

**Keywords:** *Antilocapra americana*, RSF, species distribution models, context dependence, scale, model transferability

## **Abstract**

Species distribution and habitat selection models frequently use data collected from a small geographic area over a short window of time to extrapolate patterns of relative abundance to unobserved areas or periods of time. However, these types of models often poorly predict how animals will use habitat beyond the place and time of data collection because space-use behaviors vary between individuals and are context-dependent. Here, we present a modelling workflow to advance predictive distribution performance by explicitly accounting for individual variability in habitat selection behavior and dependence on environmental context. Using global positioning system (GPS) data collected from 238 individual pronghorn, (*Antilocapra americana*), across 3 years in Utah, USA, we combine individual-year-season-specific exponential habitat-selection models with weighted mixed-effects regressions to both draw inference about the drivers of habitat selection and predict space-use in areas/times where/when pronghorn were not monitored. We found a tremendous amount of variation in both the magnitude and direction of habitat selection behavior across seasons, but also across individuals, geographic regions, and years. We were able to attribute portions of this variation to season, movement strategy, sex, and regional variability in resources, conditions, and risks. We were also able to partition residual variation into inter- and intra-individual components. We then used the results to predict population-level, spatially and temporally dynamic, habitat-selection coefficients across Utah, resulting in a temporally dynamic map of pronghorn distribution at a 30x30m resolution but an extent of 220,000km<sup>2</sup>. We believe our transferable workflow can provide managers and researchers alike a way to turn limitations of traditional RSF models - variability in habitat selection - into a tool to improve understanding and predicting animal distribution across space and time.

# 1 Introduction

One of the central aims of ecology is to understand why species have their observed spatio-temporal distributions (Yates et al. 2018a). Ecologists draw inference about why an organism is present at a particular geographic location by comparing environmental attributes of that location to attributes of locations that are available to the organism. This comparison between what habitat units (pixels or patches) organisms use and what habitat units they could use is facilitated by a class of models that we will refer to as species-habitat association analyses (SHAAs; Matthiopoulos, J. R. Fieberg, and Aarts 2020). SHAAs include species-distribution models (SDMs), habitat-selection functions (HSFs, also known as resource-selection functions or RSFs), and their respective variations developed to accommodate different data types and relax model assumptions (e.g., step-selection functions or SSFs; Matthiopoulos, J. Fieberg, et al. 2015; Matthiopoulos, J. R. Fieberg, and Aarts 2020; J. Fieberg, Signer, et al. 2021). Drivers of species presence inferred from SHAAs can be used to guide habitat improvements through the manipulation of resources, risks, and conditions to meet population management objectives (Matthiopoulos, J. Fieberg, et al. 2015). Still, the allure of SHAAs and their prevalence in the ecological literature is tied to the promise of their predictive capabilities, rather than their capacity for inference (Matthiopoulos, Field, and MacLeod 2019). Using correlations between an organism’s presence and habitat attributes in environmental space, SHAAs can be used to predict the probability of habitat use in geographic space outside of the space and time the organism was observed (Matthiopoulos, J. Fieberg, et al. 2015). The predictive capabilities of SHAAs have been used to address fundamental questions in both applied and theoretical ecology, including delineating habitat for conservation (C. J. Johnson, Seip, and Mark S. Boyce 2004), prioritizing translocations (Antoine Guisan et al. 2013), assessing anthropogenic impacts on wildlife (Street et al. 2015), forecasting species’ responses to climate change (Kleiven et al. 2018), evaluating the potential for disease outbreaks (C. M. Beale and Lennon 2012) or spread of an invasive species (Barbet-Massin et al. 2018), and quantifying niche overlap (Buckley et al. 2010). However, a recent emphasis on the validation of predictive SHAA models reveals that most fall short of their promised powers of projection, suffering from poor model transferability when

results are extrapolated beyond the observation extent (Paton and Matthiopoulos 2016; Aldossari, Husmeier, and Matthiopoulos 2022; Heit et al. 2023; Gantchoff et al. 2022).

The transferability of SHAAs is often limited by availability dependence, biological variation among individuals and populations. The habitat that an organism could use — the spatial extent of its availability domain — is typically defined by the species biology and the sampling design, which is question-specific (J. R. Fieberg et al. 2018; J. Fieberg, Matthiopoulos, et al. 2010; Bowersock et al. 2023; Bastille-Rousseau, Potts, et al. 2015). However, the inference drawn from SHAAs about the drivers of space-use behavior may change based on the habitat deemed available to an organism. For example, an obligate grazer may strongly select for habitat with more grass when grasses are scarce. As grass becomes increasingly prevalent on the landscape, the grazer will no longer need to select habitat based on grass presence because it is widely available (i.e., they still use habitats with grass, but that use is no longer disproportionate to the availability of the habitats with grass). This shift in selection behavior with resource availability is known as availability-dependent habitat selection (also called a ‘functional response’; Mysterud et al. 1999; McLoughlin, D. W. Morris, et al. 2010; Matthiopoulos, Hebblewhite, et al. 2011). Availability dependence constrains the predictive potential of SHAAs because correlations between attributes of environmental space and habitat use may only be relevant for the place, time, and spatial scale of the data used to fit the model. Conversely, if adequately accounted for, availability and scale dependence can be harnessed to enhance our capacity to transfer SHAAs across space and time.

Individual organisms in SHAAs are often treated as sampling units to draw inference about the habitat-selection patterns of a population or a species. However, individual variation is commonly observed (J. Fieberg, Matthiopoulos, et al. 2010; Bastille-Rousseau, Potts, et al. 2015; Bastille-Rousseau and Wittemyer 2022). Within an individual, external environmental variation interacts with an organism’s physiological condition and cognitive state to change the predominant drivers of habitat selection across space and time (Hirzel and Le Lay 2008) causing space use behavior to vary across space and time. Behavioral variation can occur between aggregations of individuals (populations, subspecies, etc.) that arises because of differences within and between organisms and

their experiences in environmental space. Behavioral variation limits SHAAs transferability across individuals (or their aggregations) because individuals may exhibit different responses to identical attributes of environmental space. Whereas SHAAs are typically used to draw inference and/or make predictions at the population or species levels, behavioral variation may act to attenuate or even invalidate SHAAs predictions. For SHAAs to realize their full predictive potential, availability dependence, and individual variation must all be adequately accounted for.

