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Research article

Differential effects of environmental predictability on ungulate movement behavior in disparate ecosystems

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Increasing ecological perturbations resulting from global change processes are altering the environmental predictability (EP) of critical forage and water resources for wildlife. While research has furthered our understanding of how EP both underlies and directs animal movement, studies have mainly focused on relationships between EP and large-scale movement behaviors (e.g. migration) at the species level, neglecting the mediating influence that environmental context has on the behavior of wide-ranging species. We address these knowledge gaps by examining how EP of forage in mule deer *Odocoileus hemionus* – a cosmopolitan species of the American southwest – seasonal home ranges relates to average daily movement distance, focusing on two female populations inhabiting disparate ecoregions in Utah, USA (n = 225, 2015–2022). We employed two separate metrics of EP, representing spatial and temporal constancy of vegetation productivity, and explored how home range (HR) area, forage availability, and season modulate the relationships between EP and daily movement distance. We found spatial constancy of an individual's HR significantly impacted movement during the summer and had significant interactions with HR area and forage availability. Interestingly, individuals inhabiting spatially constant HRs moved more in resource-limited seasonal environments, and less in non-limiting environments. Temporal constancy was a significant predictor of movement in non-limiting seasonal environments, resulting in shorter daily movements of deer with temporally constant HR areas. Finally, we found a significant interaction between spatial and temporal constancy, resulting in shorter daily movements of individuals inhabiting resource-limited HRs that were spatially and temporally constant. Interactions between HR area, forage availability, and constancy metrics demonstrate how the EP may become a larger driver of movement decisions as habitat quality is reduced. Understanding how EP drives movement of

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mule deer aids our ability to predict how global change will impact individual fitness, space use requirements and population demographics of ungulates.

Keywords: climate change impacts, environmental predictability, intraspecific variation, movement ecology, mule deer *Odocoileus hemionus*, spatiotemporal resource availability

Introduction

Animal movements are the product of interactions between an organism and its environment (Mueller and Fagan 2008). Environmental predictability (EP) – reliability of an area in terms of resource availability – has garnered attention as an overarching driver of habitat use and large-scale movement tactics of a wide variety of taxa (bears, Ferguson et al. 1999; giant tortoises, Bastille-Rousseau et al. 2017; whales, Abrahms et al. 2019). Fundamentally, an individual's survival depends on its ability to locate resources, and so EP provides fitness benefits to individuals who are able to exploit it (Albon and Langvatn 1992, Middleton et al. 2018). As such, EP underlies the evolution of cognitive abilities relating to navigation, perception, memory and learning (Mery 2013, Morand-Ferron et al. 2016) which ultimately determine where, when, how, and *if* an organism moves and dictate the degree of plasticity in movement behavior (Mueller and Fagan 2008, Riotte-Lambert and Matthiopoulos 2020). In turn, these abilities direct movement by allowing animals to respond to the contemporary predictability of their environment (Ferguson et al. 1999), which represents a crucial form of environmental information. Under this framework, EP both underlies and directs animal movement and space use, and increasing appreciation for the dual role of EP has produced a fast-growing body of literature on the topic (Mueller and Fagan 2008, Jonzén et al. 2011, Riotte-Lambert and Matthiopoulos 2020).

Ungulates frequently face resource limitations that impact their survival (Bender et al. 2007) and therefore environmental conditions and dynamics play a substantial role in their movement decisions (Senft et al. 1987). At large scales, ungulates' movement tactics allow them to maximize access to high quality forage by timing relocations or life-history events in accordance with vegetation dynamics and choosing areas with available resources (Jonzén et al. 2011, Stoner et al. 2016, Peters et al. 2019). These strategies – observed at the species, population and individual level – necessitate cognitive abilities and movement tactics that are, in theory, reliant on EP of resources. However, research regarding ungulate movement has often included the concept of EP as a factor posited to be encapsulated by the qualitative conditions of the study system (e.g. presumed dynamics of resource-availability within an ecoregion, as in Joly et al. 2021) rather than as a quantitative metric that is empirically tested. To make more conclusive statements about the influence of EP on animal movement, appropriate quantitative measures of EP must be identified and calculated, and their relationship to various movement metrics should be modeled directly. This necessity is underscored by the increasing scale and pace of environmental change occurring under global change processes.

Where predictability has been defined and empirically considered in analyses, a large degree of variation exists. Most studies calculate EP by quantifying some form of spatial or temporal variability or deviation of an environmental variable (most commonly forage) (Mueller et al. 2011, Bastille-Rousseau et al. 2017). Notably, predictability can be decomposed into two separate metrics (Colwell 1974): constancy, the inverse of the variability of resource conditions across space and throughout time; and contingency, the regularity of seasonal cycling. These metrics capture unique components of an organism's resource landscape, by identifying inter- and intra-annual predictability, respectively, and can be used to summarize EP at different spatial and temporal scales.

As movements occur at a wide range of spatial and temporal scales (Senft et al. 1987), predictability must be considered and calculated at the appropriate spatial scale for the type of animal movement considered. Research to date has mainly focused on the relationships between predictability and large-scale movement behaviors, by examining predictability across a populations' range area and relating that to behaviors such as migration (Mueller et al. 2011). Much less is known about EP in regard to its impact on animal movement at finer scales (e.g. its relationships with daily movement distance), where foraging decisions are predicated on food item value and costs associated with movement and digestion (Stephens and Krebs 1986). Understanding how EP impacts daily movements of ungulates is important for management, as it is indicative of time budget and energy balance which can impact overwinter survival (Bender et al. 2007) and litter size (Parker et al. 2009). Daily movement is also a gauge of space required by an individual to meet its daily nutritional needs (Senft et al. 1987), which dictates the carrying capacity of the environment in question (Pastor et al. 1997).

Despite technological advancements in animal-borne sensors and the improved resolution of remote sensing products, many unexplored questions remain about how species respond to EP at ecologically relevant spatial and temporal scales. The response of a species to the predictability of its environment may not be consistent throughout the year, as individuals' ecological requirements fluctuate seasonally (Johnson et al. 2021). Seasonal conditions can alter associated costs and benefits of movement (Robinson and Merrill 2012), which may change animals' proclivity to use EP as a source of information when making movement decisions (Jonzén et al. 2011) or shift whether spatial or temporal predictability provides the most relevant information. Additionally, although research has examined the relationship between predictability and

movement behaviors at the species level, the mediating influence of environmental context is rarely considered despite the gradient of climatic and ecological conditions faced by populations of wide-ranging, habitat generalists. Populations of a given species inhabiting disparate landscapes are confronted with different suites of conditions that impose unique constraints on moving individuals (Singh et al. 2012). As such, movement decisions – and the weight of factors incorporated into those decisions – may vary greatly from one population to another. Indeed, in many ungulate species we observe variation between populations in movement and space use tactics (Bolger et al. 2008, Singh et al. 2012), but the extent to which differences in EP – and its use as a form of information – drives intraspecific variation is seldom examined (but see research on roe deer, Peters et al. 2019). Examining intraspecific variation in movement behavior and its plasticity is important, as differences at the population level can impact large-scale community and ecosystem processes (Des Roches et al. 2018, Shaw 2020).

