covers and slope gradients: A field experiment in Southern Shaanxi Province, China. CATENA. 105:1–10. doi:10.1016/j.catena.2012.12.012

[B] Morbidelli R, Corradini C, Saltalippi C, Flammini A, Dari J, Govindaraju RS. 2019. A New Conceptual Model for Slope-Infiltration. Water. 11(4):678. doi:10.3390/w11040678

[C] Lee J-K, Hwang H-S, Eum T-K, Bae H-K, Rhim S-J. 2020. Cascade effects of slope gradient on ground vegetation and small-rodent populations in a forest ecosystem. Anim Biol. 70(2):203–213. doi:10.1163/15707563-20191192

[D] Singh S. 2018. Understanding the role of slope aspect in shaping the vegetation attributes and soil properties in Montane ecosystems. Tropical Ecology. 59(3):417–430.

[E] Beers, T. W., Dress, P. E. & Wensel, L. C. Notes and Observations: Aspect Transformation in Site Productivity Research. *J. For.* **64**, 691–692 (1966).

[F] O'Donnell MS, Ignizio DA. 2012. Bioclimatic Predictors for Supporting Ecological Applications in the Conterminous United States. US Geological Survey Data Series. 691:10.

[G] Wang T, Hamann A, Spittlehouse D, Carroll C. 2016. Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America.Álvarez I, editor. PLOS ONE. 11(6):e0156720. doi:10.1371/journal.pone.0156720

[H] Schwalm D, Epps CW, Rodhouse TJ, Monahan WB, Castillo JA, Ray C, Jeffress MR. 2016. Habitat availability and gene flow influence diverging local population trajectories under scenarios of climate change: a place-based approach. Glob Change Biol. 22(4):1572–1584. doi:10.1111/gcb.13189

Table 6 (continued). Plot-level covariates considered in models of lagomorph occupancy. Asterisks (*) indicate variables that were also considered as covariates of detection.

Plot variable	Description	Justification
precipTotalWarmQtrLag1	Total precipitation during the warmest quarter of the previous year (June through August of 2021)	Affects vegetation health and the potential for evaporative cooling in the previous summer
precipTotalColdQtrNormal	Yearly average of total precipitation during the coldest quarter (December, January, February), calculated as in Bioclim 19, but using monthly normals from 1991-2020 [G]	Affects the normal winter microclimate, potential subnivean microclimate, vegetation type, and the potential for chronic stress in plants and animals
precipTotalColdQtrLag1	Total precipitation during the coldest quarter of the previous year (December 2021 through February 2022)	Affects recent winter microclimate, potential subnivean microclimate, and the potential for recent stress in plants and animals
precipSeasonalityNormal	Yearly average of the annual variation in monthly precipitation totals, calculated as in Bioclim 15, but using monthly normals from 1991-2020 [G]	Affects the normal potential for (snow) drought and acute stress in plants and animals
precipSeasonalityLag1	Variation in monthly precipitation totals during the previous year	Affects the recent potential for (snow) drought and acute stress in plants and animals
potsnowNormal	Yearly average of total precipitation from September through May in grid cells with mean temperature < 0 °C (potential snow), calculated as in Schwalm et al. (2016) [H] but using September-May normals from 1991-2020 [G]	Affects normal snowpack, water availability, infiltration, vegetation type, and the potential for a subnivean microclimate or chronic stress in plants and animals

[A] El Kateb H, Zhang H, Zhang P, Mosandl R. 2013. Soil erosion and surface runoff on different vegetation covers and slope gradients: A field experiment in Southern Shaanxi Province, China. CATENA. 105:1–10. doi:10.1016/j.catena.2012.12.012

[B] Morbidelli R, Corradini C, Saltalippi C, Flammini A, Dari J, Govindaraju RS. 2019. A New Conceptual Model for Slope-Infiltration. Water. 11(4):678. doi:10.3390/w11040678

[C] Lee J-K, Hwang H-S, Eum T-K, Bae H-K, Rhim S-J. 2020. Cascade effects of slope gradient on ground vegetation and small-rodent populations in a forest ecosystem. Anim Biol. 70(2):203–213. doi:10.1163/15707563-20191192

[D] Singh S. 2018. Understanding the role of slope aspect in shaping the vegetation attributes and soil properties in Montane ecosystems. Tropical Ecology. 59(3):417–430.

[E] Beers, T. W., Dress, P. E. & Wensel, L. C. Notes and Observations: Aspect Transformation in Site Productivity Research. *J. For.* **64**, 691–692 (1966).

[F] O'Donnell MS, Ignizio DA. 2012. Bioclimatic Predictors for Supporting Ecological Applications in the Conterminous United States. US Geological Survey Data Series. 691:10.

[G] Wang T, Hamann A, Spittlehouse D, Carroll C. 2016. Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America.Álvarez I, editor. PLOS ONE. 11(6):e0156720. doi:10.1371/journal.pone.0156720

[H] Schwalm D, Epps CW, Rodhouse TJ, Monahan WB, Castillo JA, Ray C, Jeffress MR. 2016. Habitat availability and gene flow influence diverging local population trajectories under scenarios of climate change: a place-based approach. Glob Change Biol. 22(4):1572–1584. doi:10.1111/gcb.13189

Table 6 (continued). Plot-level covariates considered in models of lagomorph occupancy. Asterisks (*) indicate variables that were also considered as covariates of detection.

Plot variable	Description	Justification
potsnowLag1	Total precipitation from September through May in grid cells with mean temperature < 0 °C (potential snow), calculated as in Schwalm et al. (2016) [H] but using a date range of 9/1/2021 to 5/31/2022	Affects recent snowpack, water availability, infiltration, vegetation health, and the potential for a subnivean microclimate or recent stress in plants and animals

[A] El Kateb H, Zhang H, Zhang P, Mosandl R. 2013. Soil erosion and surface runoff on different vegetation covers and slope gradients: A field experiment in Southern Shaanxi Province, China. CATENA. 105:1–10. doi:10.1016/j.catena.2012.12.012

[B] Morbidelli R, Corradini C, Saltalippi C, Flammini A, Dari J, Govindaraju RS. 2019. A New Conceptual Model for Slope-Infiltration. Water. 11(4):678. doi:10.3390/w11040678

[C] Lee J-K, Hwang H-S, Eum T-K, Bae H-K, Rhim S-J. 2020. Cascade effects of slope gradient on ground vegetation and small-rodent populations in a forest ecosystem. Anim Biol. 70(2):203–213. doi:10.1163/15707563-20191192

[D] Singh S. 2018. Understanding the role of slope aspect in shaping the vegetation attributes and soil properties in Montane ecosystems. Tropical Ecology. 59(3):417–430.

[E] Beers, T. W., Dress, P. E. & Wensel, L. C. Notes and Observations: Aspect Transformation in Site Productivity Research. *J. For.* **64**, 691–692 (1966).

[F] O'Donnell MS, Ignizio DA. 2012. Bioclimatic Predictors for Supporting Ecological Applications in the Conterminous United States. US Geological Survey Data Series. 691:10.