Recent improvements have been made to SHAAs to increase their predictive performance. Matthiopoulos, Hebblewhite, et al. (2011) proposed a generalized functional response SHAA that accounts for availability dependence by allowing selection coefficients to interact with habitat availability. An expansion of this model, the point-by-point generalized functional response permits each used location to have its own defined area of availability, acknowledging that an organism most likely makes a behavioral decision based on its immediate surroundings (Paton and Matthiopoulos 2016). Moreover, the proliferation of mixed models in ecology and their integration into SHAAs has helped to account for individual variability in habitat selection behavior. However, these model corrections are opaque to most users because they operate behind layers of statistical machinery. The “black box” formulation of many SHAAs prevents users from partitioning the sources of variation that restrict model transferability. Understanding why a model is not generalizable is the first and most essential step for addressing issues of transferability that are species- and system-specific. Further, most current SHAAs do not allow habitat selection coefficients to vary in space and time. Developing spatially and temporally explicit SHAAs that allows users to partition sources of variation is the next step to realizing the predictive potential of these powerful analytical tools.

To address this need, we introduce an improved workflow for conducting SHAAs with large and diverse datasets — an approach we’ve termed ‘Variance- Partitioning Species-Habitat Association Analysis’ (VP-SHAA). This workflow consists of data preparation, modeling, and inferential and/or predictive stages for generating results. First, we partition the data into temporal data subdivisions (e.g., parts of the diurnal cycle, seasons, years, or any combination of these) and fit an exponential habitat-selection function to each unique individual-temporal combination. Second, we quantify



the relationship between population-level habitat-selection coefficients and a set of spatio-temporal predictors (e.g., season and habitat availability) using mixed-effects linear regression with inverse-variance weighting. Third, we use the relationships derived in stage 2 to project habitat selection coefficients across space and time, and demonstrate both how transferability can be quantified and predictive maps generated. Our goal is to improve the transferability of SHAA models to unobserved places and times to enable wildlife managers, working with limited fiscal and manpower resources for species monitoring, to make data-driven conservation decisions in a rapidly changing world. We apply the VP-SHAA workflow to pronghorn (*Antilocapra americana*) monitoring data from the state of Utah, USA, to scale localized species-habitat relationships into state-wide predictions of species distribution.

## 2 Methods

### Methodological approach

Before discussing our specific application to pronghorn in Utah, we provide a concise overview of the VP-SHAA workflow (Figure 1). The workflow consists of three main stages: data preparation (Steps 1-3), modeling (Steps 4-5), and generating inferential and/or predictive results (Steps 6-7). Our objective was to develop predictive models of probability of use based on remotely-sensed landscape data and GPS telemetry data that consider multiple orders of selection (D. H. Johnson 1980; Buderman et al. 2023). These orders of selection are inherently nested, and thus our estimates are conditional (i.e., when we estimate third-order selection, it is conditional on second-order selection). We integrate second- and third-order selection to account for temporally varying landscape characteristics that are available for use during within-home-range movements (third-order selection), while also considering individual home range selection (second-order selection) during biologically relevant periods of the year. Steps 1-7 listed below outline our framework for constructing third-order SHAA model and predictive maps. In Step 1, we define temporal availability domains by identifying important biological events and predictable environmental variation, such

as seasons. We then divide the data into within-individual temporal subdivisions based on these domains. Step 2 is delineating spatial availability domains for each temporal subdivision. These domains are squares of the same size but each is positioned on the landscape so that it is centered on the mean position of a specific individual at a specific temporal subdivision. In Step 3, we re-project remotely sensed habitat covariates onto a template raster clipped to each spatial availability domain, with temporally-dynamic covariate values averaged across each temporal subdivision. After these initial steps, we have multiple data subdivisions, each with a set of habitat covariates observed across a constant number of pixels for each individual. We also identify a subset of pixels as 'used' based on observed animal positions. In Step 4, we use logistic regression to estimate the parameters of an exponential habitat-selection function fitted to each data subdivision independently. In Step 5, we employ a mixed-effects model, with inverse-variance weights, to partition variability (obtained in step 4) between individual, environmental, and temporal sources. Step 6 is drawing inferences about pronghorn habitat associations based on model results. In Step 7, we use the fitted models to predict expected selection coefficients across a raster covering the regions of interest, creating our third order selection maps. In Appendix A, we describe our workflow for creating our second-order projections, which closely followed the workflow described here but defining the entire state as 'available'. Finally, we calculated the pixel-by-pixel product of the second- and third-order projections for each season, status, sex combination in our dataset (Appendix B). This process resulted in the creation of what we term 'unconditional third-order' probability of use maps. These maps provide spatio-temporally explicit, fine-scale predictions of habitat selection behavior and allow us to map the expected distribution of the species in the region. Overall, our VP-SHAA workflow offers researchers a flexible method to evaluate population-level habitat selection by considering individual habitat-selection behaviors while also accounting for temporal, scale, and availability dependencies.

## 2.1 Data preparation

### 2.1.1 Pronghorn captures

The Utah Division of Wildland Resources (UDWR) captured pronghorn across the state from 2017 – 2021 in eight wildlife management units (WMUs) as a part of the Utah Wildlife Migration Initiative. During December and early January, helicopter-capture crews net-gunned pronghorn and processed individuals at the capture site without the aid of chemical immobilization agents, sexing pronghorn and fitting each animal with a GPS collar set to record the individual's location every two hours. Over the course of this study, UDWR captured 447 pronghorn and tracked individuals for an average of 380 days (range: 1 – 1465 days). All animal handling procedures were conducted and approved by the UDWR.

#### *Step 1. Defining the appropriate temporal data subdivision*

Since an organism's habitat selection behavior may vary with predictable shifts in environmental resources, risks, and conditions, or physiological events with consistent timing (e.g., birth pulses or migration), the first step in our workflow is to define an appropriate temporal grain within our temporal extent for the GPS and habitat covariate data. Focal species biology, environmental seasonality, data availability, and our research question informed our choice of temporal grain and extent.

**Pronghorn application:** Given that we were interested in pronghorn habitat selection year-round, we used a monthly temporal grain within an annual extent and selected four focal months that capture a pronghorn's winter ranging (February), spring migration (April), summer ranging (July), and fall migration (November), to represent seasonal behavior in our analysis.