As environmental predictability and habitat quality wane or exhibit increased spatiotemporal variation under the increasing intensity of climate change and human development, integrating measures of EP into wildlife studies will become increasingly critical for making reliable inferences. In this study, we examine how EP acts as a source of environmental information driving seasonal movement of two populations of mule deer *Odocoileus hemionus* inhabiting disparate environments in Utah, USA. Mule deer are well suited to serve as a model species with which to test unstudied relationships between EP and animal movement. Mule deer are a wide-ranging species adapted to extreme environmental gradients, and there is a breadth of knowledge about their biology, ecology, and physiology (Heffelfinger 2006). In addition, the small rumen to body size ratio of mule deer requires them to be more selective than other ungulates in their forage intake (Cox et al. 2009), which may result in strong, observable responses to the EP of the landscape. Finally, changes in precipitation and temperature impacting plant phenology and resource availability in mountainous regions (IPCC 2007, Post and Forchhammer 2008) and causing low elevation, water-limited systems to become even more arid (Seager et al 2007, Cayan et al 2010) will directly affect the summer and winter range areas of mule deer in this study. Acceleration of sprawling urbanization and anthropogenic land use change occurring in lower-elevation areas and high rates of population increase (Polfus and Krausman 2012, Hollingshaus et al. 2024) will also likely increasingly impact winter ranges of mule deer in the populations considered here. As these human-driven impacts shift the quality, availability, and predictability of forage resources for deer in this system, quantifying how EP drives daily movement will prove important for predicting changes in the time budget, energy balance, and population demographics of these animals.

Specifically, the objectives of this study were to 1) assess how spatial and temporal predictability of forage in an individual's seasonal home range (HR) affect average daily movement distance and 2) explore how contrasting environmental conditions modulate these relationships. We hypothesized that predictable HRs would necessitate less movement and so predicted that average daily movement distance would have an inverse relationship with both spatial and temporal HR predictability. We also hypothesized that relationships between daily movement and predictability would vary in relation to four general factors: environment, seasonality, forage availability, and HR area. We predicted that individuals inhabiting an environment with greater strength in seasonality would have more detectable responses to EP and that across both populations, responses to EP would be greater during the summer. Finally, given the mechanistic relationships between forage availability, movement, and HR size (Rivrud et al. 2010, Moorcroft and Lewis 2013, Stoner et al. 2018), we also predicted that responses to EP would grow as HR area increases and lessen with greater forage availability.

Material and methods

Mule deer GPS data

We utilized GPS data from female mule deer from two management units in Utah, USA, one in the northeast corner of the state, the north slope of the Uinta Mountains (~306 470 ha, hereafter 'North Slope'), and one in the southwest, the Pine Valley Mountains (~350 980 ha, hereafter 'Pine Valley') (Fig. 1). Mule deer were captured using the helicopter net-gun technique (Jacques et al. 2009) and fitted with GPS collars (model type G2110E2H, G5-2DH, or W300, Advanced Telemetry Systems, Isanti, MN, USA) by the Utah Division of Wildlife Resources (UDWR) spanning the years 2015–2022 (see Van de Kerk et al. 2020 for details). GPS collars acquired fixes at intervals between 2–24 hours, however, the majority (>80% of individuals) collected locations at either 2-hour or 12-hour frequencies. Professional capture and ground crews handled animals following the most current version of the guidelines for the use of wild mammal species laid out by the American Society of Mammologists (Sikes et al. 2011). GPS data span the years 2018–2022 for North Slope and 2015–2022 for Pine Valley.

Study sites and seasonal home range characteristics

Mule deer are a cosmopolitan species with a wide distribution covering many habitat types and climatic zones, and the two populations examined here offer an interesting contrast. Like most ungulate species in the Intermountain West, mule deer in these populations spend the summer months in high elevation areas and return to lower elevation areas in the winter (Monteith et al. 2011). Characteristics of summer and winter HR areas for both populations are summarized in the Supporting information, including details regarding climate and hydrology, vegetation and land use and ownership.

Drivers and energetics of movement in each season are markedly different for individuals in these two populations. North Slope has a deep snowpack that can function to hinder movement and restrict access to forage (Parker et al. 1984, Robinson and Merrill 2012), and cold temperatures that