[G] Wang T, Hamann A, Spittlehouse D, Carroll C. 2016. Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America.Álvarez I, editor. PLOS ONE. 11(6):e0156720. doi:10.1371/journal.pone.0156720

[H] Schwalm D, Epps CW, Rodhouse TJ, Monahan WB, Castillo JA, Ray C, Jeffress MR. 2016. Habitat availability and gene flow influence diverging local population trajectories under scenarios of climate change: a place-based approach. Glob Change Biol. 22(4):1572–1584. doi:10.1111/gcb.13189

Table 7. Parameter values used in the ArcGIS Area Solar Radiation Tool.[A]

Parameter	Value	Reasoning
Input raster	Digital Elevation Model (DEM) projected as NAD83 UTM 13T	Required
Output global radiation raster	areaRadStdSky.tif	Required
Latitude	37.80929067537346	Automatically calculated by the tool
Sky size / Resolution	200	Default value
Time configuration	WholeYear 2022	Calculates the average incoming solar radiation during 2022
Day interval	14	Default value
Hour interval	0.5	Default value
Create outputs for each interval	NO INTERVAL	Outputs for each interval were not needed

[A] ESRI. 2023. ArcGIS Pro [Internet]. [accessed 2023 Nov 17]. https://support.esri.com/en-us/patches-updates/2023/arcgis-pro-3-1-patch-3-3-1-3-announcement

Table 7 (continued). Parameter values used in the ArcGIS Area Solar Radiation Tool.[A]

Parameter	Value	Reasoning
Z factor	1	Default value
Slope and aspect input type	FROM_DEM	Slope and aspect for internal model calculated by the tool using the DEM
Calculation directions	32	The default value is suggested for complex topography
Zenith divisions	8	Default value
Azimuth divisions	8	Default value
Diffuse model type	STANDARD_OVERCAST_SKY	Assumes incoming diffuse radiation flux varies with the zenith angle
Diffuse proportion	0.3	Default value
Transmittivity	0.5	Default value

[A] ESRI. 2023. ArcGIS Pro [Internet]. [accessed 2023 Nov 17]. https://support.esri.com/en-us/patches-updates/2023/arcgis-pro-3-1-patch-3-3-1-3-announcement

Appendix B: 2022 pika detection history matrix

Table 8 shows detections and non-detections of pika sign during surveys.

Table 8. Detections (1) and non-detections (0) of the American pika or fresh pika sign at n=115 plots surveyed throughout Great Sand Dunes National Park and Preserve in late summer of 2022. Pikas were also detected at Site5-001, Site5-002 and Site5-003, but no leporid or plot variable data were recorded *in situ* at those plots, so those three plots were dropped from this analysis.

Plot ID	First survey	Second survey
Site1-001	1	–
Site1-002	1	–
Site1-003	1	–
Site1-004	1	1
Site1-006	1	–
Site1-007	1	–
Site1-009	1	–
Site1-010	1	1
Site1-011	1	0
Site1-012	1	–
Site1-013	1	–
Site1-014	1	–
Site1-016	1	1
Site1-017	1	–
Site1-018	1	–
Site1-020	1	–
Site1-021	1	–
Site1-022	1	–
Site1-023	1	–
Site1-024	1	–
Site1-025	1	1
Site1-027	1	1
Site1-032	1	–
Site1-033	1	–
Site1-034	1	–
Site1-035	1	–
Site1-037	0	–
Site1-038	1	–
Site1-041	1	1

Table 8 (continued). Detections (1) and non-detections (0) of the American pika or fresh pika sign at n=115 plots surveyed throughout Great Sand Dunes National Park and Preserve in late summer of 2022. Pikas were also detected at Site5-001, Site5-002 and Site5-003, but no leporid or plot variable data were recorded *in situ* at those plots, so those three plots were dropped from this analysis.

Plot ID	First survey	Second survey
Site1-043	1	1
Site1-044	1	–
Site1-046	1	1
Site1-049	1	1
Site1-050	1	–
Site1-053	1	–
Site1-055	1	–
Site1-056	1	–
Site1-057	1	–
Site1-058	1	–
Site1-062	1	1
Site1-063	1	–
Site1-065	1	–
Site1-066	1	–
Site1-068	1	1
Site2-001	1	–
Site2-005	0	–
Site2-007	1	–
Site2-009	1	–
Site2-012	1	–
Site2-013	1	–
Site2-014	1	–
Site2-015	1	–
Site2-016	1	–
Site2-017	1	–
Site2-018	1	–
Site2-019	1	–
Site2-020	1	–
Site2-021	1	–
Site2-022	1	–
Site2-023	1	–
Site2-024	1	–
Site2-026	1	–

Table 8 (continued). Detections (1) and non-detections (0) of the American pika or fresh pika sign at n=115 plots surveyed throughout Great Sand Dunes National Park and Preserve in late summer of 2022. Pikas were also detected at Site5-001, Site5-002 and Site5-003, but no leporid or plot variable data were recorded *in situ* at those plots, so those three plots were dropped from this analysis.

Plot ID	First survey	Second survey
Site2-027	1	–
Site2-028	1	–
Site2-029	1	–
Site2-030	1	–
Site2-031	1	–
Site2-032	1	–
Site2-033	1	–
Site2-036	1	–
Site2-037	1	–
Site2-038	1	–
Site2-041	1	–
Site2-044	1	–
Site2-052	1	–
Site2-053	1	–
Site2-055	1	–
Site2-057	0	–
Site2-061	1	–
Site2-064	1	–
Site2-065	1	1
Site2-066	1	–
Site2-067	0	–
Site2-069	1	–
Site3-002	0	–
Site3-003	0	–
Site3-004	0	–
Site3-005	0	0
Site3-006	1	–
Site3-007	0	–
Site3-008	1	–
Site4-002	1	–
Site4-003	1	1
Site4-005	1	–
Site4-006	1	–

Table 8 (continued). Detections (1) and non-detections (0) of the American pika or fresh pika sign at n=115 plots surveyed throughout Great Sand Dunes National Park and Preserve in late summer of 2022. Pikas were also detected at Site5-001, Site5-002 and Site5-003, but no leporid or plot variable data were recorded *in situ* at those plots, so those three plots were dropped from this analysis.

Plot ID	First survey	Second survey
Site4-008	1	–
Site4-011	1	–
Site4-014	1	–
Site4-015	0	–
Site4-016	1	–
Site4-019	1	–
Site5-005	1	–
Site5-006	1	–
Site6-001	0	0
Site6-002	0	0
Site6-004	0	–
Site6-005	0	–
Site6-006	1	1
Site6-007	1	1
Site6-008	0	0
Site6-009	0	0
Site6-010	1	1
Site6-011	1	1
Site6-012	1	1
Site6-014	1	1

Appendix C: 2022 leporid detection history matrix

Table 9 shows detections and non-detections of leporid sign during surveys.

Table 9. Detections (1) and non-detections (0) of leporid sign at n=115 pika habitat plots surveyed throughout Great Sand Dunes National Park and Preserve in late summer of 2022.

Plot ID	First survey	Second survey
Site1-001	1	–
Site1-002	1	–
Site1-003	0	–
Site1-004	0	0
Site1-006	0	–
Site1-007	1	–
Site1-009	0	–
Site1-010	0	0
Site1-011	0	0
Site1-012	0	–
Site1-013	0	–
Site1-014	0	–
Site1-016	1	0
Site1-017	0	–
Site1-018	0	–
Site1-020	1	–
Site1-021	1	–
Site1-022	0	–
Site1-023	0	–
Site1-024	1	–
Site1-025	1	0
Site1-027	0	0
Site1-032	0	–
Site1-033	0	–
Site1-034	0	–
Site1-035	1	–
Site1-037	0	–
Site1-038	0	–
Site1-041	0	0
Site1-043	0	0
Site1-044	0	–

Table 9 (continued). Detections (1) and non-detections (0) of leporid sign at n=115 pika habitat plots surveyed throughout Great Sand Dunes National Park and Preserve in late summer of 2022.