#### *Step 2. Defining the spatial extent*

The spatial extent of an availability domain should include the majority of habitat an animal could have used while excluding parts of the landscape that are not habitat, unavailable to the focal species, or unrelated to the research question. We recommend using the same spatial extent to

define availability domains for all individuals to minimize the influence of scale-driven availability dependence (McLoughlin, Case, et al. 2002; Van Beest et al. 2010; Prokopenko, Mark S. Boyce, and Avgar 2017).

**Pronghorn application:** We delineated a 10x10km square availability domain centered on the pronghorn's position mid-month for each individual-month-year data subdivision. We chose to use a 100km<sup>2</sup> extent based on typical monthly home range size.

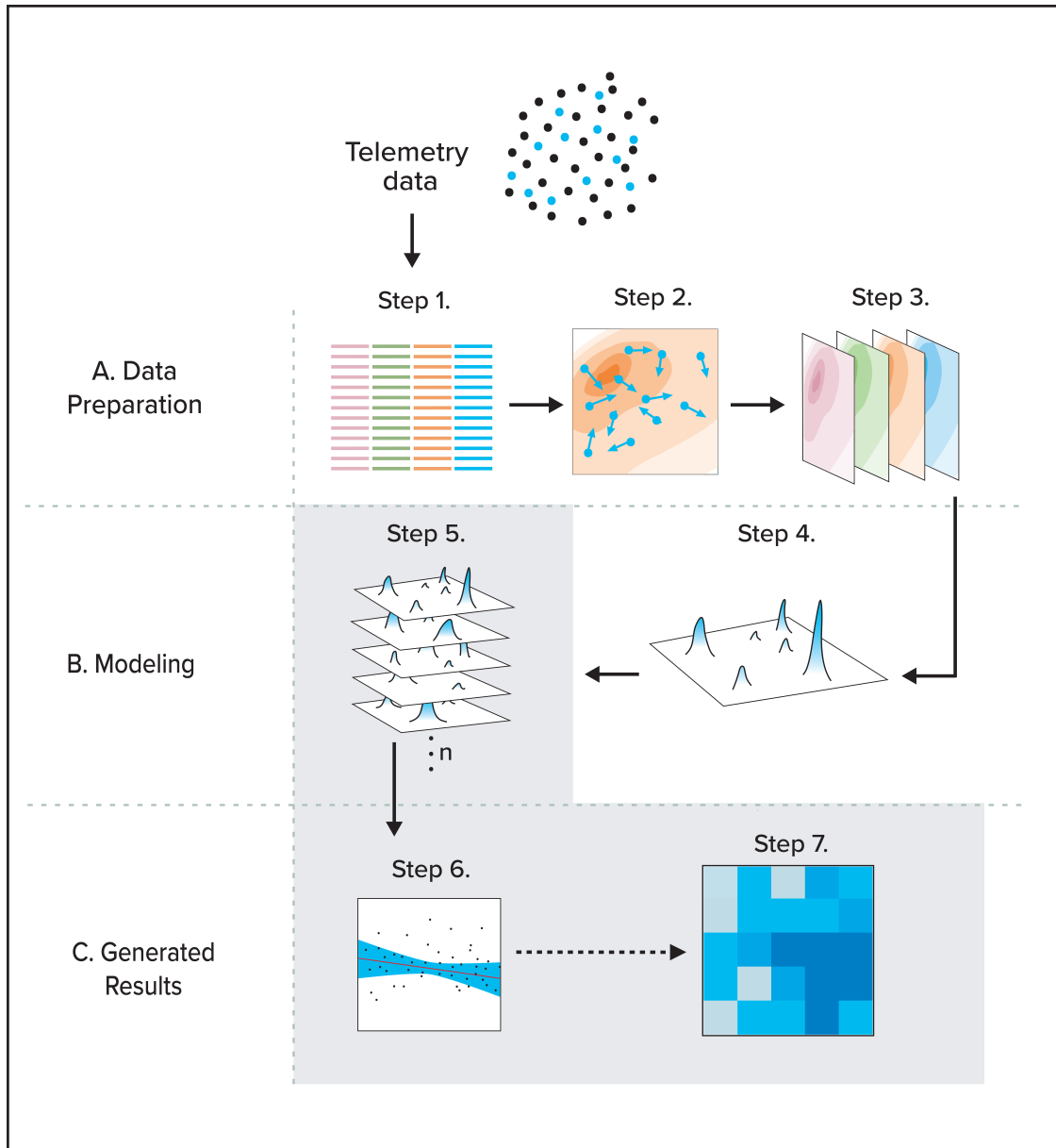


Figure 1: VP-SHAA workflow with three stages; A. data preparation, B. modeling, and C. results (see 'Methodological Approach'). White and gray background denotes individual- and population-level inference, respectively.

**Step 3. Determine the habitat covariates to be included and their temporal resolution**

Environmental covariates representing resources, risks, or conditions fundamental to a species' biology or tied to the central research question should be considered for inclusion in the exponential habitat selection function (eHSF) models. Covariates should then be standardized to the same spatio-temporal resolution to account for scale dependence in the analysis.

**Pronghorn application:** After reviewing the primary literature, we selected a suite of environmental covariates representing known drivers of ungulate space-use (Appendix B: Table 4). Since habitat selection is, in part, a behavioral response to environmental variation, the spatio-temporal grain used to measure environmental attributes will affect our inference. We recommend using the temporal grain chosen in step 1 and a single spatial grain for all covariates. For pronghorn, we extracted covariate values from remotely-sensed products at a 30x30m spatial resolution within the spatial extent of the availability domain. For habitat covariates with a temporal grain finer than one season, we calculated the mean covariate value by pixel across the time interval.

## 2.1.2 Modeling

### *Step 4: Accounting for individual behavioral variability in eHSFs*

With standardized habitat covariates, we can begin to partition individual and temporal variability in habitat selection behavior by estimating selection coefficients for each study organism temporal data fold. Using eHSF models, we can compare the environmental attributes of used vs. available points within each individual-season-year subdivision to estimate selection coefficients for each covariate (Appendix B: Table 4).

**Pronghorn application:** Given that a single 30x30m pixel within our availability domain contained the same covariate values, we assigned one available point per pixel. Used points were then determined by the number of GPS points collected per individual in that particular season. Used points were given weights of 1 and available points were given weights of 5000 following the guidance of J. Fieberg, Signer, et al. (2021).