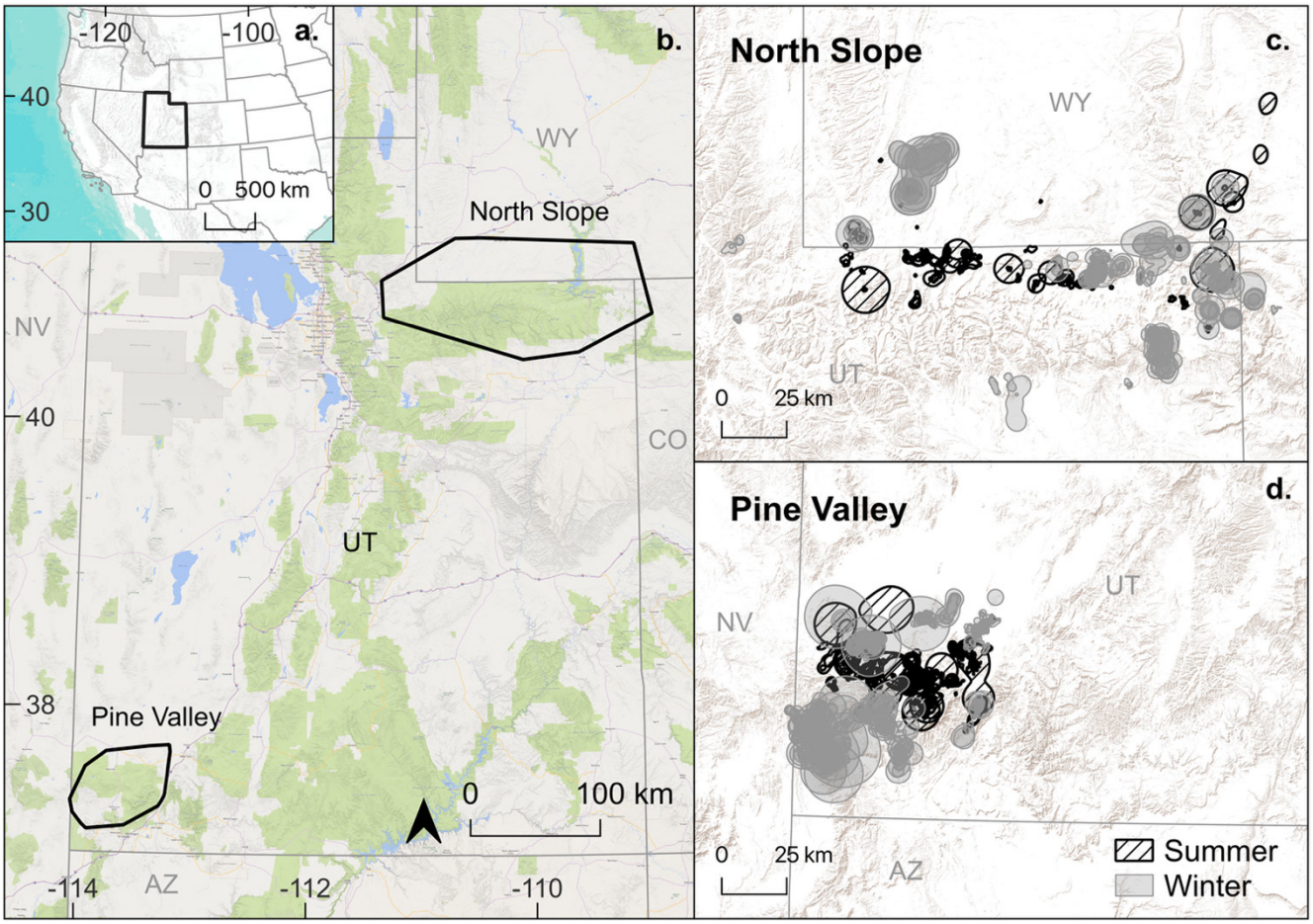

Figure 1. (a) Map of study areas and individual seasonal HR areas in Utah, USA. Minimum convex polygons used to denote study areas (outlined in black) were created from HR centroids. (b–c) Summer and winter individual HR areas represent 95% kernel utilization distributions.

require increased energy to maintain homeostasis. In Pine Valley, winter snow is ephemeral, and temperatures are mild enough to provide forage, although of a lower quality than during the summer months, for most of the winter season. Higher altitude summer HRs of deer in North Slope have prolonged snowmelt and cooler temperatures, which produce higher quality forage and lengthen the growing season (Albon and Langvatn 1992, Parker et al. 2009); however, during the summer, deer in this population must maintain a favorable energy ratio to accumulate enough body fat to support lactation for newborn fawns and survive the harsh North Slope winter (Loudon et al. 1983, Parker et al. 2009). In contrast, in the semi-arid environment of Pine Valley, water is often a key limiting resource for organisms during the summer and for the forage upon which they depend(Cox et al. 2009, Nandintsetseg et al. 2016). As such, mule deer movements in Pine Valley during the summer are likely constrained by proximity to water rather than driven by the need to gain fat.

Animal home range and daily movement

Prior to analysis, all GPS trajectories were re-sampled to a frequency of 12-hours to minimize frequency impacts on calculated individual HR areas and movement distances and to maximize the number of individuals we could include in the analysis. We assigned movement data to summer and winter seasons by identifying migration dates between seasonal range areas using average net squared displacement values (Calenge et al. 2009, Wal and Rodgers 2009). More information on season determination is available in the Supporting information. We excluded seasonal data for an individual if it did not have fixes on at least 2/3 of the days within a season. We estimated each individual's yearly summer and winter HR using a 95% kernel density estimate. Our final set of HRs included 225 unique animals (NS, n = 66; PV, n = 159) for a total of 880 individual seasonal HRs (NS_{Summer}, n = 119; NS_{Winter}, n = 151; PV_{Summer}, n = 248; PV_{Winter}, n = 362). We used these seasonal HR bounds to extract remotely sensed metrics used to calculate habitat indices.

We then calculated the average daily movement distance for each individual within each seasonal HR by summarizing the total distance traveled between each 12-hour fix and dividing this by the number of unique fix dates for each animal in the season. There are many metrics of fine-scale movement that would have been interesting to investigate and may have added nuance to our study on the effect of EP on seasonal movement of mule deer (Seidel et al. 2018); however,

we elected to use average daily movement distance as our response variable for this study as it 1) was both feasible and appropriate given our movement data and 2) allowed us to accomplish the objectives of our study. The various sampling frequencies of our data meant that we were faced with a tradeoff between quantifying distance traveled more accurately or retaining as many individuals as possible in the study; we chose to resample our GPS trajectories to the largest and most common frequency (12-h) and prioritize a robust sample size of individuals. While our quantification of daily movement distance is potentially negatively biased by this 12-hour sampling frequency (Johnson et al. 2008, Gautestad 2012), this frequency still allowed us to capture a range of distances from short relocations (which could result from behaviors such as area restricted search; Dorfman et al. 2022) to larger relocations (potentially indicative of exploratory movements; Morales et al. 2005). Our metric of average daily movement distance summarizes these movements over the course of a season and serves as our response variable, allowing us to test for effects of EP quantified at the seasonal HR level. The number of fixes obtained for an individual within a season was not significantly correlated with HR area or daily movement distance (see the Supporting information). Variables of daily movement distance and HR area were log-transformed for subsequent analyses.

Habitat indices: predictability, forage availability and snow cover

To quantify metrics for predictability and forage availability, we used normalized difference vegetation index (NDVI) composite images derived from MODIS satellite imagery (MOD13Q1.061 product; Didan 2021) with a 250-m spatial resolution and a 16-day temporal resolution. NDVI imagery was collected via Google Earth Engine spanning the years 2015–2022 (Gorelick et al. 2017) and rescaled from −1.0 to 1.0. NDVI is commonly used as a metric of vegetation productivity and has been demonstrated to be accurate at predicting resource quality and availability for herbivores such as ungulates (Pettorelli et al. 2011, Ryan et al. 2012, Stoner et al. 2016).

Following Colwell's (1974) definition of predictability and the described methodologies of Morrison et al. (2021), constancy (C) of NDVI values was calculated using Shannon's (1948) entropy (H) for each individual seasonal HR. For our constancy calculations, 100 intervals were employed in the Shannon's entropy calculation to find the proportion (P_i) of NDVI values falling within each interval (i) between the minimum and maximum NDVI value.

$$H = -\sum P_i \times \log\left(P_i\right)$$

$$C = 1 - \frac{H}{\log\left(n\right)}$$

Temporal constancy, which here represents the average variance in the NDVI value of an individual pixel throughout a given season, was calculated on a pixel basis, using a pixel's values from all 16-day NDVI composites included within a given season (clipped to the HR bounds), and then averaged across all pixels included in the HR (Fig. 2a). Spatial constancy, which here represents the 'instantaneous homogeneity' of NDVI across a HR, was calculated for each 16-day NDVI composite (clipped to the HR bounds) using NDVI values from all pixels in that clipped composite, and then averaged across all composites included within a given season (Fig. 2b). Both spatial and temporal constancy ranged from 0 to 1, representing increasing predictability. We quantified forage availability by calculating the mean NDVI value in the HR using all composites included in a given season (clipped to the HR bounds). Metrics for predictability and mean forage availability were calculated for each individual seasonal HR.

For winter HRs in North Slope and Pine Valley, we calculated an additional habitat-level variable for snow cover using mean normalized difference snow index (NDSI) also calculated from MODIS satellite imagery (MOD09GA product; Vermote and Wolfe 2015) with a 500-m spatial resolution and daily temporal resolution. NDSI imagery, scaled from −1 to 1 with values of 0.5–1 representing snow cover, was collected via Google Earth Engine spanning the years 2015–2022 (Gorelick et al. 2017). NDSI has proven an effective predictor of snow cover (Salomonson and Appel 2004) and is widely understood to impact ungulate movement through direct costs and impacts to forage availability (Parker et al. 1984, Rivrud et al. 2010, Robinson and Merrill 2012).