Plot ID	First survey	Second survey
Site1-046	0	0
Site1-049	0	0
Site1-050	0	–
Site1-053	0	–
Site1-055	0	–
Site1-056	0	–
Site1-057	0	–
Site1-058	0	–
Site1-062	0	0
Site1-063	1	–
Site1-065	0	–
Site1-066	0	–
Site1-068	0	0
Site2-001	0	–
Site2-005	0	–
Site2-007	0	–
Site2-009	0	–
Site2-012	0	–
Site2-013	0	–
Site2-014	0	–
Site2-015	0	–
Site2-016	0	–
Site2-017	1	–
Site2-018	0	–
Site2-019	0	–
Site2-020	1	–
Site2-021	0	–
Site2-022	0	–
Site2-023	0	–
Site2-024	0	–
Site2-026	0	–
Site2-027	0	–
Site2-028	0	–
Site2-029	0	–

Table 9 (continued). Detections (1) and non-detections (0) of leporid sign at n=115 pika habitat plots surveyed throughout Great Sand Dunes National Park and Preserve in late summer of 2022.

Plot ID	First survey	Second survey
Site2-030	0	–
Site2-031	0	–
Site2-032	0	–
Site2-033	0	–
Site2-036	0	–
Site2-037	0	–
Site2-038	0	–
Site2-041	0	–
Site2-044	0	–
Site2-052	0	–
Site2-053	0	–
Site2-055	0	–
Site2-057	0	–
Site2-061	0	–
Site2-064	0	–
Site2-065	1	0
Site2-066	0	–
Site2-067	0	–
Site2-069	0	–
Site3-002	0	–
Site3-003	0	–
Site3-004	1	–
Site3-005	1	1
Site3-006	0	–
Site3-007	1	–
Site3-008	1	–
Site4-002	1	–
Site4-003	1	0
Site4-005	1	–
Site4-006	1	–
Site4-008	0	–
Site4-011	1	–
Site4-014	1	–
Site4-015	1	–

Table 9 (continued). Detections (1) and non-detections (0) of leporid sign at n=115 pika habitat plots surveyed throughout Great Sand Dunes National Park and Preserve in late summer of 2022.

Plot ID	First survey	Second survey
Site4-016	1	–
Site4-019	0	–
Site5-005	1	–
Site5-006	0	–
Site6-001	0	1
Site6-002	1	1
Site6-004	1	–
Site6-005	1	–
Site6-006	0	0
Site6-007	1	1
Site6-008	1	1
Site6-009	1	1
Site6-010	0	0
Site6-011	1	0
Site6-012	1	1
Site6-014	0	0

Appendix D: Exploratory data analysis for the pika dataset

Figures 11—14 show exploratory data analysis for the 2022 pika dataset.

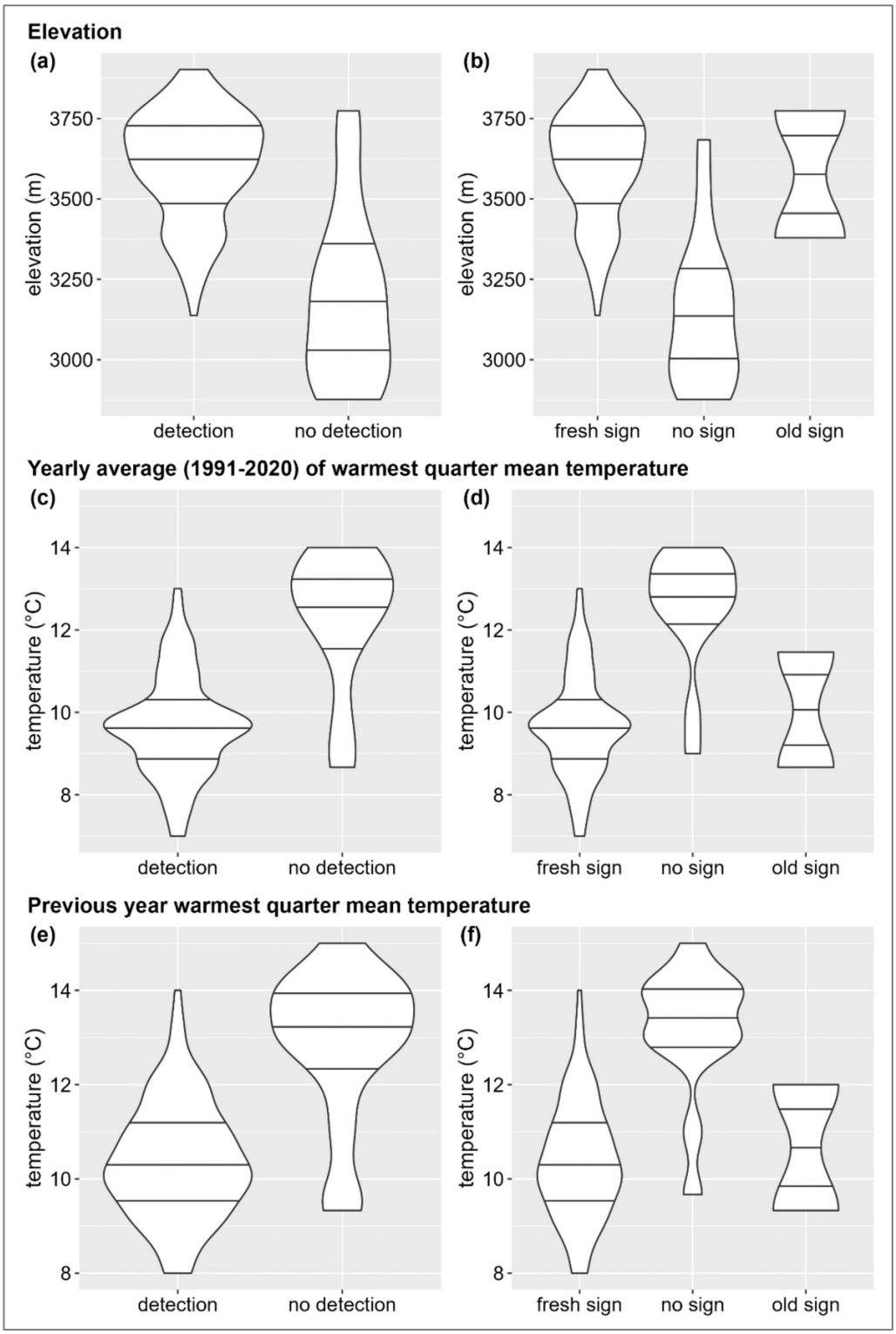

Figure 11. Covariate values at n=115 survey plots in late summer of 2022 at Great Sand Dunes National Park and Preserve, summarized by pika detection metrics using a binary classification (detection or no detection of fresh sign; panels a, c and e) or distinguishing fresh from old and no sign (panels b, d and f). "Yearly average" panels (c and d) are based on 1991-2020 normals. "Previous year" panels (e and f) are based on June-August 2021 summaries (see Appendix A for details of each plot covariate).

