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Determinants of pika population density vs. occupancy in the Southern Rocky Mountains

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Abstract. Species distributions are responding rapidly to global change. While correlative studies of local extinction have been vital to understanding the ecological impacts of global change, more mechanistic lines of inquiry are needed for enhanced forecasting. The current study assesses whether the predictors of local extinction also explain population density for a species apparently impacted by climate change. We tested a suite of climatic and habitat metrics as predictors of American pika (*Ochotona princeps*) relative population density in the Southern Rocky Mountains, USA. Population density was indexed as the density of pika latrine sites. Negative binomial regression and AIC_c showed that the best predictors of pika latrine density were patch area followed by two measures of vegetation quality: the diversity and relative cover of forbs. In contrast with previous studies of habitat occupancy in the Southern Rockies, climatic factors were not among the top predictors of latrine density. Populations may be buffered from decline and ultimately from extirpation at sites with high-quality vegetation. Conversely, populations at highest risk for declining density and extirpation are likely to be those in sites with poor-quality vegetation.

Key words: *American pika; climate change; forbs; graminoids; habitat quality; latrines; occupancy;* Ochotona princeps; *population density; Southern Rocky Mountains, USA; vegetation quality.*

Introduction

Climate change is a key driver of species distributional shifts worldwide (e.g., Lenoir et al. 2008, Chen et al. 2011). Occupancy studies documenting local extinctions and range shifts have been vital to our understanding of the ecological effects of climate change (Chen et al. 2011). However, it is not enough to understand which habitat metrics best predict occupancy; some occupied sites may be "sinks" that receive immigrants from suitable habitat (Pulliam 1988). Studies of population density may be required to presage populations at risk (Pimm et al. 1988).

In order to better manage species threatened by global change, scientists must move toward a more mechanistic line of inquiry (Guralnick et al. 2011). Explaining patterns in population density represents one step toward inferring the mechanics of range shift, given that dwindling populations are often a precursor to local extinction (Pimm et al. 1988, Gaston et al. 2000). More generally, studies of population density are needed to better illustrate the occupancy–abundance relationship, which has been characterized as mainly positive but sometimes variable across taxa (Gaston et al. 2000, Holt et al. 2002). Here we ask whether the determinants of occupancy align with those of population density, using data from a species widely noted for recent declines in occupancy.

The American pika (*Ochotona princeps*), a small lagomorph, is closely associated with rocky debris such as talus slopes and lava beds and is further limited to relatively cool summer and wet winter climates in western North America (Smith and Weston 1990, Hafner 1994). Although pikas can escape extreme weather by using the subsurface microclimates created by large-diameter rocky debris (MacArthur and Wang 1974, Millar and Westfall 2010), they are sensitive to variation in summer temperature and winter snowpack (Smith 1974, Beever et al. 2011). Pika distribution is often predicted by both climatic and vegetation-based factors (Millar and Westfall 2010, Jeffress et al. 2013) and there is accumulating evidence linking decline in pika occupancy to climatic and microclimatic factors (Beever et al. 2010, Erb et al. 2011). However, frequency of extirpation varies by region. In the Southern Rocky Mountains, relatively few extirpations have been documented (Erb et al. 2011), providing an opportunity to investigate the drivers of density among intact populations.

Occupancy patterns in the Southern Rockies indicate that climatic and habitat factors structure pika distribution. In an assessment of the predictive power of multiple habitat and climatic variables, recent (2008–2011) occupancy patterns were best explained by precipitation, vegetation quality, and summer tempera-