### *Step 5. Mixed-effect model structure for variance decomposition*

To understand the drivers of habitat selection, we employed a covariate-specific linear mixed-effects model, one for each estimated eHSF coefficient. This model allowed us to partition the variance in habitat selection among individual, temporally-dependent, availability-dependent, and environmental factors. The fixed-effects component of the model captured individual-level char-

acteristics, such as sex, season, age, and reproductive status, as well as the availability of habitat covariates on the landscape. By considering availability, we could differentiate between the preference for a specific habitat and its actual availability (availability dependence), enabling us to identify the underlying mechanisms driving habitat-selection variation. To account for habitat availability and distinguish between preference and availability driven variation, we included mean values of habitat covariates and anthropogenic features, such as fences and roads, across each availability domain. To address residual unexplained individual variation, we incorporated random effects for individual and WMU-year combinations. Finally, response variables (selection coefficients) were all weighted by their respective inverse variance, giving less influence to coefficient estimates associated with higher uncertainty.

**Pronghorn application:** In the fixed effects component of the pronghorn covariate models, we included sex, movement strategy (i.e., was the individual a ‘mover’ or a ‘resident’ individual in a given season-year; Appendix B), season, mean habitat and precipitation covariates for each availability domain in the focal season, and anthropogenic features that may alter habitat selection behavior. We incorporated interactions between precipitation covariates, sex, movement strategy, and season to absorb additional temporal variability. We addressed individual variation by including random selection coefficient intercepts for each pronghorn in each year. We estimated seven eHSF coefficients across eight season-status-sex groups, resulting in a total of 56 population-level averages (after controlling for availability dependencies, correlations with other selection coefficients, random effects, and uncertainty).

### 2.1.3 Generated results

#### *Step 6. Draw habitat selection inference using the VP-SHAA workflow*

For questions that require an understanding of the drivers of population-level habitat selection behavior, our workflow can be used to draw inference by plotting selection coefficients derived from the fixed effects of the variance-partitioning models described in step 5 against the overall availability of that covariate (J. Fieberg, Matthiopoulos, et al. 2010). To assess the goodness-of-fit

of the model, we used the *r.squareGLMM()* function ((Bartoń 2022)) to calculate the pseudo- $R^2$  values of the model output. These values are specifically adapted for use with generalized linear models.

#### ***Step 7. Make spatial predictions using the VP-SHAA workflow***

Step 7 aims to generate a fine-scale relative probability of use map of habitat selection behavior, allowing for an understanding of the factors that influence a particular species' habitat selection, such as elevation, vegetation, and anthropogenic activities. By mapping the species' habitat selection behavior at the appropriate spatial and temporal grain, we can gain insight into their ecological requirements and behavior, which can inform conservation and management efforts.

**Pronghorn application:** Using standardized parameters from step 5, we created a fine spatio-temporal resolution map that reconciles second- (home range) and third-order (within home range) habitat selection, enabling us to predict habitat selection behavior in locations or periods where the species was not observed for each season-status-sex classification in our data-set. To ensure that our predictions were made at the same scale the model was fit, we overlaid a grid of 10x10km pixels across Utah, corresponding to the size of the pronghorn availability domain in step 2.

For mapping third-order selection, we used the fixed effects from the VP-SHAA model (step 5) to predict habitat selection within each 10x10km pixel during each season. To estimate the relative probability of pronghorn use, we downscaled our predictions to 30x30m by substituting our expected coefficient values into our eHSFs (step 4) within each 10x10km pixel. We normalized our third-order habitat selection rasters so that they sum to 1 within each 10x10km pixel (McLoughlin, D. W. Morris, et al. 2010).

## **2.2 Unconditional third-order mapping**

In our methodology, we incorporated the concept of nestedness across selection orders, (see DeCesare et al. 2014; Joseph M. Northrup et al. 2013; McGarigal et al. 2016), as this nested structure leads to conditional estimates. For example, when estimating third-order selection, it



relies on the conditions established by second-order selection. Likewise, second-order selection depends on first-order selection, or selection of the geographic range of a species (which we have assumed to be uniform across the state, meaning every location has an equal probability of selection; D. H. Johnson 1980). Consequently, attempting to predict third-order selection without the inclusion of second-order information may yield projections that lack ecological coherence (Buderman et al. 2023).

To address this limitation, we generated seasonally varying second-order projections by utilizing the covariates from step 3 and the estimated selection coefficients from our mixed-effect models step 5. This allowed us to integrate large-scale environmental context into our projections. In these second-order projections, we defined the entire state as 'available' to pronghorn, with the GPS points from each pronghorn in that season considered as 'used' (Appendix A).

We then used both second- and third-order projections to calculate the pixel-by-pixel product of these two layers for each season. This process resulted in the creation of what we term 'unconditional third-order' probability of use maps. These maps provide spatially and temporally explicit, fine-scale predictions of pronghorn habitat selection behavior (L. R. Morris, Proffitt, and Blackburn 2016; Buderman et al. 2023).

## 2.3 Validation

The recognition of a need for transferable models to accurately predict in environments that differ greatly from those used during model training has shed light on the shortcomings of current SHA models, particularly for wild animals (Aldossari, Husmeier, and Matthiopoulos 2022; J. R. Fieberg et al. 2018). Properly evaluating predictive model performance is therefore critical, especially as we develop management and conservation plans that depend on how animals respond to accelerating changes in the environment (Yates et al. 2018b). There have been many methods suggested for validating model predictive performance in the literature (Mark S Boyce et al. 2002; Aldossari, Husmeier, and Matthiopoulos 2022; Roberts et al. 2017). For this study, we use out-of-sample data of a withheld year, 2021, consisting of 293 individuals, 77 of which were new to the study, and two

WMUs not represented in previous years. This has been suggested as the ideal method for validating predictions because, for models to provide robust inference on ecological processes, they need to be able to predict processes in data that is independent from data used to fit the model (Joseph M Northrup et al. 2022; Coe et al. 2011). Additionally, pronghorn differ from other ungulates, such as elk and mule deer, in that they have low site fidelity and are facultative migrants, where their behavioral tactics vary within or across years (Morrison et al. 2021; Jakes et al. 2018), supporting the relative independence of the training data sets.