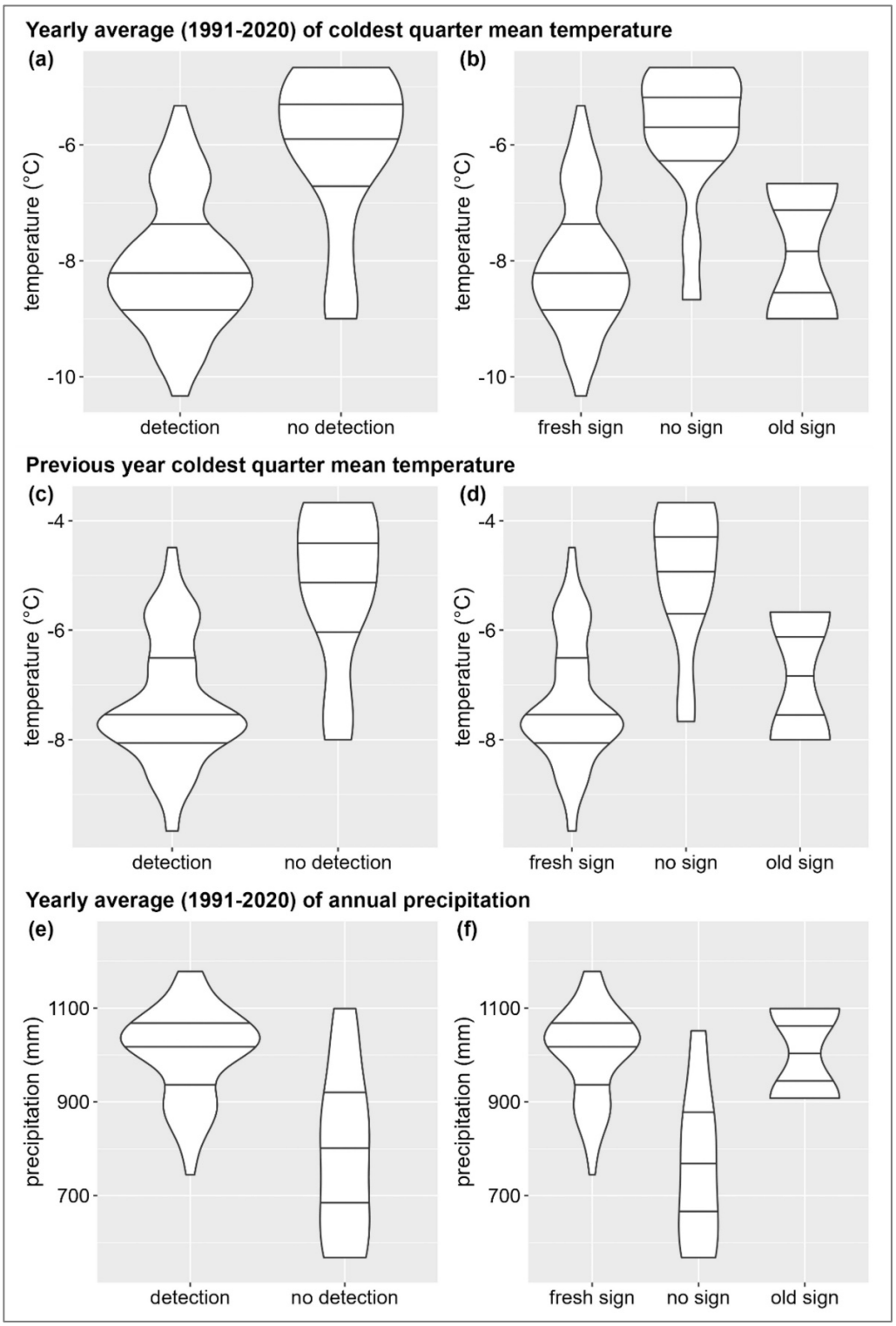

Figure 12. Covariate values at n=115 survey plots in late summer of 2022 at Great Sand Dunes National Park and Preserve, summarized by pika detection using a binary classification (detection or no detection of fresh sign; panels a, c and e) or distinguishing fresh from old and no sign (panels b, d and f). "Yearly average" panels (a, b, e and f) are based on 1991-2020 normals. "Previous year" panels (c and d) are based on December 2021-February 2022 summaries (see Appendix A for details of each plot covariate).