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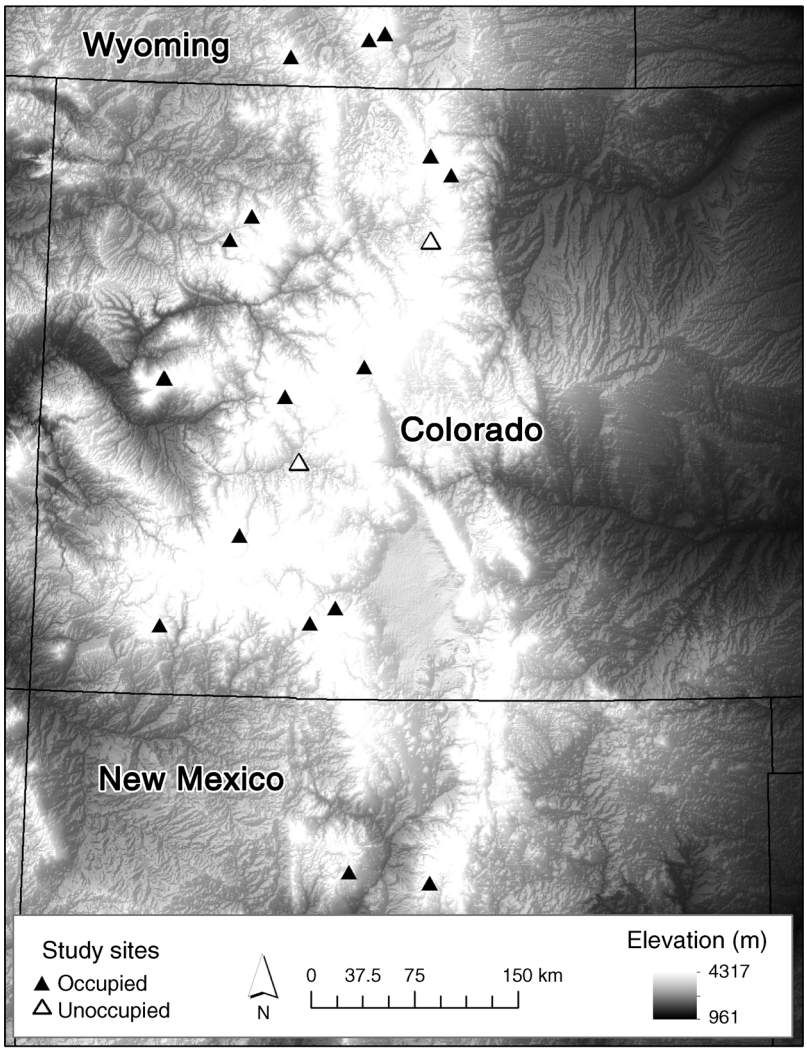

FIG. 1. Map of 18 study sites in the Southern Rocky Mountains, USA, at which pika (*Ochotona princeps*) latrine density was evaluated. All study sites were occupied by pikas at some point prior to 1980.

ture metrics (Erb et al. 2011; L. P. Erb, R. Guralinick, and C. Ray, *unpublished manuscript*). Here we employ the same suite of potential predictors to model pika latrine density, as a metric of relative population density, using generalized linear models ranked via AIC_c (Akaike's information criterion corrected for small sample sizes). If similar factors predict both occupancy and relative density, these predictors could be used to determine which populations are at highest risk of extirpation in the near future.

METHODS

Study area

Pika latrine density was assessed at 18 sites in the Southern Rocky Mountains of New Mexico, Colorado, and southern Wyoming, USA (35°20′ to 41°30′ N and 104°54′ to 108°17′ W). These sites were selected from among 69 historically occupied sites (see Erb et al. 2011) via random sampling stratified by latitude, longitude, and elevation. These 18 sites represented a similar distribution of climatic predictors as the original 69 (Appendix A). Vegetation varied among sites from upper montane forest to alpine meadow. Selected sites ranged from 2703 to 3708 m in elevation (3250 ± 302 m, mean ± SD; Fig. 1) and each was sampled for pika latrine density in both 2009 and 2010. At sites with multiple talus patches, the largest talus patch was selected for pika sampling as well as habitat characterization (Erb et al. 2011).

Quantifying pika latrine density

The density of fresh scat piles (latrines) was assessed using a transect-based design, with transects positioned relative to a "control point" located at the lowest instance of rocky debris at the site. A base transect was established 10 m upslope of the control point running

perpendicular to the dominant site aspect (e.g., toward 120°/300° if the dominant site aspect was 30°). Subsequent transects were established upslope and parallel to the base transect at 60-m intervals (distances are actual, not elevational). The number of transects per site varied between one and six, depending on the extent of rocky debris (hereafter, "talus"). A spacing of 60 m between transects ensured that each pika sign was counted only once in our surveys, given an average pika territory diameter of 25 m (Smith and Weston 1990). Each transect was just as long as the talus was wide. Most transects were <150 m long (62.3 ± 46.1 m, mean ± SD); however, where transects were longer than 150 m ($n = 3$), only the middle 100 m and 25 m at each end were sampled.