Regression of predictability and home range area

We accounted for the inherent positive relationship between area and environmental heterogeneity by using third-degree polynomial regressions between log-transformed HR area and both spatial and temporal constancy, regressing both EP metrics separately for each season and population (see the Supporting information). We then extracted the residuals of each regression which served as our final predictability metrics, representing the relative EP of a HR given its size. Positive EP values indicate a more predictable HR area, and negative values represent a less predictable HR area. It is important to note that while these metrics of spatial and temporal constancy were calculated using NDVI values, they do not represent a metric of resource quality. A positive value of spatial or temporal constancy does not correspond to high NDVI; rather, it indicates that resources are consistent, either in space or time – from a nutritional standpoint, these resources could be predictably 'bad' or 'good'.

Modeling approach

We employed linear mixed-effects models for each combination of population and season to test for relationships between log-transformed average daily movement distance and predictability and assess how these relationships vary under contrasting forage availability and HR area (Bates et al. 2015). All steps of analysis were completed in R (www.r-project.org). Our null model for each seasonal range included a

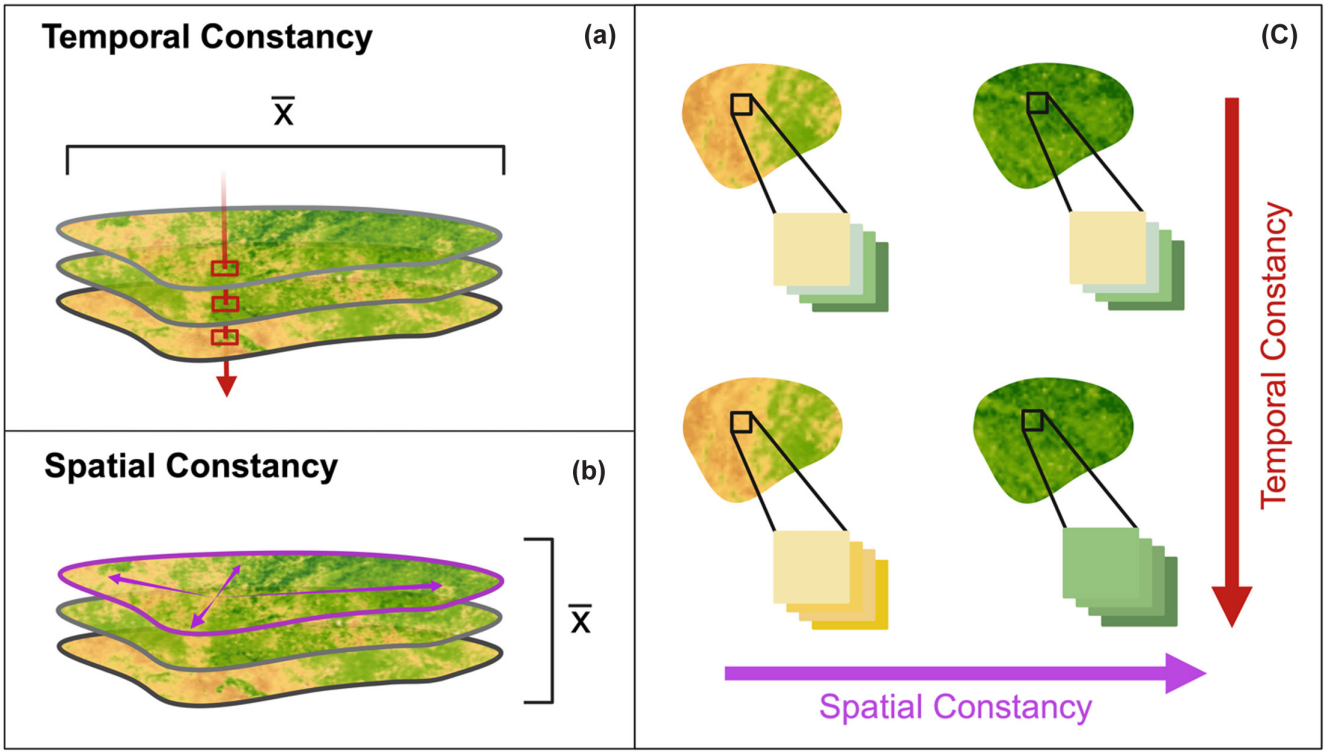

Figure 2. Diagram of temporal and spatial constancy calculation and visualization of constancy of hypothetical HRs. X-bar represents the final average taken (a) across all pixels of the entire HR or (b) across all composites included in a given season to produce the final temporal and spatial constancy values for each individuals' seasonal HR. In (c), spatial constancy increases moving from left to right and temporal constancy increases moving from top to bottom; therefore, maximum theoretical predictability is represented by the bottom right HR.

single non-linear fixed effect of log-HR area to account for the mechanistic correlation between HR area and movement (Moorcroft and Lewis 2013), modeled using natural spline (df=3). Model selection was performed using an information theoretic approach by comparing support for models with the following three structures using AICc (Hurvich and Tsai 1989, Harrison et al. 2018) to select a best model for each seasonal range:

$$\text{Null}: \text{ddist} \sim \text{ns}(\text{area}, 3) \ \ldots$$

$$\text{A)}\ \text{ddist} \sim \text{ns}(\text{area}, 3) + \text{NDVI}(\text{NDSI}) \ \ldots$$

$$\text{B)}\ \text{ddist} \sim \text{ns}(\text{area}, 3) + \text{NDVI}(\text{NDSI}) + \text{spatC} + \text{tempC} \ldots$$

$$\begin{aligned}\text{C)}\ \text{ddist} \sim\ & \text{ns}(\text{area}, 3) + \text{NDVI}(\text{NDSI}) \\ & + \text{spatC} + \text{tempC} + \text{area} \times \text{spatC} \\ & + \text{area} \times \text{tempC} + \text{NDVI}(\text{NDSI}) \times \text{spatC} \\ & + \text{NDVI}(\text{NDSI}) \times \text{tempC} + \text{spatC} \times \text{tempC}\end{aligned} \quad \ldots$$

where *ddist* is our response variable of mean daily movement distance, *area* is HR area, *spatC* is spatial constancy and *tempC* is temporal constancy. For our two winter seasonal range models, we first compared models with additive effects of either NDVI or NDSI (A) to our null model. Then, we compared models containing NDVI or NDSI to those that also had additive effects of spatial constancy (*spatC*) and temporal constancy (*tempC*) (B) and to global models containing additive fixed effects of either NDVI or NDSI and spatial constancy and temporal constancy and interactions between these fixed effects and HR area (C). All models, including the null model, also included random intercepts for animal ID and year. All numeric predictors were scaled and centered using the mean and standard deviation of the entire dataset (i.e. populations and seasons combined) to allow comparison of effect sizes both within and between models. It is important here to note that we fit these models to our data for the purpose of inference, not prediction, and while we included multiple interactive effects within our global model, they are all plausible. Authors have argued that 'global' models such as this are sufficient if the inclusion of covariates is hypothesis driven and parsimonious (Tredennick et al. 2021).