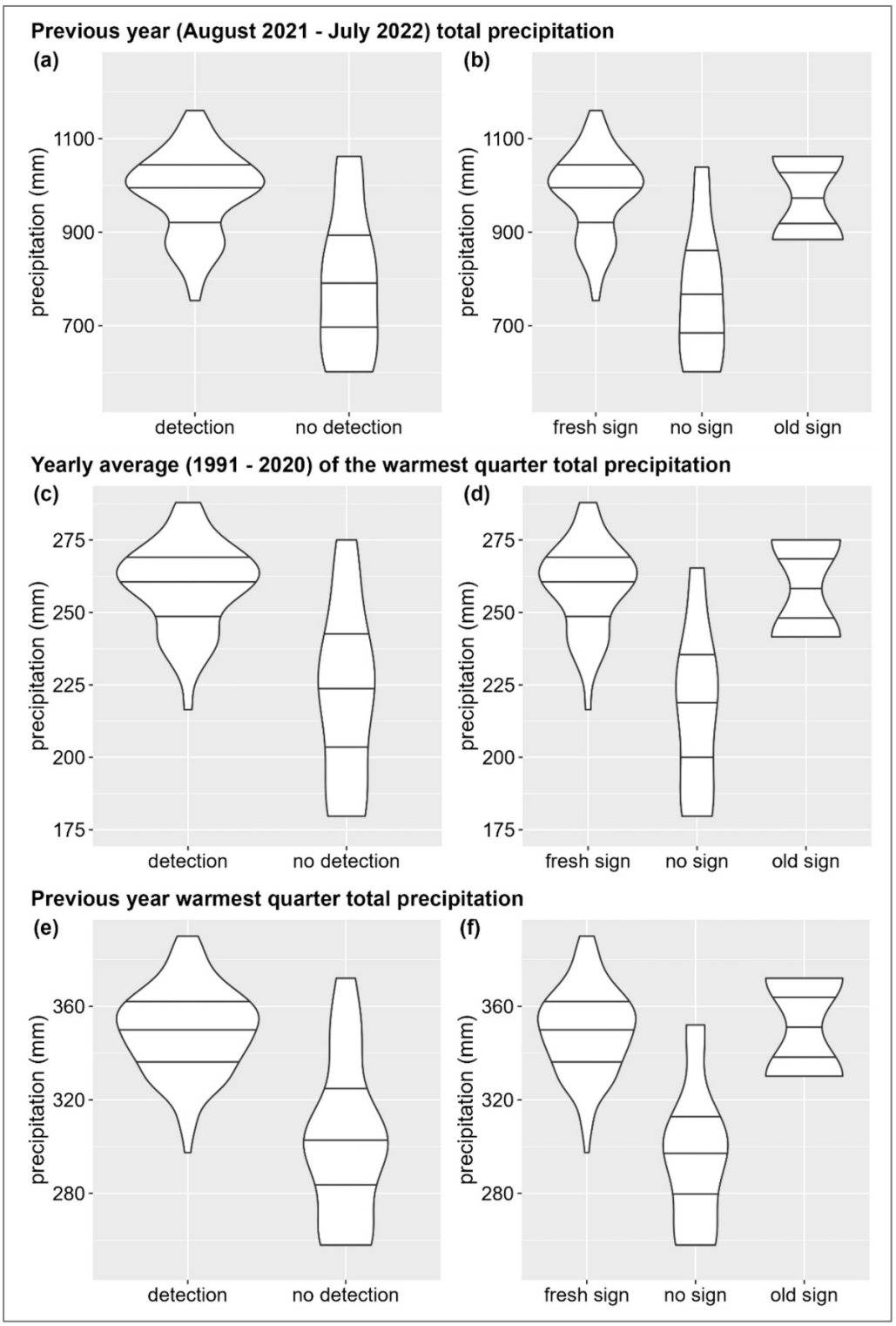

Figure 13. Covariate values at n=115 survey plots in late summer of 2022 at Great Sand Dunes National Park and Preserve, summarized by pika detection metrics using a binary classification (detection or no detection of fresh sign; panels a, c and e) or distinguishing fresh from old and no sign (panels b, d and f). "Yearly average" panels (c and d) are based on 1991-2020 normals. "Previous year" panels (e and f) are based on June-August 2022 summaries (see Appendix A for details of each plot covariate).

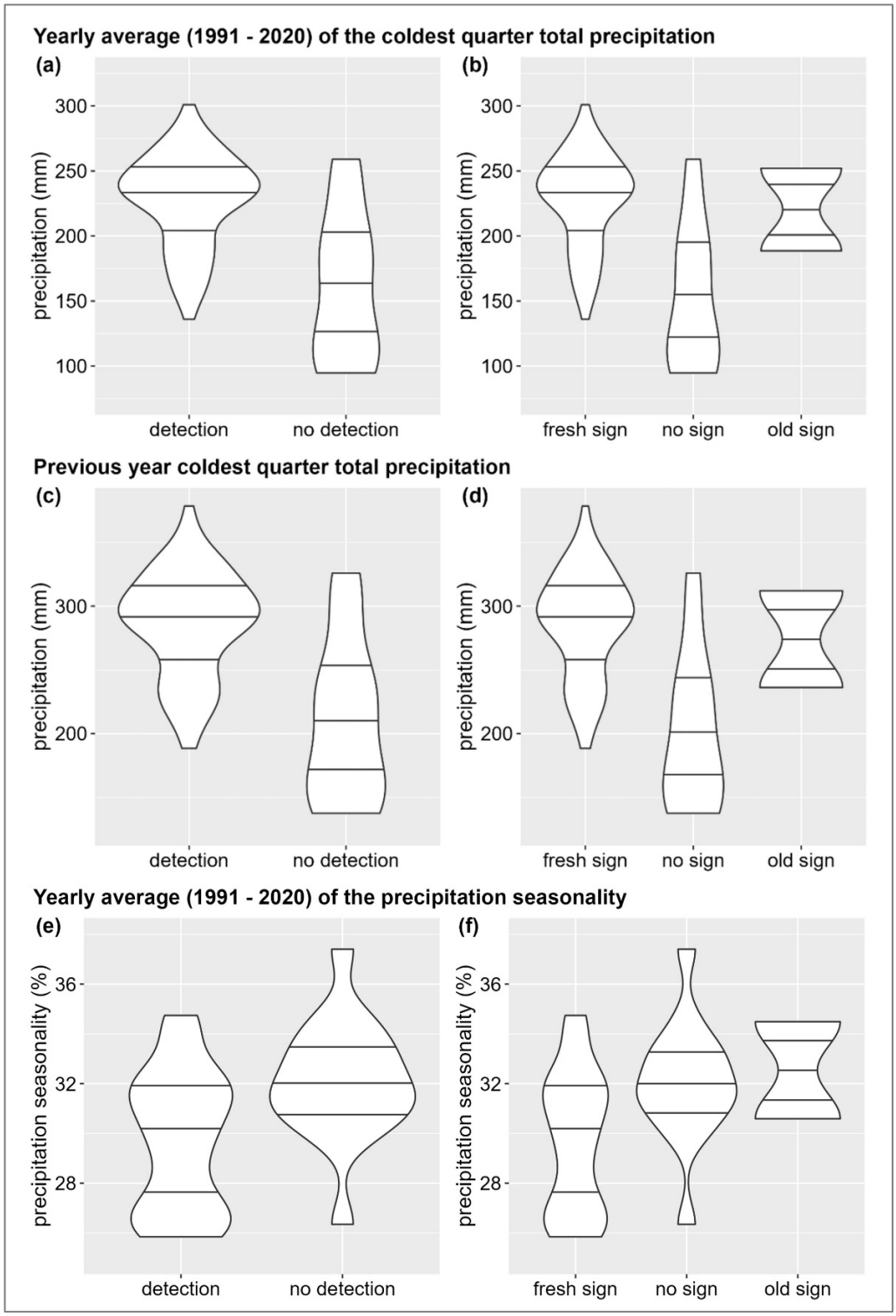

Figure 14. Covariate values at n=115 survey plots in late summer of 2022 at Great Sand Dunes National Park and Preserve, summarized by pika detection metrics using a binary classification (detection or no detection of fresh sign; panels a, c and e) or distinguishing fresh from old and no sign (panels b, d and f). "Yearly average" panels (a, b, e and f) are based on 1991-2020 normals. "Previous year" panels (c and d) are based on December 2021-February 2022 summaries (see Appendix A for details of each plot covariate).

Appendix E: Exploratory data analysis for the leporid dataset (Figures 15—17)

Figures 15—17 show exploratory data analysis for the 2022 leporid dataset.