In our pilot year of 2009, crews recorded all fresh haypiles (pika food stores), fresh latrines, and individual pikas observed within 30 m of transects. Fresh hay and latrines were determined by the presence of green pigment in constituent plant material. Pikas are coprophagous and produce both caecal feces, which are reingested, and fecal pellets, which are not. In our study of latrines, only fecal pellets were examined for evidence of deposition within the current year. The green color within fecal pellets has been documented to disappear within months of deposition (Nichols 2010). Paired observers walked each transect, with one observer focused downslope and the other focused upslope, while both observed sign directly on the transect. Paired observers conferred frequently and recorded each sign only once. Independent observations were obtained by having two independent pairs walk each transect on different days. Averaging across sites in 2009, 82% of fresh latrines were recorded by the observer looking upslope. Because pika scat is generally deposited under sheltering rocks, making latrines easier to see when looking upslope, we discontinued downslope observations in 2010 and omitted downslope data from all analyses.

Fresh latrine counts were the most consistently available sign of current pika activity, probably due to variation in pika behavior at different population densities (C. Ray and L. Erb, *personal observations*) and in different weather conditions (Hayes and Huntly 2005), as well as climatic and seasonal effects on pika haying behavior (Smith and Weston 1990, Dearing 1996). Consequently, we used the density of fresh pika latrines as our metric of relative population density.

To limit the influence of observer error, density analyses were based on observations within 2 m of transects, where most latrines (mean ± SE = 84.4% ± 15.8%) were observed in this study. Given a standard transect length of 150 m, latrine density (number per standard transect) was calculated as $y = N/L \times 150$, where N was the total number of fresh latrines observed at the site and L was the total length of transects surveyed at the site. All density estimates (two from 2009 and two from 2010) were averaged to generate our response variable, minimizing effects of environmental stochasticity and observer bias.

Characterization of climate

For each site, we calculated five climate metrics representing potential stressors (Table 1). Mean annual precipitation and mean summer temperature maxima were obtained for the years 2008–2011 (4-km grid cell) via the PRISM interpolated climate data set (*available online*).[5] Pika occupancy has been predicted in part by mean annual precipitation in the Southern Rocky Mountains (Erb et al. 2011; L. P. Erb, R. Guralnick, and C. Ray, *unpublished manuscript*) and high summer temperatures in the Great Basin (Beever et al. 2011, Wilkening et al. 2011).

Subsurface temperatures were used to characterize the microclimate in the talus at these sites. HOBO temperature data loggers (Onset U10-003, Natick, Massachusetts, USA) were buried in the talus at a mean depth of 75 cm. Four loggers were installed at each site, one under each of four randomly selected haypiles. Where fewer than four fresh haypiles were available ($n = 4$ sites), remaining loggers were buried under old haypiles or latrines. Where no pika sign occurred ($n = 2$ sites), loggers were buried in locations with large rocks and deep talus to mimic pika haypile site selection (C. Ray and L. Erb, *personal observations*). Loggers were installed between July 2008 and July 2009 and recorded temperature every 30 minutes until removal in September 2011.

Cold stress was quantified as the percentage of subsurface temperatures below −10°C recorded at each site, a metric that predicted pika occupancy patterns in the Great Basin (Beever et al. 2010). Subsurface heat stress was quantified as the percentage of temperatures above 25°C and (alternatively) as the mean summer (June–August) temperature recorded at each site. Mean summer temperature has explained pika occupancy patterns in the Great Basin (Beever et al. 2010) and the Southern Rockies (L. P. Erb, R. Guralnick, and C. Ray, *unpublished manuscript*), and pikas held above the talus have died at surface temperatures as low as 25.5°C (Smith 1974).

Characterization of habitat

Maximum talus depth was estimated visually at the deepest crevice observed within each site. Subsurface water was categorized as present where it was seen or heard or where riparian vegetation was observed at the base of the site (Erb et al. 2011). Deeper taluses and those with subsurface water sources should provide a more stable microclimate (Ray et al. 2012).