### **2.3.1 Predictive model validation**

To assess the predictive performance of the VP-SHAA workflow, we fit the model using the selection coefficients output from the three years of pronghorn data for the withheld data set to obtain "true" selection coefficients. We compared the 2021 predicted coefficients to the "true" selection coefficients obtained using weighted Pearson's correlation coefficients with inverse variance weights. To evaluate the improvement in model transferability, we compared the VP-SHAA full model predictions to predictions from season-only and null models. We quantified the difference using a goodness-of-prediction metric (Burzykowski 2023). Specifically, we subtracted the null model's weighted correlation estimates from the full model's correlation estimates and divided by 2 for each model in Step 5.

### **2.3.2 Spatial predictive validation**

We calculated the out-of-sample Boyce Index (BI) for the predicted third-order and unconditional projections (Mark S Boyce et al. 2002). This assessment was conducted using the 10x10km pixels, where GPS points were available for each season and year. We only used 10x10km pixels with greater than 30 GPS locations and reported the number of pixels used for each season-status-sex classification.

In the case of third-order maps, we began by computing the number of locations within each pixel, subsequently grouping them into a fixed number of bins (specifically, 5 bins). Next, we

divided these values by the number of individuals present in those bins, enabling us to gauge the accuracy of our model's geographic space predictions. To conduct a thorough evaluation at a fine scale, we examined eHSF values for all 30x30m pixels within a 10x10km pixel for each season-status-sex classification. To measure model transferability, we applied Spearman's rank correlation (Nielsen et al. 2010) for each 10x10km cell and calculated the mean and standard deviation for each season-status-sex classification.

For unconditional third-order maps, we calculated the number of points within each pixel and organized them into predetermined bins. However, to account for variation in the number of 10x10km pixels used in our third-order validation for each classification, we scaled the bin count by multiplying it by 5. This scaling ensured consistency across classifications. Additionally, we normalized these values by the number of individuals to assess the accuracy of our model's geographic space predictions. We evaluated model transferability using Spearman's rank correlation (Nielsen et al. 2010).

### **2.3.3 Functional response validation**

To properly assess the importance of controlling for functional responses for enhanced predictive capacity and transferability, we performed our BI validation on a null model where availability dependence was not controlled for. Here, the availabilities for each covariate were set as a zero in our workflow, and the spatial predictions and validations were performed as stated above.

## **3 Results**

### **3.1 Variance Decomposition and Mixed Model Results**

Results from step 5 demonstrate that the fixed effects of the full covariate models explained an average of 34.1% of the selection coefficient variation while the season only models explained an average of 9% of variation (marginal  $R^2$ , Table 2). We assessed an intercept only model as a benchmark for comparison. With the addition of random effects for individual and WMU-year,

357 the full, season only, and null (intercept-only) models captured an average of 99% of the variation  
358 (conditional  $R^2$ , Table 2).

Table 1: Goodness-of-fit: Marginal and conditional  $R^2$  percentage values for each Full, Null, and Season only covariate model output for pronghorn (*Antilocapra americana*), Utah, USA.

Covariates	Full model		Season only Model		Null Model	
	$R^2$ (marginal)	$R^2$ (conditional)	$R^2$ (marginal)	$R^2$ (conditional)	$R^2$ (marginal)	$R^2$ (conditional)
Elevation	57	99	02	99	0	99
Roughness	43	99	20	99	0	99
Aspect (Easting)	12	99	02	99	0	99
Aspect (Northing)	33	99	20	99	0	99
Herbaceous cover	21	99	01	99	0	99
Shrub cover	50	99	12	99	0	99
Tree cover	23	99	06	99	0	99

## 3.2 Habitat Selection Inference

A visualization of the distributions of the seven eHSF coefficients show tremendous variability, with coefficients encompassing both positive (selection) and negative (avoidance) values across data subdivisions (Figure 2). Hence, if we had not subdivided the data, we might have expected to see no effect of most of the covariates (i.e., the positive and negative values would cancel out). Further, estimates obtained from one data subdivision of movement tactic, season, or sex seem to tell us little about the effects on other subdivisions.

The graphical output from inference drawn at step 6 demonstrates 42 of the 56 population-level averages had confidence bounds that overlapped 0, indicating a lack of significance (Figure 2). Selection for herbaceous cover was evident for females during winter ( $\beta = 0.488$ ) and movers during both spring ( $\beta = 0.343$ ) and fall ( $\beta = 0.499$ ). However, summer residents avoided herbaceous cover ( $\beta = -0.300$ ). Spring movers ( $\beta = -0.244$ ) and winter females ( $\beta = -0.0232$ ) avoided shrub but spring residents select for shrub ( $\beta = 0.302$ ). Movers avoided tree cover during spring ( $\beta = -0.815$ ), residents in the fall ( $\beta = -0.278$ ), and by females in winter ( $\beta = -1.15$ ). Winter females ( $\beta = -0.108$ ) and spring movers ( $\beta = -0.139$ ) selected against north-facing slopes.