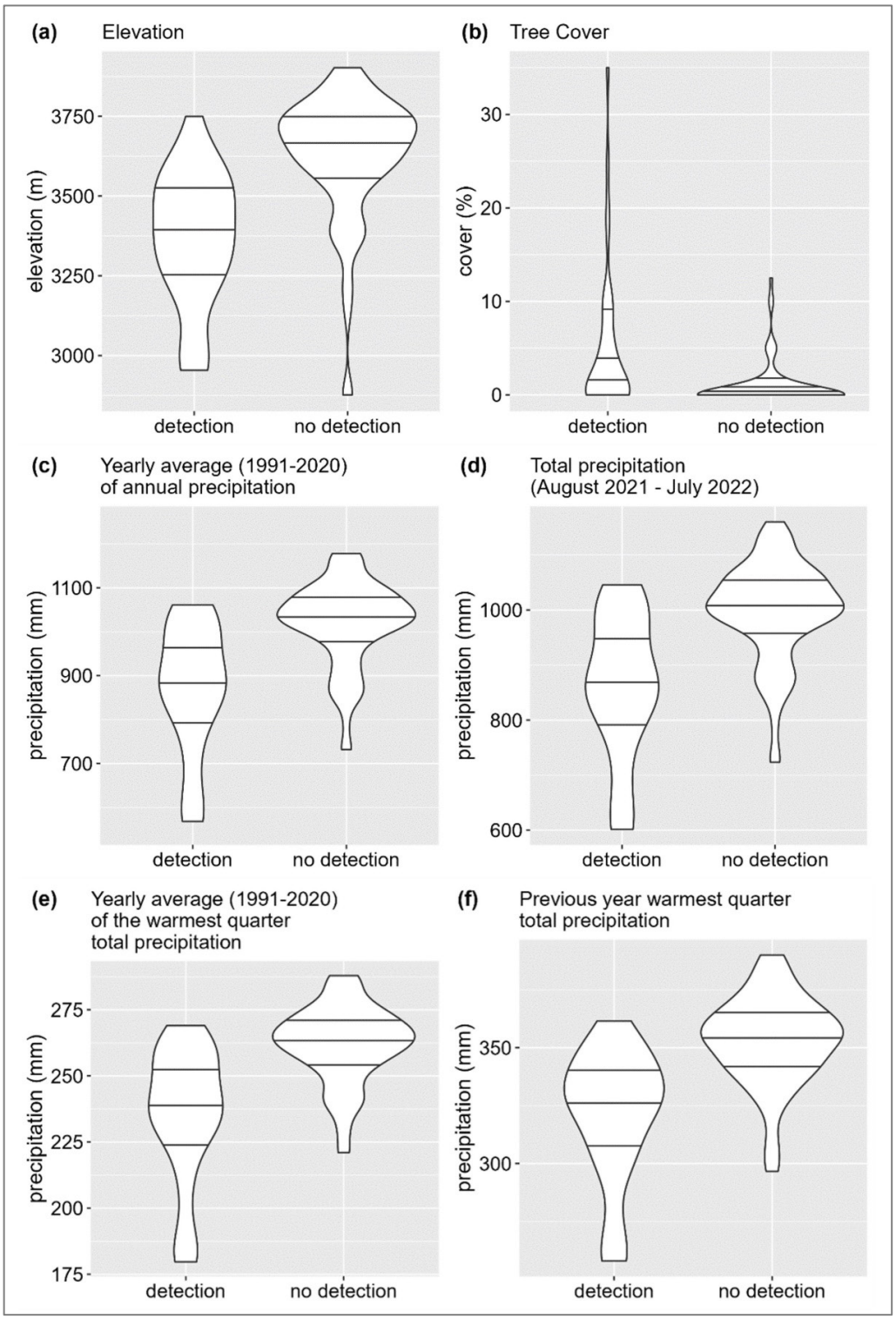

Figure 15. Covariate values at n=115 survey plots in late summer of 2022 at Great Sand Dunes National Park and Preserve, summarized by leporid detection. “Tree cover” refers to percent cover of trees in the pika plot (12 m in diameter). “Yearly average” panels (c and e) are based on 1991-2020 normals. “Previous year” panels (f) are based on June-August 2021 summaries (see Appendix A for details of each plot covariate).

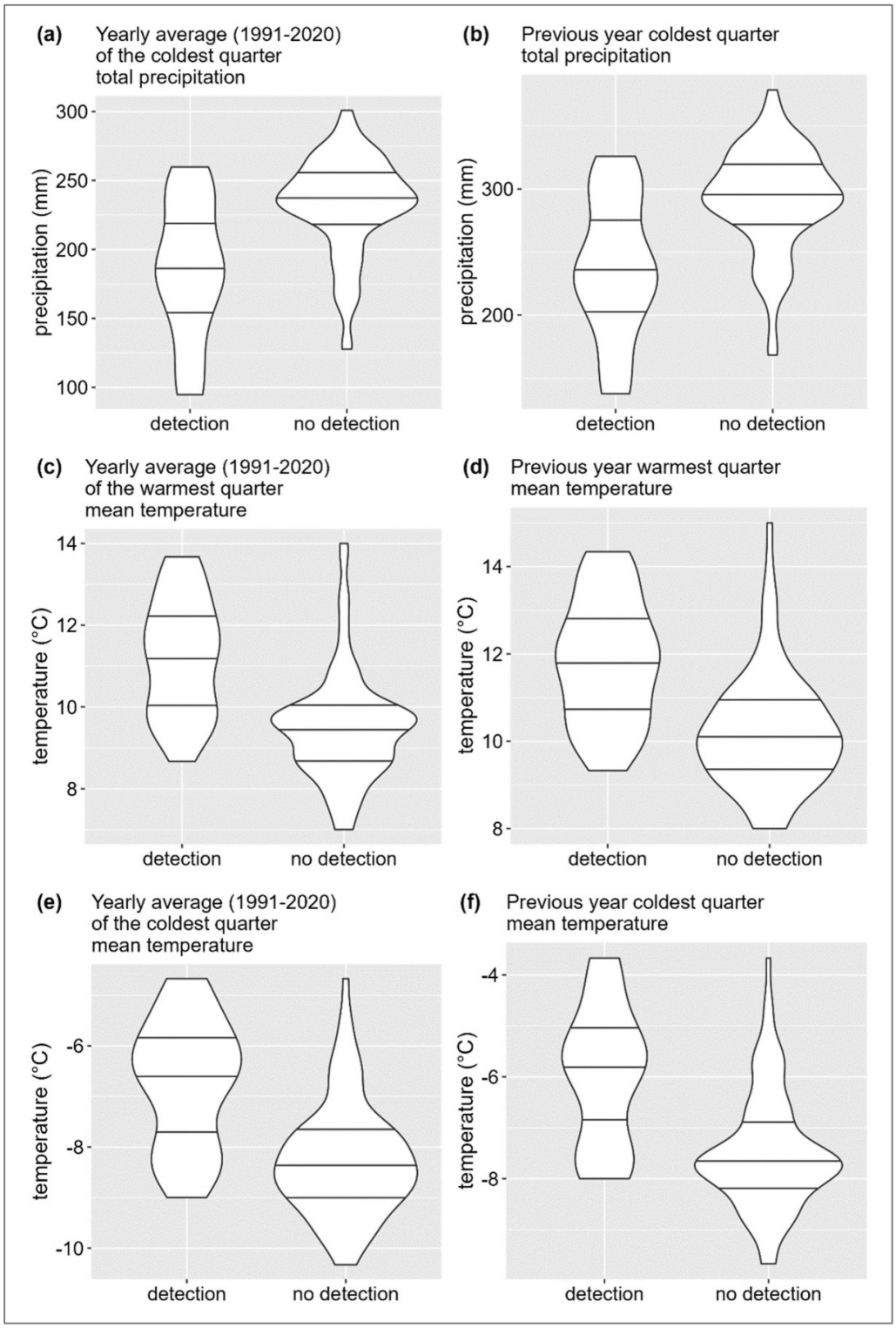

Figure 16. Covariate values at n=115 survey plots in late summer of 2022 at Great Sand Dunes National Park and Preserve, summarized by leporid detection. “Yearly average” panels (a, b, e and f) are based on 1991-2020 normals. “Previous year” panels (c and d) are based on December 2021-February 2022 summaries (see Appendix A for details of each plot covariate).