Results

Forage availability was higher in summer range areas than winter for both populations, but values were more variable during summer (Table 1, Fig. 3a). Snow cover was higher

Table 1. Observed mean (x) and standard deviation (σ) of forage availability (mean NDVI), snow cover (mean NDSI), home range (HR) area (ha), and average daily movement distance (m) for each seasonal range.

Range			Forage availability	Snow cover	HR area (ha)	Daily distance (m)
North Slope	Summer	x	0.589		1583.54	1139.52
		σ	0.085		5127.89	393.69
	Winter	x	0.290	0.214	5989.80	1046.22
		σ	0.047	0.306	9809.27	259.51
Pine Valley	Summer	x	0.543		1787.41	831.51
		σ	0.069		5470.86	499.85
	Winter	x	0.380	-0.336	3559.36	1315.00
		σ	0.036	0.130	9780.10	495.09

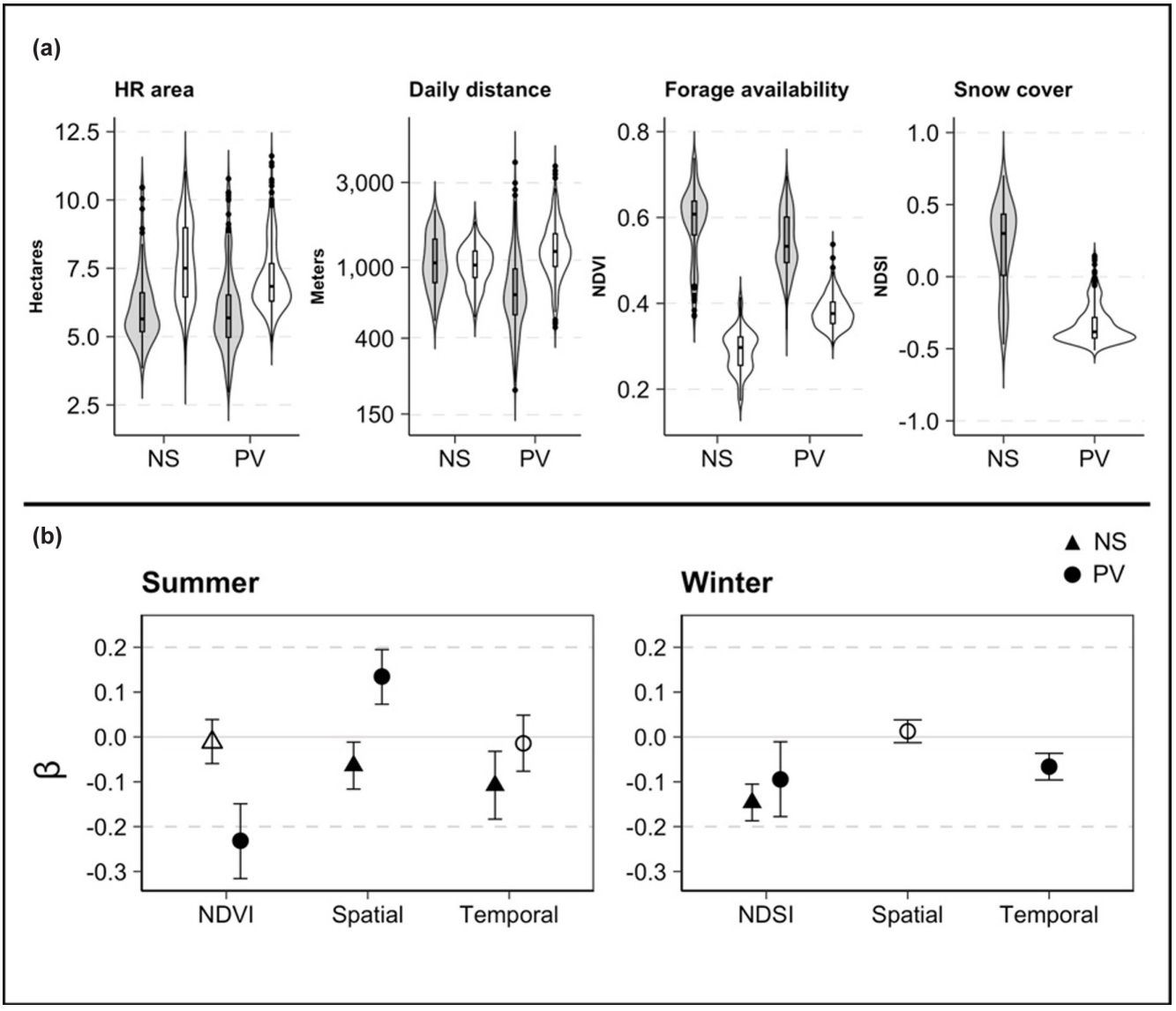

Figure 3. (a) Summary violin plots of HR forage availability (mean NDVI), snow cover (mean NDSI), area, and average daily movement distance values for each seasonal range. Values for area and distance are natural log transformed for visualization. (b) Effect plot for main effects in mixed effects models. Black fill indicates significance at the $p = 0.05$ level, with triangle symbols used for North Slope (NS) and circular symbols used for Pine Valley (PV). The main effect of HR area is not presented here for easier visualization of effects of interest but was included in all top seasonal range models using a spline effect ($df = 3$).

in North Slope than in Pine Valley in winter range areas (Table 1, Fig. 3a). HR areas were smaller in summer than winter for both populations (Table 1, Fig. 3a). Average daily movement distance was similar between seasons in the North Slope, but individuals in Pine Valley moved greater distances per day during the winter than during the summer on average (Table 1, Fig. 3a).

The top model of average daily movement distance for summer range areas in both populations included forage availability, predictability metrics, and interaction terms (our global model) (Table 2). For winter ranges, the top model for movement in North Slope included only snow cover, while the top model for Pine Valley included snow cover and predictability metrics, but no interaction terms (Table 2).

HR area was a significant predictor of average daily movement distance in all seasonal environments (NS_{Summer}, $\beta = 7.14$, $p = <0.001$*; NS_{Winter}, $\beta = 6.88$, $p = <0.001$*; PV_{Summer}, $\beta = 6.68$, $p = <0.001$*; PV_{Winter}, $\beta = 7.13$, $p = <0.001$*) (the asterisk denotes statistical significance at the $p = 0.05$ level). Increased snow cover within an individual's seasonal HR resulted in shorter average daily movement distances in winter (NS, $\beta = -0.146$, $p = <0.001$*; PV, $\beta = -0.095$, $p = 0.021$*) and increased forage availability resulted in shorter average daily movement distances during summer (NS, $\beta = -0.012$, $p = 0.628$; PV, $\beta = -0.231$, $p = <0.001$*) (Table 3, Fig. 3b). Across both seasons, mule deer in Pine Valley moved greater distances per day with greater estimated spatial constancy – representative of the average 'instantaneous homogeneity' of NDVI values across an area over time – at the HR scale (PV_{Summer}, $\beta = 0.135$, $p = <0.001$*; PV_{Winter}, $\beta = 0.013$, $p = 0.326$) (Table 3, Fig. 3b). In North Slope during summer, greater spatial constancy was associated with significantly shorter daily movement (NS_{Summer}, $\beta = -0.064$, $p = 0.017$*). Daily movement of deer decreased with greater temporal constancy – representative of the average variability of a single NDVI pixel over the entire season – in all seasonal environments for which it was included in the best model (NS_{Summer}, $\beta = -0.108$, $p = 0.003$* ; PV_{Summer}, $\beta = -0.014$, $p = 0.649$; PV_{Winter}, $\beta = -0.066$, $p = <.001$*) (Table 3, Fig. 3b).