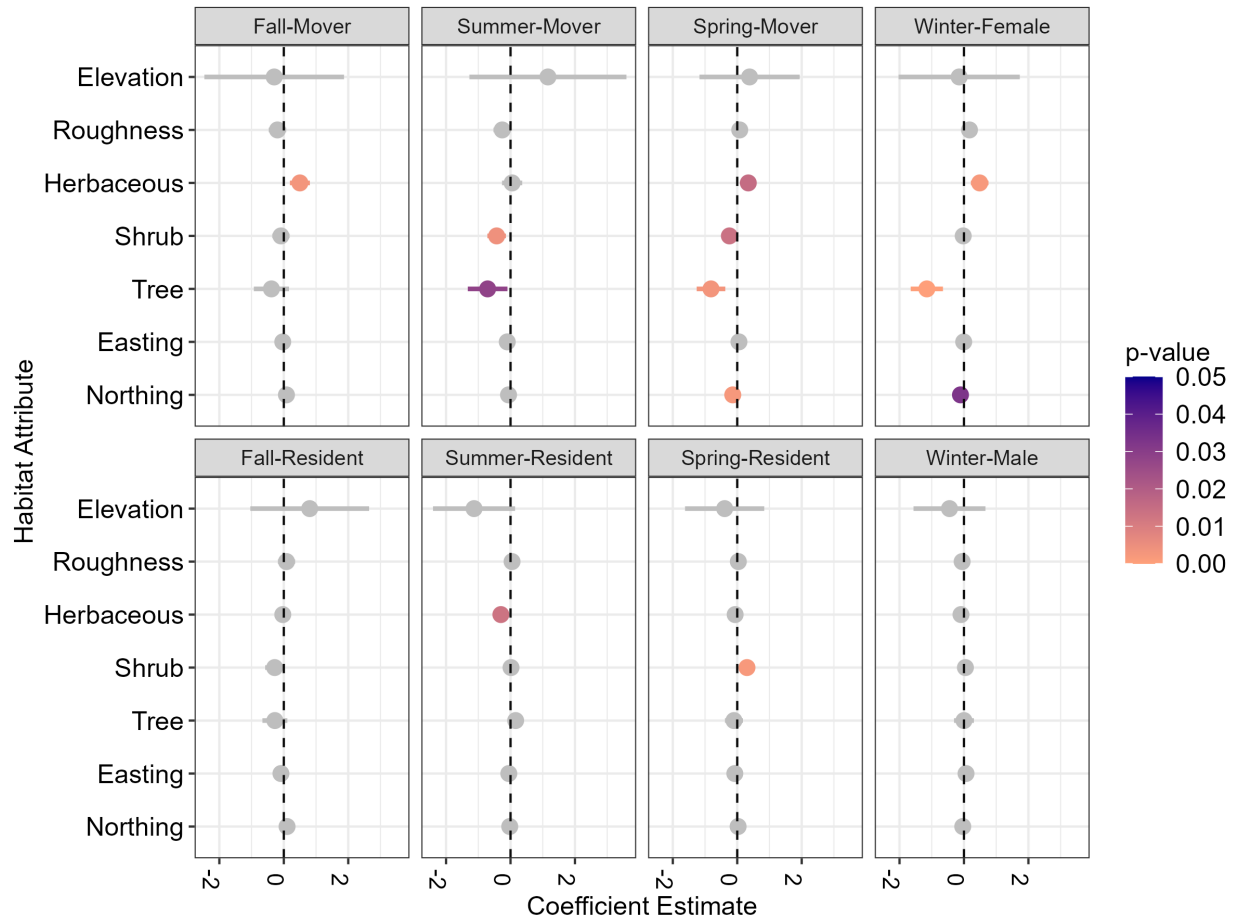


Figure 2: Estimates and 95% confidence intervals for relative habitat selection strength in pronghorn (*Antilocapra americana*, 2018-2020, Utah, USA) based on seven covariates. Significance is a color-coded gradient, with lighter shades indicating lower significance, darker shades indicating higher significance, and gray indicating non-significance. The dashed horizontal line represents zero.

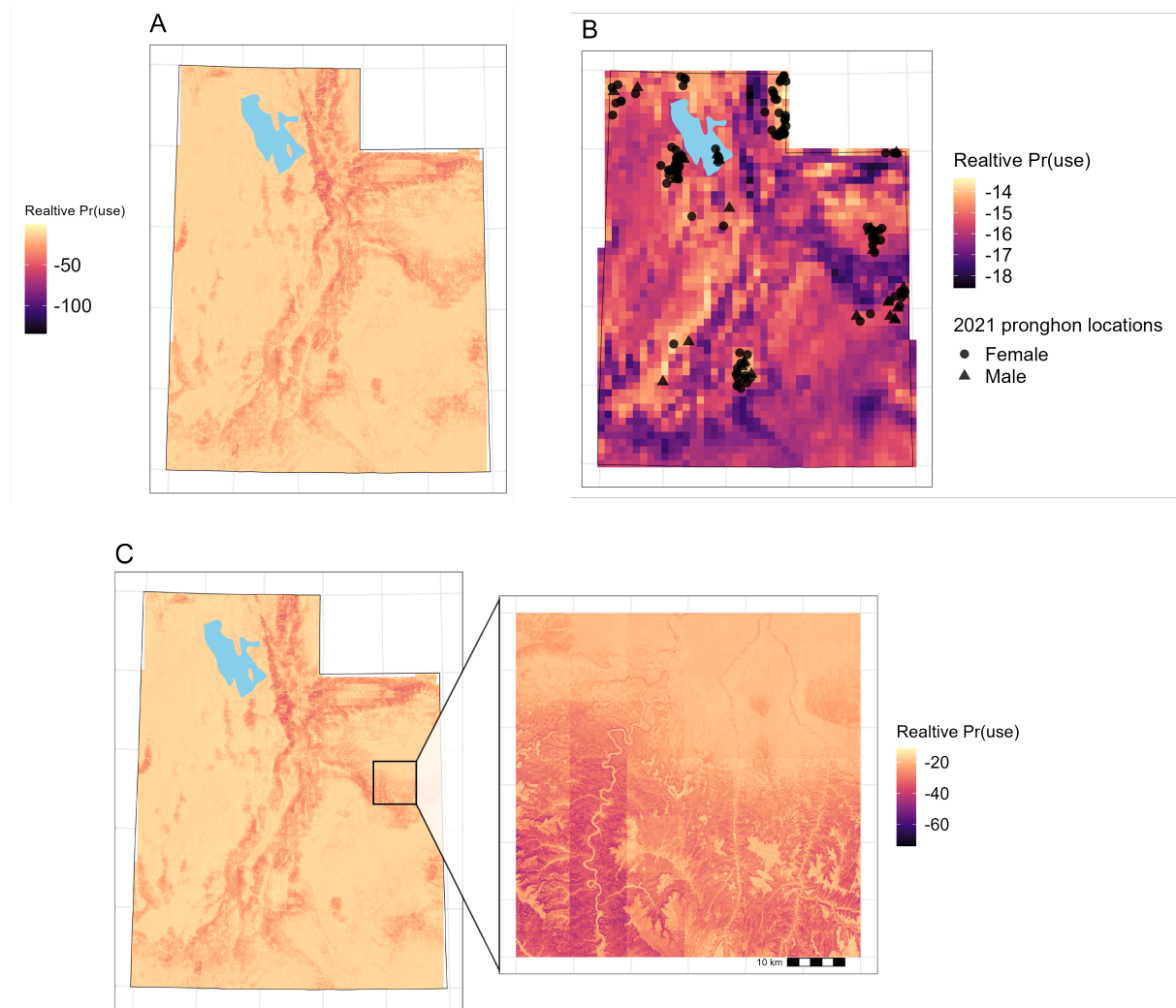


Figure 3: Spatially predictive summer habitat selection maps for female pronghorn across Utah using VP-SHAA framework, with eHSF results mapped following McLoughlin, D. W. Morris, et al. (2010). Panels A-C display third-order, second-order, and unconditional third-order selection mapping, respectively, with the points in panel B representing the mean GPS location for pronghorn monitored during the summer of 2021. Panel C provides a fine-scale enhancement of unconditional third-order mapping. The blue polygon represents the Great Salt Lake. Color intensity reflects relative probability of use and darker shades indicating lower probability of use.