Vegetation communities were characterized using methods modified from Wilkening et al. (2011). Three data logger locations at each site were randomly selected

[5] www.prism.oregonstate.edu

TABLE 1. Predictor descriptions, expected relationships to pika population density, weighted average coefficients, and Akaike weights; top predictors are in boldface.

Predictor description	Expected relationship with density	Weighted average coefficient	CV of coefficient estimate	Akaike weight
Climate				
Mean annual precipitation, PRISM 2008–2011 (mm)	+	0.539	0.217	0.209
Subsurface summer mean temperature; mean June, July, August temperatures from data loggers 2009–2011 (°C)	−	−0.340	−0.710	0.113
Subsurface summer maximum temperature; percentage of recorded temperatures above 25°C	−	−0.096	−4.212	0.055
Surface summer maximum temperature; mean June, July, August monthly PRISM maxima 2008–2011 (°C)	−	−0.292	−0.87	0.092
Subsurface winter minimum temperature; percentage of recorded subsurface temperatures below −10° C	−	−0.442	−0.383	0.204
Habitat quality: talus				
Talus depth (m)	+	0.198	0.783	0.067
Sub-talus water source	+	−0.078	−0.713	0.057
Habitat quality: vegetation				
Vegetation cover (%)	+	−0.188	2.64	0.078
Graminoid : forb (cover ratio)	−	**−0.642**	**−0.367**	**0.251**
Forb species richness (no. species)	+	**0.594**	**0.335**	**0.260**
Percent cover of forbs, grasses, and shrubs	+	0.415	0.410	0.137
Percentage of vegetation consisting of forbs	+	0.427	2.39	0.173
Habitat quantity				
Rock cover (%)	−	−0.504	−0.520	0.131
Talus area (m^2)	−	**−0.698**	**−0.15**	**0.661**
Overall habitat quality				
Rock cover × vegetation cover	+	−0.434	−0.415	0.123

for vegetation sampling. At each of these three logger locations, vegetation was sampled along three parallel transects, each 50 m long: a central transect, centered on the logger and running perpendicular to the dominant aspect of the site, along with transects 15 m upslope and downslope of the logger. Vegetation was quantified at 1-m intervals using the line-point-intercept method (as in Wilkening et al. 2011), resulting in 150 points per logger location and 450 points per site. All trees, shrubs, and forbs were identified to species level, while grasses, sedges, and rushes were classed as graminoids. We considered several vegetation metrics consistent with recent studies of pika occupancy (Rodhouse et al. 2010, Wilkening et al. 2011, Jeffress et al. 2013). Total percent cover of vegetation was our measure of available forage for this generalist species. Forage highly accessible to pikas was represented by the combined percent cover of forbs, graminoids, and shrubs, omitting only tree cover. Percent forb cover, forb species richness, and the ratio of graminoids to forbs (gram : forb) were all considered metrics of forage quality.

Cover at ground level was also classed at each transect point as soil, rock, or litter. Although highly associated with talus, pikas occur mainly at the edges of rocky habitats where forage is easily accessed (Smith and Weston 1990). Thus, we anticipated a negative relationship between rock cover and latrine density, sites with lower rock cover providing greater foraging opportunities. Similarly, talus patch size effects were expected to follow Kawamichi (1982), who showed a trend in *O. princeps* toward smaller home ranges resulting in higher densities in small patches. Patch size was measured as the area of large-diameter (>20 cm) rocky debris contained within each talus patch surveyed for latrine density.

Statistical analysis

Negative binomial models of latrine density were developed and compared using AIC_c (Burnham and Anderson 2002). Our goal was to evaluate the relative support for each of 15 predictor variables (Table 1). We considered all possible models incorporating three or fewer predictors. By considering each predictor in a variety of contexts, we developed an unbiased ranking to facilitate the comparison of predictors of latrine density with predictors of habitat occupancy. Models were fitted in R (R Development Core Team 2012) using function glm.nb (Venables and Ripley 2002). We considered a mixed-distribution model to address pika occupancy and density as separate processes, but a Kolmogorov-