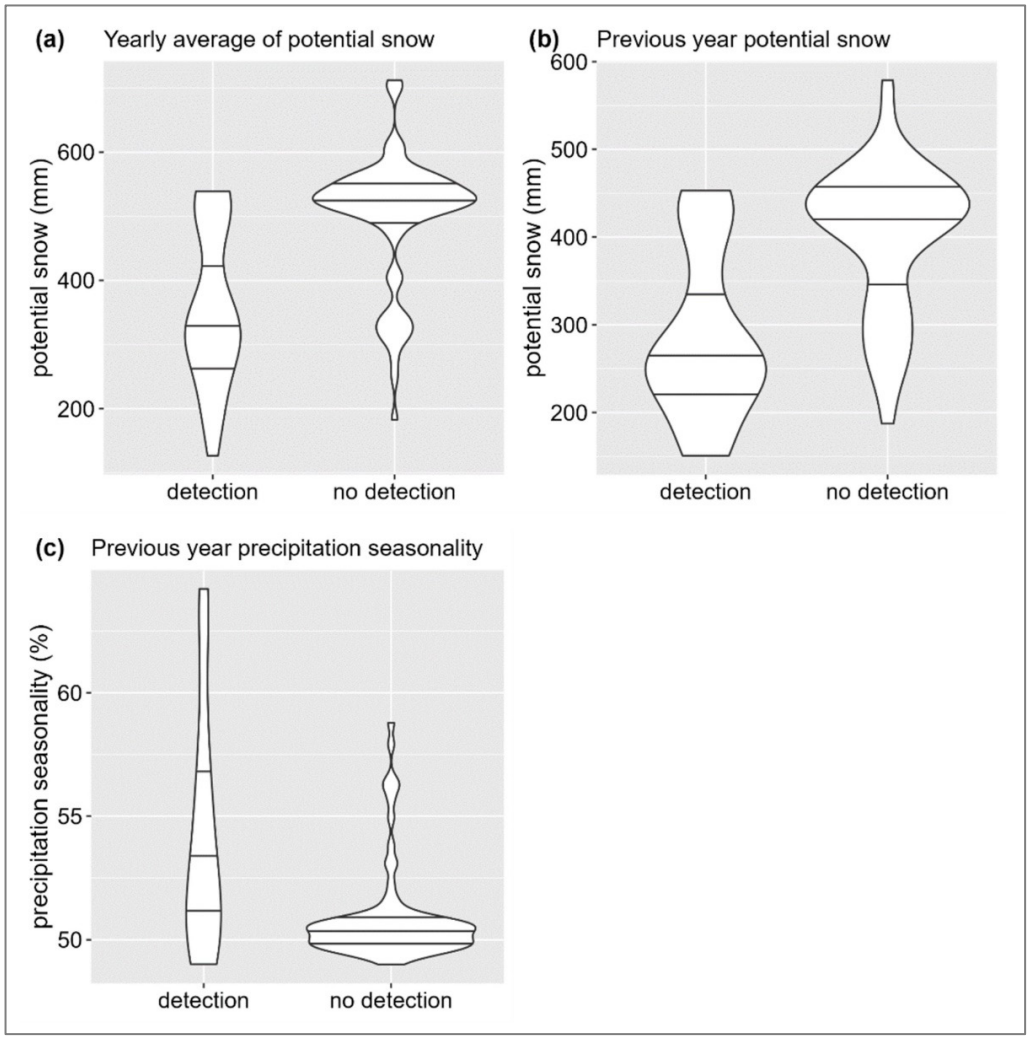

Figure 17. Covariate values at n=115 survey plots in late summer of 2022 at Great Sand Dunes National Park and Preserve, summarized by leporid detection. Yearly average of potential snow (a) is based on 1991-2020 normals from September through May. Previous year potential snow (b) is based on September 2021-May 2022 summaries. Previous year precipitation seasonality (c) is based on 2021 monthly precipitation totals. See potsnowNormal (a), potsnowLag1 (b) and precipSeasonalityLag1 (c) in Appendix A for details of each plot covariate.

Appendix F: Occupancy models

Tables 10—12 show occupancy model statistics.

Table 10. Logistic regression models of naïve pika occupancy (y, uncorrected for detection probability) based on single surveys of 115 plots conducted in late summer of 2022 at Great Sand Dunes National Park and Preserve. Models were designed based on previous studies and ranked by AIC_c, Akaike's information criterion corrected for small sample size. Lower AIC_c values indicate better (more parsimonious) models containing more information per degree of freedom (DF) used in model fit. The weight of evidence (Akaike Wt) in support of model i is a function of $\Delta AIC_{c,i}$, the difference in AIC_c values between model i and the best model.

Model code: ~ logit(*y*) covariates	**DF**	**AIC_c**	**ΔAIC_c**	**Akaike Wt**
~ elevation + precipTotalWarmQtrLag1 + solRad1100m	4	57.16	0.00	0.31
~ elevation + precipTotalWarmQtrNormal + solRad1100m + slope12m + I(slope12m^2) [A]	6	58.45	1.29	0.16
~ elevation + precipTotalWarmQtrLag1 + northeastness	4	58.69	1.53	0.15
~ elevation + precipTotalWarmQtrLag1 + solRad1100m + slope12m + I(slope12m^2)	6	59.28	2.12	0.11
~ elevation + precipTotalWarmQtrLag1 + solRad12m	4	59.50	2.34	0.10
~ elevation + precipTotalColdQtrLag1 + tempColdQtrLag1 + solRad12m	5	60.24	3.08	0.07
~ elevation + precipTotalWarmQtrLag1 + tempWarmQtrLag1 + solRad12m	5	60.94	3.78	0.05
~ elevation + precipTotalColdQtrNormal + tempColdQtrNormal + solRad12m	5	61.67	4.51	0.03
~ elevation + precipTotalWarmQtrNormal + tempWarmQtrNormal + solRad12m	5	62.33	5.17	0.02
~ tempWarmQtrNormal + solRad1100m + grassCover + I(grassCover^2) + forbCover + I(forbCover^2)	7	74.11	16.95	0.00
~ tempWarmQtrLag1 + solRad1100m + grassCover + I(grassCover^2) + forbCover + I(forbCover^2)	7	74.63	17.47	0.00
~ precipTotalWarmQtrLag1 + precipSeasonalityLag1 + solRad1100m + precipTotalColdQtrLag1 + potsnowLag1	6	78.54	21.38	0.00
~ precipTotalWarmQtrNormal + precipSeasonalityNormal + solRad1100m + potsnowNormal	5	81.57	24.41	0.00
~ tempWarmQtrLag1 + solRad12m + grassCover + I(grassCover^2) + forbCover + I(forbCover^2)	7	89.67	32.51	0.00

[A] Terms of the form I(x^2) are equivalent to x^2

Table 10 (continued). Logistic regression models of naïve pika occupancy (y, uncorrected for detection probability) based on single surveys of 115 plots conducted in late summer of 2022 at Great Sand Dunes National Park and Preserve. Models were designed based on previous studies and ranked by AIC_c, Akaike's information criterion corrected for small sample size. Lower AIC_c values indicate better (more parsimonious) models containing more information per degree of freedom (DF) used in model fit. The weight of evidence (Akaike Wt) in support of model i is a function of $\Delta AIC_{c,i}$, the difference in AIC_c values between model i and the best model.

Model code: ~ logit(*y*) covariates	**DF**	**AIC_c**	**ΔAIC_c**	**Akaike Wt**
~ tempWarmQtrLag1 + northeastness + grassCover + I(grassCover^2) + forbCover + I(forbCover^2)	7	90.59	33.43	0.00
~ tempWarmQtrNormal + solRad12m + grassCover + I(grassCover^2) + forbCover + I(forbCover^2)	7	90.91	33.75	0.00
~ tempWarmQtrNormal + northeastness + grassCover + I(grassCover^2) + forbCover + I(forbCover^2)	7	91.43	34.27	0.00
~ precipTotalWarmQtrNormal + precipSeasonalityNormal + solRad12m + potsnowNormal	5	92.62	35.46	0.00
~ precipTotalWarmQtrLag1 + precipSeasonalityLag1 + solRad12m + precipTotalColdQtrLag1 + potsnowLag1	6	93.67	36.51	0.00
~ 1	1	94.81	37.65	0.00

[A] Terms of the form I(x^2) are equivalent to x^2

Table 11. Hierarchical logistic regression models of leporid detection probability (p) and occupancy (ψ) based on 115 plots surveyed once (n = 90) or twice (n = 25) in late summer of 2022 at Great Sand Dunes National Park and Preserve. Using an intercept-only model of occupancy (~ 1), these models were ranked by AIC_c to select a single detection model for use in all candidate models of occupancy (Table 12). See Table 10 for column definitions.