The predictive habitat selection maps produced by step 7 demonstrate differences in relative probability of selection for each season-status-sex classification (Appendix B). Here, third-order (Figure 3A), second-order (Figure 3B), and unconditional third-order mapping (Figure 3C) indicate predicted habitat selection in each 30x30m pixel within the 100km pixels across the study area for female movers and residents in summer. Although Figure 3c and Figure 3A look visually similar, Figure 3c selection has greater variation and definition at the 30m spatial resolution. Female resident selection is representative of third-order pronghorn habitat selection across all season-status-sex data subdivisions, with lower expected use of high elevation areas, depicted in purple (Figure 3A).

### **3.4 Transferability**

We assessed model transferability for our predicted selection coefficients in our three mixed effects models in step 5 as well as our spatial predictions for mapping selection for 2021 data. Positive correlations between predicted and observed pronghorn habitat coefficients demonstrate that both the full and null models of habitat selection are predictive, but the magnitude of the selection coefficients suggests that their predictive performance is poor. The full model was able to better predict pronghorn habitat selection for six of the seven covariates when compared to the null model and three of the seven when compared to the model containing seasonal effects only (Table 2).

Table 2: Out-of-sample validation using Pearson's weighted correlation to estimate predictive capacity for the full vs. season only and full vs. null models, along with the goodness-of-prediction metric. Positive values indicate better predictive performance in the full and season only covariate model compared to the null covariate model, while negative values suggest the opposite.

Observed vs Predicted Selection Coefficients	Full model	Season model	Null model	Goodness-of-prediction (Full vs Season)	Goodness-of-prediction (Full vs Null)
Elevation	0.088	-0.094	-8.20E-17	0.091	0.045
Roughness	0.254	-0.015	1.16E-16	0.137	0.130
Aspect (Easting)	-0.0365	0.056	-2.96E-16	-0.046	-0.018
Aspect (Northing)	0.336	0.360	3.99E-16	-0.022	0.158
Herbaceous cover	0.040	-0.001	-9.02E-17	0.30	0.030
Shrub cover	0.156	0.353	-4.40E-16	-0.10	0.077
Tree cover	0.216	0.076	-1.03E-16	-0.030	0.108

To evaluate model transferability to novel environments, we used the BI index to assess predictive capabilities on our third-order, unconditional-order, and a null model containing no availability dependence. The BI correlation values differed between resident and mover individuals in each season-status-sex classification (table 3). Mover status demonstrated higher rank correlation estimates than residents across all mapping order-season-sex classification.

Table 3: Out of sample validation: Spearman’s rank correlation estimations applied to out-of-sample data for estimating predictive capacity of third-, unconditional third-order, and a null, no availability dependence model for each season-status-sex combination. Values closer to one demonstrate higher association of prediction, and a negative value demonstrates a negative association of prediction.

Season	Status	Sex	Third-order			Unconditional third-order	Null
			Mean	SD	n	Rank value	Rank value
Winter	Resident	F	0.17	0.73	77	0.40	0.35
	Resident	M	-0.01	0.69	49	0.22	0.63
Spring	Resident	F	0.56	0.55	11	0.70	0.54
	Resident	M	-0.48	0.73	7	-0.6	0.80
	Mover	F	0.38	0.67	92	0.82	0.85
	Mover	M	0.46	0.60	31	0.89	0.76
	Resident	F	0.15	0.60	6	0.2	0.61
Summer	Resident	M	-0.33	0.65	7	-0.61	-0.13
	Mover	F	0.22	0.73	91	0.58	0.95
	Mover	M	0.15	0.85	27	0.62	0.61
	Resident	F	0.56	0.38	7	0.89	0.86
Fall	Resident	M	0.84	0.19	2	0.67	0.87
	Mover	F	0.27	0.73	79	0.70	0.62
	Mover	M	0.14	0.72	37	0.66	0.83

## 4 Discussion

Habitat selection behavior arises from an interaction between an individual’s internal state and the external environment, both of which can vary in space and time. As we have demonstrated here,

habitat selection is typically observed at the individual level, and it may be challenging to draw any generalizable conclusions at the population-level. In the absence of careful variance partitioning, we might have concluded that, on average, pronghorn in Utah did not strongly select for or avoid any habitat components within their seasonal home ranges (Figures 3). Looking only at the third-order selection, we may have also drawn the conclusion that accounting for availability at the individual-level was insufficient to make inference at the population-level (Figure 3a). Using the VP-SHAA workflow however, we were able to tease apart the drivers of variability in individual-level habitat-selection to draw inference about population-level patterns. Accounting for availability dependence and differences in sex and movement strategy between individuals were particularly important for drawing accurate inference about habitat selection behavior. To make accurate predictions from fine-scale data across large management regions, our results suggest corrections for scale dependence is necessary and adjustments for availability dependence can be useful.

#### **4.1 Drivers of pronghorn habitat selection in Utah**

To our knowledge, our study provides the first comprehensive analysis on pronghorn habitat selection considering an array of temporally static and dynamic habitat covariates across a large environmental gradient. Of the environmental covariates previously explored as drivers of pronghorn habitat selection, our findings are largely corroborated by the body of existing literature. Sawyer et al. (2019) found that pronghorn strongly avoid trees, which is supported by our findings that females in winter, movers in spring, and residents in fall avoid tree cover. After conducting a fecal analysis, Jacques et al. (2006) found pronghorn demonstrate a preference for grasses over shrubs, but with selection for shrubs increasing in the winter, which aligns with our results. Movers during spring and females during winter avoided shrub cover and selected instead for herbaceous resources. Our study was also able to expand on additional environmental factors that might contribute to pronghorn habitat selection; for example, we found evidence of no selection or avoidance for elevation across all seasons and movement types. We also found selection for rougher terrain by residents during spring and avoidance by movers during fall. Overall, few studies on ungulates,

let alone pronghorn, have been able to draw inference on selection across multiple populations or across a study area with as much climatic and topographical diversity as Utah.