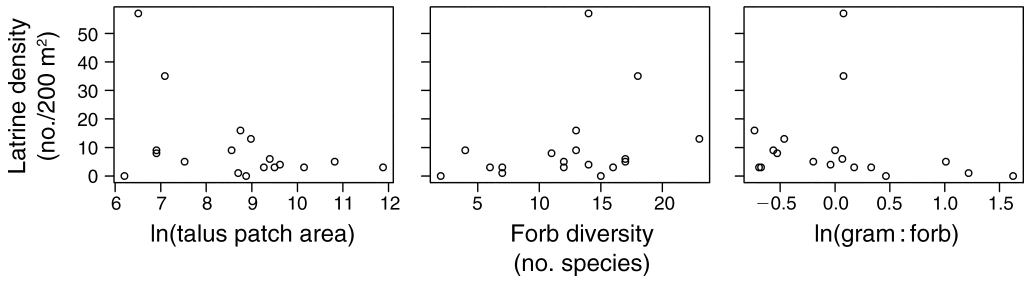

FIG. 2. Pika latrine density vs. the top three density predictor variables, determined by Akaike weights. Predictor variable units appear in Table 1; gram : forb refers to the ratio between percent cover of graminoids vs. forbs.

Smirnov test indicated no excess zeros (absences) in our response variable. Several variables were log-transformed to reduce skew, and each continuous predictor variable X_i was standardized as $Z_i = (X_i - \mu(X_i))/\sigma(X_i)$, allowing for intuitive interpretation of model coefficients (β_i): each β_i measures the effect of X_i in units of standard deviation in X_i. Model rank was determined using AIC_c and predictor influence was assessed via Akaike weights. Model fit was evaluated using Nagelkerke's maximum-rescaled R^2 (R^2_N), which measures model performance relative to the null model (Nagelkerke 1992).

RESULTS

Across our 18 study sites, the range in pika latrine densities was 0–57 latrines/200 m^2 (10 ± 14.3 latrines/200 m^2; all data reported as mean ± SD unless otherwise noted; Appendix B). Two of our sites lacked any fresh pika sign throughout our survey period (Fig. 1). The range in mean PRISM summer maximum temperatures was 15.9–22.3°C (18.9° ± 1.6°C); the range in mean subsurface summer maximum temperatures was 8.57–20.6°C (13.3° ± 3.1°C). Mean subsurface summer temperatures had a range of 6.4–16.8°C (10.6° ± 2.9°C) and the precipitation range was 432.9–1476.5 mm (890.9 ± 259.8 mm). One site experienced no subsurface temperatures below −10°C. At the remaining 17 sites, the percentage of subsurface temperatures below −10°C ranged from 0.01% to 8% (1.7% ± 2.2%).

Talus patch area ranged from 495 to 144 000 m^2 (17 180 ± 33 831 m^2) and rock cover ranged from 24% to 83% (54% ± 17%) among sites. Vegetation cover ranged from 18% to 55% ($\mu = 35\%$, $\sigma = 11\%$) and accessible forage cover (omitting trees) ranged from 7% to 54% (28% ± 11%). Vegetation composition was highly variable, with cover values ranges of 9–59% (32% ± 18%) for forbs, 0.5–5.1% (1.4% ± 1.2%) for gram : forb, and 2–23% (12.3% ± 5.4%) for forb species richness.

Results of modeling showed that the best predictor of pika latrine density in the Southern Rockies was patch area. After area, vegetation quality metrics were the best predictors among other climate and habitat variables. Of our 15 predictors, 12 demonstrated expected relationships with density (Table 1). Sites with smaller patch area, higher forb species richness, and lower gram : forb ratios demonstrated the highest pika densities (Table 1, Fig. 2). The top model included patch area and subsurface minimum temperature, with $R^2_N = 0.47$; however, there were 13 additional models that were equally explanatory, with $\Delta AIC < 2$ and $R^2_N > 0.30$ (Appendix C). Predictor weights supported the importance of patch area and forage quality in determining pika latrine densities (Table 1).

DISCUSSION

Our results indicate that patch area and vegetation metrics determine pika latrine density in the Southern Rocky Mountains. The importance of patch area, the ratio of graminoids to forbs, and forb diversity indicates that forage accessibility and quality drive relative pika density patterns in this region. This finding is consistent with studies of occupancy in the western United States, which indicate that *Ochotona princeps* occupancy and/or persistence are predicted by graminoid cover (negative effect; Rodhouse et al. 2010, Jeffress et al. 2013; L. P. Erb, R. Guralinick, and C. Ray, *unpublished manuscript*), forb cover (positive effect; Wilkening et al. 2011, Jeffress et al. 2013; L. P. Erb, R. Guralinick, and C. Ray, *unpublished manuscript*), and forb richness (positive effect; L. P. Erb, R. Guralinick, and C. Ray, *unpublished manuscript*). Our results support the likelihood of a positive occupancy–abundance relationship for pikas, as has been found for many other taxa (Gaston et al. 2000, Holt et al. 2002).