Model code: ~ logit(*p*) covariates ~ logit(*ψ*) intercept only	DF	AIC_c	ΔAIC_c	Akaike Wt
~ shrubCover + grassCover + (1|observer)[A] ~ 1	5	160.45	0.00	0.20
~shrubCover + (1|observer) ~ 1	4	161.47	1.03	0.12
~ shrubCover + forbCover + (1|observer) ~ 1	5	162.06	1.62	0.09
~ shrubCover + grassCover + temperature + (1|observer) ~ 1	6	162.20	1.76	0.08
~ shrubCover + grassCover + temperature2 + (1|observer) ~ 1	6	162.20	1.76	0.08
~ shrubCover + grassCover + forbCover + (1|observer) ~ 1	6	162.22	1.77	0.08

[A] Random effect of observer on the intercept of the detection sub-model.

Table 11 (continued). Hierarchical logistic regression models of leporid detection probability (p) and occupancy (ψ) based on 115 plots surveyed once (n = 90) or twice (n = 25) in late summer of 2022 at Great Sand Dunes National Park and Preserve. Using an intercept-only model of occupancy (~ 1), these models were ranked by AIC_c to select a single detection model for use in all candidate models of occupancy (Table 12). See Table 10 for column definitions.

Model code: ~ logit(p) covariates ~ logit(ψ) intercept only	DF	AIC_c	ΔAIC_c	Akaike Wt
~ grassCover + (1|observer) ~ 1	4	162.45	2.01	0.07
~ shrubCover + temperature + (1|observer) ~ 1	5	162.81	2.36	0.06
~ shrubCover + temperature2 + (1|observer) ~ 1	5	162.81	2.36	0.06
~ temperature2 + (1|observer) ~ 1	4	164.63	4.19	0.03
~ temperature + (1|observer) ~ 1	4	164.63	4.19	0.03
~ (1|observer) ~ 1	3	165.14	4.70	0.02
~ forbCover + (1|observer) ~ 1	4	165.89	5.45	0.01
~ surveyTime + (1|observer) ~ 1	4	166.22	5.77	0.01
~ rock10thLargest + (1|observer) ~ 1	4	166.87	6.42	0.01
~ bareCover + (1|observer) ~ 1	4	166.89	6.45	0.01
~ rockLargest + (1|observer) ~ 1	4	167.94	6.49	0.01
~ 1 ~ 1	2	167.16	6.72	0.01
~ skies + (1|observer) ~ 1	4	168.78	8.33	0.00
~ (1|observer) + (1|plotID) ~ 1	4	169.31	8.66	0.00

[A] Random effect of observer on the intercept of the detection sub-model.

Table 12. Hierarchical logistic regression models of leporid detection probability (p) and occupancy (ψ) based on 115 plots surveyed once (n = 90) or twice (n = 25) in late summer of 2022 at Great Sand Dunes National Park and Preserve. Using the best model of detection from Table 11, candidate occupancy models were ranked by AIC_c. See Table 10 for column definitions. All candidate models with AIC_c less than the null model are shown here.

Model code: ~ logit(p) covariates ~ logit(ψ) covariates	**DF**	**AIC_c**	**ΔAIC_c**	**Akaike Wt**
~ shrubCover + grassCover + (1|observer) ~ elevation + solRad12m	7	130.21	0.00	0.10
~ shrubCover + grassCover + (1|observer) ~ elevation	6	130.26	0.05	0.10

Table 12 (continued). Hierarchical logistic regression models of leporid detection probability (p) and occupancy (ψ) based on 115 plots surveyed once (n = 90) or twice (n = 25) in late summer of 2022 at Great Sand Dunes National Park and Preserve. Using the best model of detection from Table 11, candidate occupancy models were ranked by AIC_c. See Table 10 for column definitions. All candidate models with AIC_c less than the null model are shown here.

Model code: ~ logit(p) covariates ~ logit(ψ) covariates	**DF**	**AIC_c**	**ΔAIC_c**	**Akaike Wt**
~ shrubCover + grassCover + (1|observer) ~ elevation + northern_exposure	7	130.53	0.32	0.08
~ shrubCover + grassCover + (1|observer) ~ elevation + precipTotalAnnualLag1	7	130.56	0.34	0.08
~ shrubCover + grassCover + (1|observer) ~ elevation + potsnowLag1	7	130.74	0.53	0.08
~ shrubCover + grassCover + (1|observer) ~ elevation + tempColdQtrLag1	7	130.75	0.54	0.08
~ shrubCover + grassCover + (1|observer) ~ elevation + tempWarmQtrLag1	7	130.94	0.73	0.07
~ shrubCover + grassCover + (1|observer) ~ elevation + potsnowNormal	7	131.08	0.87	0.06
~ shrubCover + grassCover + (1|observer) ~ elevation + eastern_exposure	7	131.36	1.15	0.06
~ shrubCover + grassCover + (1|observer) ~ elevation + precipSeasonalityLag1	7	131.48	1.27	0.05
~ shrubCover + grassCover + (1|observer) ~ elevation + grassCover	7	131.72	1.51	0.05
~ shrubCover + grassCover + (1|observer) ~ elevation + forbCover	7	131.98	1.77	0.04
~ shrubCover + grassCover + (1|observer) ~ elevation + northeastness	7	131.99	1.78	0.04
~ shrubCover + grassCover + (1|observer) ~ elevation + shrubCover	7	132.04	1.83	0.04
~ shrubCover + grassCover + (1|observer) ~ elevation + precipTotalWarmQtrLag1	7	132.07	1.86	0.04
~ shrubCover + grassCover + (1|observer) ~ elevation + slope12m + I(slope12m^2)	8	132.42	2.21	0.03
~ shrubCover + grassCover + (1|observer) ~ biome	6	140.36	10.14	0.00
~ shrubCover + grassCover + (1|observer) ~ treeCover	6	150.77	20.55	0.00
~ shrubCover + grassCover + (1|observer) ~ precipSeasonalityNormal	6	156.43	26.22	0.00
~ shrubCover + grassCover + (1|observer) ~ shrubCover	6	157.69	27.48	0.00
~ shrubCover + grassCover + (1|observer) ~ precipTotalWarmQtrNormal	6	159.31	29.10	0.00
~ shrubCover + grassCover + (1|observer) ~ precipTotalWarmQtrLag1	6	159.50	29.28	0.00
~ shrubCover + grassCover + (1|observer) ~ forbCover	6	160.25	30.04	0.00
~ shrubCover + grassCover + (1|observer) ~ 1	5	160.45	30.23	0.00
~ shrubCover + grassCover + (1|observer) ~ eastern_exposure	6	160.74	30.53	0.00

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