In North Slope, we found significant interactive effects between summer HR area and both metrics of predictability (Table 3, Fig. 4a). As summer HR area increased, the negative significant effects of both spatial and temporal constancy on daily movement distance became greater (area:spatC, $\beta = -0.048$, $p = <0.001$*; area:tempC, $\beta = -0.094$, $p = 0.002$*), and daily movement of deer decreased further. We found a similar synergistic interaction in Pine Valley between summer HR area and temporal constancy (area:tempC, $\beta = -0.041$, $p = 0.126$), however this relationship was not statistically significant.

During summer, the effect of spatial constancy on daily movement distance was modulated by forage availability (Table 3, Fig. 4b). In the North Slope, high spatial constancy tended to result in less daily movement; however, as forage availability increased, deer inhabiting spatially predictable HRs moved significantly more than deer with unpredictable HRs (NDVI:spatC, $\beta = 0.045$, $p = 0.019$*). In Pine Valley, spatial constancy resulted in larger daily movements; however, as forage availability increased, deer inhabiting spatially predictable HRs moved shorter distances per day than deer with unpredictable HRs (NDVI:spatC, $\beta = -0.091$, $p = 0.014$*). Finally, In Pine Valley during summer, increased temporal constancy functioned to significantly reduce the positive effect of spatial constancy on daily movement distance (spatC:tempC, $\beta = -0.043$, $p = 0.025$*) (Table 3, Fig. 4c). We did not observe significant interactions between these predictability metrics in any other models. See the Supporting information for plots depicting non-significant interactions and random effects.

Table 2. Results of model selection to identify the best model of daily distance for each seasonal range area from three candidate models including (A) additive effects of NDVI or NDSI, (B) additive effects of NDVI or NDSI and spatial (spatC) and temporal (tempC) constancy, or (C) additive effects of NDVI or NDSI and spatial and temporal constancy and interactions between these fixed effects and HR area. Bold entries denote the 'best' model selected based on AICc.

Range		Model	AICc	Δ AICc
North Slope	Summer	Null: ddist ~ ns(area,3) + animal + year	−77.13	↑ 4.70
		A: + NDVI	−74.83	↑ 7.00
		B: + spatC + tempC	−71.87	↑ 9.96
		C: + NDVI:spatC + NDVI:tempC + area:spatC + area:tempC + spatC:tempC	**−81.83**	0
	Winter	Null: ddist ~ ns(area,3) + animal + year	−38.13	↑ 38.32
		A1: + NDVI	−53.23	↑ 23.21
		A2: + NDSI	**−76.45**	0
		B: + spatC + tempC	−72.70	↑ 3.74
		C: + NDSI:spatC + NDSI:tempC + area:spatC + area:tempC + spatC:tempC	−67.59	↑ 8.86
Pine Valley	Summer	Null: ddist ~ ns(area,3) + animal + year	94.44	↑ 51.21
		A: + NDVI	55.89	↑ 12.66
		B: + spatC + tempC	47.48	↑ 4.25
		C: + NDVI:spatC + NDVI:tempC + area:spatC + area:tempC + spatC:tempC	**43.23**	0
	Winter	Null: ddist ~ ns(area,3) + animal + year	106.51	↑ 18.14
		A1: + NDVI	106.48	↑ 18.12
		A2: + NDSI	103.76	↑ 15.40
		B: + spatC + tempC	**88.36**	0
		C: + NDSI:spatC + NDSI:tempC + area:spatC + area:tempC + spatC:tempC	95.19	↑ 6.82

Table 3. Summary of coefficient estimates (β) and confidence intervals (CI) for fixed effects and variance (σ^2) and standard deviation (σ) for random effects in the best linear mixed model of average daily movement distance for each range type. Effects are scaled for all models. Significant effects are in bold.

			Main effects					Random effects		
Model			NDVI	NDSI	spatC	tempC		Animal		Year
North Slope	Summer	β	−0.012		**−0.064**	**−0.108**	σ^2	0.006		0.000
		CI	−0.035, 0.012		**−0.090, −0.038**	**−0.144, −0.072**	σ	0.078		0.014
	Winter	β		**−0.146**			σ^2	0.020		0.001
		CI		**−0.167, −0.126**			σ	0.137		0.033
Pine Valley	Summer	β	**−0.231**		**0.134**	−0.014	σ^2	0.035		0.005
		CI	**−0.273, −0.190**		**0.105, 0.165**	−0.045, 0.017	σ	0.188		0.068
	Winter	β		**−0.095**	0.013	**−0.066**	σ^2	0.074		0.002
		CI		**−0.000, −0.025**	−0.000, 0.026	**−0.081, −0.051**	σ	0.272		0.048
			Interactions							
			NDVI:spatC	NDVI:tempC	area:spatC	area:tempC			tempC:spatC	
North Slope	Summer	β	**0.045**	0.034	**−0.047**	**−0.094**			0.003	
		CI	**0.026, 0.064**	−0.014, 0.055	**−0.060, −0.035**	**−0.125, −0.064**			−0.019, 0.025	
Pine Valley	Summer	β	**−0.091**	−0.036	−0.025	−0.041			**−0.043**	
		CI	**−0.128, −0.055**	−0.064, 0.008	−0.042, 0.008	−0.067, 0.014			**−0.063, −0.024**	

Discussion

Empirical studies have related metrics of EP to animal movement behaviors at multiple scales (Mueller et al. 2011, Bauer et al. 2020, Morrison et al. 2021), but the relationship between the predictability of forage and movement within an individual's seasonal HR has not been investigated until now. Our study demonstrates that EP impacts fine scale movement of mule deer and reveals variation in their response to EP under contrasting environmental conditions. Notably, we found that 1) both spatial and temporal constancy were significant predictors of the average distance moved per day by an individual within their seasonal HR, 2) these predictability metrics modulated deer movement through significant interactions with HR area, forage availability, and one another, and 3) the relationships between EP and daily movement distance were nuanced by population-level and seasonal environmental conditions. By integrating metrics of EP into our quantitative analyses, instead of attributing movement responses to inferred but unmeasured vegetation dynamics of a given environment, we gained a new understanding of how ungulates behaviorally adapt to dynamic resource landscapes and insight into the potential impacts that climate change may have on ungulate energetics and habitat carrying capacity.