It is notable that vegetation structure, especially the graminoid–forb relationship (gram : forb), may reflect local climate (Box 1996) and may be affected by the pika's selective foraging behavior (Huntly et al. 1986, Dearing 1997). If gram : forb is a more comprehensive metric of local climate than PRISM or our own local data, pikas may be responding directly to climate rather than vegetation quality. Although we cannot rule out this possibility, we can rule out effects of pika density on the gram : forb ratio. Pikas are known to prefer forbs over graminoids (Huntly et al. 1986, Dearing 1997). As suggested by Rodhouse et al. (2010), the selective removal of forbs should generate a positive relationship between the gram : forb and pika occurrence; however, our study is the first to confirm that relative pika density scales negatively with gram : forb. This result, combined with our other observations, suggest that there are direct

effects of forage quality mediating the pika's response to climate and climatic changes.

The negative relationship between patch area and latrine density is probably the result of edge effects at the rock–meadow interface. Kawamichi (1982) found a similar area–density result for this species, suggesting that reduced territory size is sustainable where a larger perimeter-to-area ratio increases access to forage. Other herbivores have been documented to show preference for smaller patches of habitat (e.g., Hester et al. 1999) and landscape ecology studies have found a similar affinity for edges among small mammals (e.g., Salek et al. 2010).

Supporting the importance of access to forage, our results also suggest that forage quality is an important predictor of relative pika density. The gram : forb ratio is likely to represent the relative abundance of low-quality (graminoid) to high-quality (forb) forage for pikas (Dearing 1997; Smith and Erb 2013). The dominant forbs in these habitats contain higher water and nitrogen content than the dominant graminoids (Smith and Erb 2013). Sites with higher forb diversity and lower gram : forb cover ratios are more likely to provide a variety of highly nutritive forage, reducing the effects of intraspecific competition and allowing relatively higher densities of pikas at such sites.

Due to the high metabolic demands on pikas (Sheafor 2003), nutrient and water availability should limit pika survival and density, especially where high summer temperatures limit foraging time. Smith and Erb (2013) found a positive correlation between mean summer temperature and pika selectivity for plants with higher water content. Thus, selective foraging behavior may mask effects of a warming climate. However, it is an open question whether, and for how long, such behavior can counter the effects of climate change. Higher summer temperatures have predicted pika extinctions in the Great Basin (Beever et al. 2010) and Southern Rockies (L. P. Erb, R. Guralinick, and C. Ray, *unpublished manuscript*).

Our results suggest that vegetation accessibility and quality are important for both occupancy and density patterns in the Southern Rockies. We also did not find strong evidence that relative pika density is predicted directly by climate. These results have theoretical and management implications, especially because summer temperature and mean annual precipitation have been important predictors of pika occupancy throughout the western United States (Beever et al. 2010, Erb et al. 2011). Combining results from pika occupancy and density studies in this region, our findings suggest that some previously suitable habitats are becoming climatically unsuitable (Erb et al. 2011), but the accessibility and quality of forage mediates population response to climate. Although selective foraging can mask the effects of climate to some extent, the buffering ability of vegetation may be limited, especially as vegetation communities show stronger responses to continuing climate change. Given the buffering capacity of higher quality sites, pika populations in regions of low forb diversity and cover are likely to be at more immediate risk of extirpation as climate change accelerates.

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Supplemental Material

Appendix A

Comparison of climatic predictors among 18 study sites and the 69 sites historically occupied by pika from which they were selected via random sampling stratified by latitude, longitude, and elevation (*Ecological Archives* A024-025-A1).

Appendix B

Pika latrine density at 18 sites in the Southern Rocky Mountains (*Ecological Archives* A024-025-A2).

Appendix C

Models predicting pika density with $\Delta AIC < 2$, along with the null model (*Ecological Archives* A024-025-A3).