Addition of predictability metrics to models of average daily movement distance improved model fit in all seasonal environments except for North Slope during the winter. We detected a similar number of significant relationships between EP and daily movement distance across populations and found that, except for one significant effect detected in winter in Pine Valley, EP had an overall more significant effect on daily movement distance in summer. These findings are counter to our second prediction, that animals inhabiting an environment with greater strength in seasonality would have more detectable responses to EP, but consistent with our third, that response to EP would be greater during the summer. Our results also highlight that predictability of forage may not be a main driver of movement in winter for these populations of mule deer. Our models of daily movement distance including NDSI outperformed those with NDVI in both North Slope and Pine Valley, consistent with previous studies showing that snow cover (indicative of habitat permeability and costs of travel) has a larger effect on ungulate movement and space use in the winter than NDVI (Nicholson et al. 1997, Avgar et al. 2013).

While our goal was to quantify spatial and temporal constancy of resources, it is important to acknowledge that our predictability metrics capture additional qualities of an individual's HR that may impact movement at various scales. Constancy, as calculated here, quantifies the similarity of NDVI values across a given area or at a given location through time, and was employed in this study to quantify spatial and temporal predictability of forage, respectively; however, the NDVI values used in these calculations also may capture functional aspects of the landscape such as aspect, slope, and cover, which determine landscape heterogeneity.

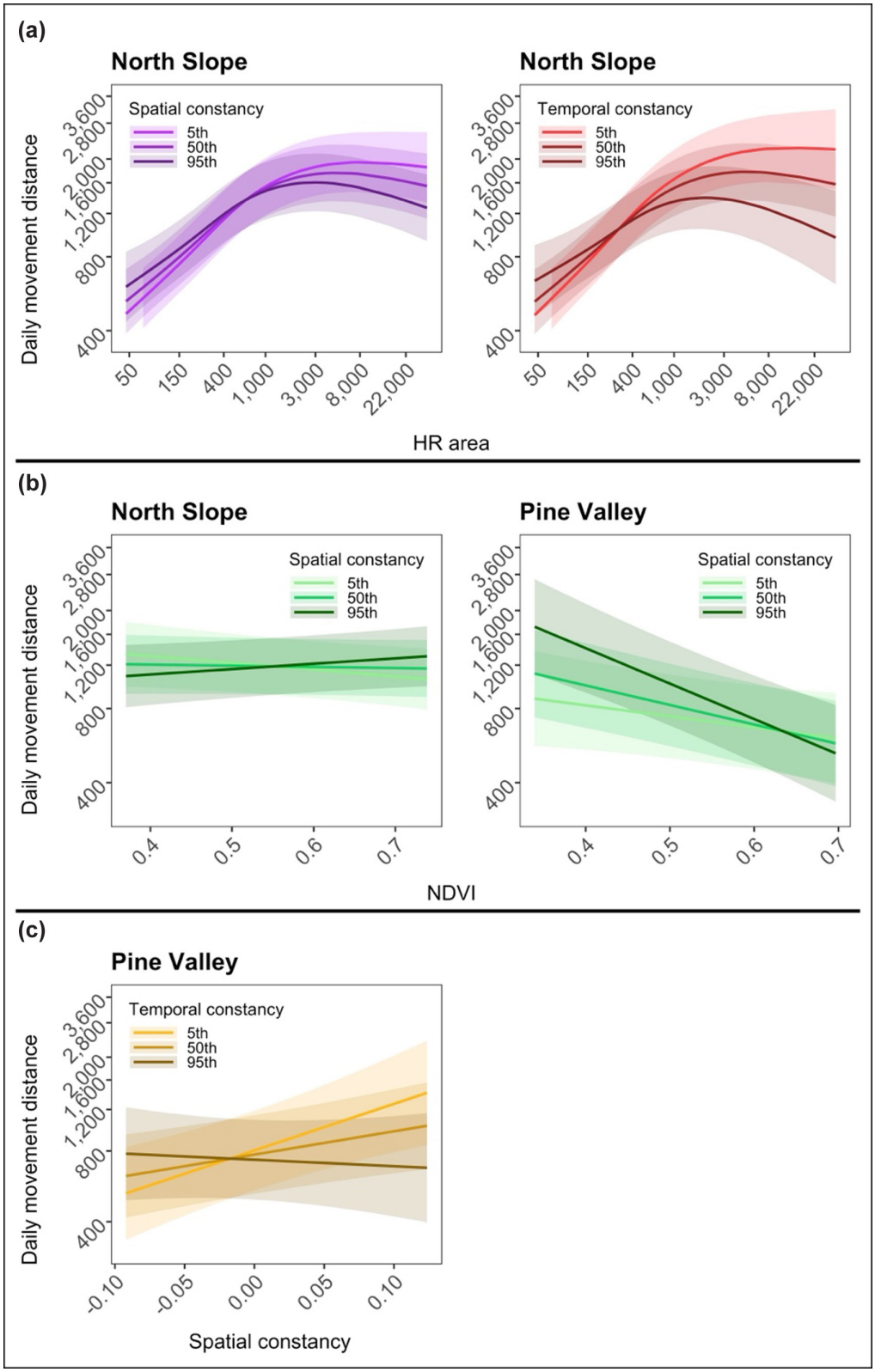

Figure 4. Plots for observed significant interactions between HR area and spatial and temporal constancy (a), forage availability and spatial constancy (b), and temporal constancy and spatial constancy (c). Lines represent the marginal effects of the 97th, 50th and 2.5th percentile values of spatial or temporal constancy, corresponding to high, normal and low predictability, respectively. Random effects were incorporated into predictions and are reflected in the confidence intervals, shown by the shaded region corresponding to each marginal effect level. Calculated confidence intervals were based on standard errors, assuming a normal distribution.

High values of spatial constancy may signify a more homogeneous home range, and high values of temporal constancy could be indicative of water sources or other landscape features sustaining vegetation productivity. Empirical studies on large herbivores have found that landscape heterogeneity impacts multiple aspects of movement and resulting fitness outcomes (Jonzén et al. 2011, Roese et al. 1991, Turner et al. 1997), and for mule deer, especially in arid regions such as Pine Valley, water is an important resource driving movement (McKee et al. 2015, Shields et al. 2012). Taking this into consideration, our discussion of our observed relationships between EP and daily distance traveled within a seasonal HR encompasses additional information plausibly captured in our predictability metrics.

Spatial constancy of resources in an individual's HR was a significant determinant of daily movement distance during summer for both populations of mule deer investigated in this study (Fig. 3b); however, it resulted in greater movements in Pine Valley and shorter movements in North Slope. These contrasting relationships did not fully support our hypothesis that predictable HRs would necessitate less movement but may demonstrate the use of EP as a source of information incorporated into practical foraging strategies that enable animals in these populations to meet nutritional and life-history requirements. The tradeoff between forage quality and biomass is documented to impact ungulate foraging behavior (Parker et al. 2009), and research suggests that deer become more selective as available forage quality decreases (Hanley 1997). Greater daily movement of deer in spatially predictable HRs in Pine Valley might reflect a strategy for dealing with this arid environment. In this population, individuals may move greater distances across spatially 'homogeneous', poor quality resource landscapes and select for nutritional quality or moisture content at the plant or bite level to reduce digestive processing capacity limitations from poor-quality forage (Collins and Urness 1983, Owen-Smith et al. 2010). The forage and water limitations of this arid environment and their constraints on deer movements are evident in the large negative effect of forage availability on average daily movement distance (Table 1).

For deer inhabiting more productive North Slope summer ranges, the benefits of movement in spatially predictable HR areas – access to forage which may be only minimally better than in their current location – may not outweigh the cost of expending energy (Switzer 1993), which depletes fat stores that individuals need for lactation and overwinter survival. This tradeoff may explain why we observed shorter daily movement in spatially predictable summer HR within this population and is supported by our weak and insignificant effect of forage availability on daily movement distance in this seasonal environment (Fig. 3b). Additionally, energy expenditure is mediated by terrain and can increase exponentially in rugged, subalpine habitats such as the North Slope (Parker et al. 1984). In summary, despite the fact that North Slope deer live in a highly productive environment, harsh winter conditions necessitate conservation of energy during summer; in contrast, Pine Valley deer live in a relatively poor yet mild habitat, and therefore must consider immediate digestive limitations rather than storing fat for overwinter survival.

Our results also reveal that during summer, the effects of spatial constancy on movement were modulated by relative forage availability within an individual's summer HR. While spatial constancy was associated with shorter daily movement in North Slope, as forage availability increased, the negative effect of spatial constancy on movement was lessened through a positive interaction between forage availability and spatial constancy (Fig. 4b). As a result, North Slope deer inhabiting areas with readily available forage that was spatially predictable moved similar distances per day as deer in areas with less forage that was unpredictable across space. In Pine Valley we observed a similar reduction in the impact of spatial predictability on daily movement distance via a negative interaction between forage availability and spatial constancy. In this environment, we found that deer moved similar distances when forage was readily available, regardless of the level of spatial predictability within their HRs (Fig. 4b).

Our finding of antagonistic interactions between forage availability and spatial constancy aligns with our prediction that deer responses to EP would lessen with greater forage availability. While deer had significantly shorter daily movements in spatially predictable HRs in North Slope during summer, as forage availability increases in spatially predictable HRs, energetic constraints on foraging may be relaxed, and individuals may forage more selectively in spatially predictable HR areas by searching for high-quality or rare species that confer the greatest benefit, increasing their average daily movement distance in the process (Stephens and Krebs 1986). In contrast, in Pine Valley, increased forage availability likely functions to release individuals from selective foraging requirements imposed by their arid environment. So, while greater forage availability within a spatially predictable summer HR may incite more movement in North Slope by providing the opportunity for animals to select high-grade forage, it may result in less daily movement in Pine Valley by releasing animals from nutritional constraints that necessitated movement-intensive foraging behavior.

Energetic considerations that may explain the negative effects of spatial and temporal constancy on summer movements of deer in North Slope are also reflected in our observed interactions between HR area and predictability in this seasonal environment. The size of mule deer HRs is negatively correlated with growing season productivity (Stoner et al. 2018), and so the establishment of a larger HR is likely indicative that an individual has higher energetic costs to acquire sufficient resources. We found that as HR area increased, individuals inhabiting HRs that were spatially or temporally predictable had increasingly shorter daily movements than those inhabiting unpredictable HRs (Fig. 4a). These significant interactions between HR area and predictability aligned with our prediction that responses to EP would grow as HR area increased.

Temporal constancy was associated with shorter daily movements in all three seasonal environments for which it

was included in the top model; in HRs with high temporal constancy of forage, deer in North Slope moved significantly less during summer and deer in Pine Valley moved significantly less during winter (and summer, although this effect was non-significant)(Fig. 3b). High temporal constancy of HRs in Pine Valley may be indicative of landscape features such as water sources that support continued plant growth and quality throughout the season and influence plant succulence (Nandintsetseg et al. 2016).

Finally, although temporal constancy was not a significant predictor of daily movement during summer in Pine Valley, it functioned to significantly reduce the positive effect of spatial constancy on daily movement distance in this environment. Individuals who inhabited spatially predictable HRs that were also highly temporally predictable moved less per day than individuals whose HR was spatially, but not temporally predictable (Fig. 4c). Our finding that spatial and temporal constancy interact to inform movement in this relatively resource-poor environment may indicate that variability of resources on the landscape may become a larger factor in movement decisions when conditions drop below a threshold of habitat quality.

Our results underscore both the utility of EP as a quantitative metric and the necessity for future EP research. Such studies could relate EP to alternative metrics of fine scale movement (e.g. tortuosity or recursion rate) or animal fitness (e.g. fat gain), or examine intra-season EP effects (e.g. effects of growing season plant phenology, Johnson et al. 2021). Our findings also have important implications when considering rapid, human-caused environmental change. As climate and land use change shift the quality, availability, and predictability of food resources in seasonal environments, the efficacy and efficiency of regionally tuned foraging tactics may vary (Roese et al. 1991, Middleton et al. 2018). Even small differences in forage quality can have a disproportionate influence on body condition and overwinter survival of ungulates (Bender et al. 2007), and for mule deer, shifts in forage quality and EP may be especially impactful, as they are more selective than other ungulates and face greater nutrient and biomass constraints (Collins and Urness 1983, Cox et al. 2009). This selectivity has the potential to reduce the carrying capacity of mule deer seasonal habitats by increasing individual space requirements (Pastor et al. 1997) or cause individuals to switch movement tactics (Robb et al. 2019). Behavioral and physiological thermoregulation costs associated with a changing climate could also compound energetic costs of foraging if increased movement is required to meet nutritional requirements under new seasonal dynamics (Aublet et al. 2009, Sears and Angilletta 2015). Ungulates have also been found to forage longer when food availability (Parker et al. 2009) and quality (Wilmshurst et al. 1995) are lower, which may increase their vulnerability to predation or hunting (Loudon et al. 1983, Lima and Bednekoff 1999). As foraging energetics at the individual level are documented to impact population parameters of ungulates (White 1983, Heffelfinger 2006, Desforges et al. 2021) shifts in EP could impact range dynamics (Joly et al. 2021) over ecological timeframes.

Mule deer populations have declined sharply in the 1990s, but the factors contributing to this decline are disputed (Heffelfinger 2006, Bergman et al. 2015). As the Intermountain West is projected to experience substantial impacts from climate change (Klein et al. 2014) and is currently observing high rates of human population growth and development expansion (Brown et al. 2005, Hansen et al. 2014), understanding how mule deer move in response to EP will prove important for effective management of this ecologically, economically, and recreationally important species. Maintenance of seasonal movement and space use of large ungulates such as mule deer is extremely crucial, as shifts in these behaviors have implications for human-wildlife conflict (e.g. vehicle collisions and crop depredation), and impact the health and functioning of larger communities and ecosystem processes (Frank 1998, Bauer and Hoye 2014, Shaw 2020). If the cascading effects of greater climatic variability include shifts in movement requirements or efficacy of foraging strategies of wildlife, there could be substantial implications in terms of human and animal welfare.

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Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.gtht76hxg (Standen et al. 2025). Mule deer are a protected species under state laws (Utah Code § 23-14-1), and as such, location data are considered proprietary and cannot be released. Inquires and data requests can be addressed to Utah Division of Wildlife Resources.

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