Pronghorn in Utah did not strongly select for or avoid habitat components within their seasonal home ranges. There are three possible explanations for this general pattern of weak, population-level habitat selection. First, the seven habitat covariates considered here could be of little importance to pronghorn as they make habitat selection decisions, but previous pronghorn habitat selection research suggests that this is likely untrue (Jacques et al. 2006; Sawyer et al. 2019; Jacques et al. 2006). Second, individual pronghorn may exhibit unique, specialized habitat selection behavior so that there are no common patterns at the population-level, although, the small magnitude of the individual-level random effects in our analysis suggests this is not the case. Lastly, pronghorn may select for seasonal ranges rather than specific habitat types within those ranges, satisfying their ecological needs through second-order habitat selection and negating the need for third-order selection (as observed in Figure 3A).

Our analysis highlights the evident link between habitat selection and an individual's behavioral state, especially when comparing the movement syndromes of migration and residency in pronghorn. While other studies have found that the direction and strength of an individual's habitat selection is dependent on their behavioral state (Picardi et al. 2022; Klappstein, Thomas, and Michelot 2023), our results demonstrate that the predictive capacity of SHAA models is also conditional on behavioral state. The differential predictive success for each movement strategy may stem from the scale in which these groups are selecting for habitat. While movers choose two separate seasonal ranges at the second-order and then select for specific habitat attributes within those ranges at the third-order, residents appear to select only for home ranges at the second-order, exhibiting little within-home range selection. It is difficult to say if habitat attributes are driving movement behavior or if movement behavior influences habitat selection, but both appear important when predicting species distribution.

Understanding the relationship between movement syndromes and habitat selection holds great importance for developing effective conservation strategies for migratory species (Matthew J

Kauffman et al. 2021). The mapping and preservation of migration corridors play a pivotal role in the conservation of migratory or partially migratory species (Merkle et al. 2022). Our unconditional selection model had high predictive accuracy for a migratory species, possibly because pronghorn are selecting for habitat at multiple scales, making our VP-SHAA workflow a valuable tool for habitat-based migratory corridor delineation (refer to Table 3). While we only have applied our model to a single species in one geographic area, we anticipate that a hybrid model of scale selection will always perform better when predicting the behavior of species who travel long distances before returning to localized movements, like migrants. Our workflow is a valuable conservation and management tool for individuals or agencies working to delineate migratory habitat, like the Utah Wildlife Migration Initiative, because of its behavioral state-dependent predictive capabilities which are exceptionally good for migrant populations or species.

## **4.2 Individual Variation in Habitat Selection and Population-level inference**

While making management decisions, it is common to consider population-level inference. However, individual animals may exhibit consistent variations in their responses to environmental cues, which can undermine the effectiveness of population-based recommendations for certain subgroups (Matthiopoulos, J. Fieberg, et al. 2015; Paton and Matthiopoulos 2016). In our VP-SHAA workflow, we comprehensively addressed individual variation by incorporating sex, movement status, and an individual random effect into our full model, capturing over three times the variation in habitat selection across populations. Additionally, we accounted for individual-specific environmental conditions by adjusting for availability dependence. By controlling for individual-level variation, we were able to draw more robust conclusions about the factors influencing pronghorn habitat selection at the population level. Additionally, by accounting for individual variation during different seasons throughout the year, we gained further insights into how individuals and subsequent groups select or avoid habitat based on its availability. This information can provide valuable insights into how these factors influence behaviors such as movement.

### 4.3 VP-SHAA workflow and model transferability

The VP-SHAA workflow generally met our expectations regarding its predictive capabilities, albeit with mixed outcomes. Notably, our unconditional third-order mapping enhanced model transferability in twelve out of the fourteen season-status-sex groups. However, our model with availability dependence yielded higher rank values in only eight of the fourteen groups compared to the null models. This discrepancy suggests that while availability dependence may prove beneficial in certain cases, its effectiveness varies across different contexts. Nonetheless, our VP-SHAA workflow, whether with or without availability dependence, consistently displayed robust predictive capabilities. Its temporal transferability equips modelers with the tools to assess the potential impacts of environmental change on species, their selection, and their distributions. This empowers conservation managers to anticipate the effects of global change more effectively.

Furthermore, the spatial transferability aspect of our models evaluates the extent to which parameterized models can be generalized to other regions, relying on predictions through interpolation rather than extrapolation (Aarts et al. 2013). The VP-SHAA framework stands out due to its adaptability to species-specific conditions and its capacity to incorporate critical factors that influence specific systems, such as conspecific density, predation pressure, and the presence of competing species. It not only enhances transferability with respect to habitat covariates for pronghorn within this ecosystem but also reveals disparities between migratory behavioral tactics and our ability to make accurate selection predictions.

Overall, the VP-SHAA has laid the foundation for a more transferable spatio-temporal framework. Our approach effectively captures the large variation in individual selection where no clear pattern could be derived, demonstrating robust predictive capabilities, and our results conclusively illustrate that the VP-SHAA workflow significantly improves model transferability for pronghorn in this system.

## 4.4 Spatial predictions across a diverse environmental gradient

When only mapping third-order predictions, we found discrepancies between our results and expectations, grounded in species biology. For example, pronghorn were predicted to strongly select for the salt flats of northeastern Utah near the Great Salt Lake. This is because at a fine spatial scale, the salt flats have habitat attributes that pronghorn do select for, like very flat areas with few trees. However, third-order selection, by definition, is within home-range selection, so by using a third-order model we are assuming that pronghorn live on the salt flats, which is highly inaccurate. Orders of selection are inherently nested and thus our estimates are conditional. Predicting without second-order information often leads to maps that are inconsistent with expected ecological patterns (Buderman et al. 2023), as we saw for pronghorn. Our findings underscore the critical importance of considering both availability and scale dependence in SHAA analyses, highlighting the need for a comprehensive approach to habitat selection modeling.

## 4.5 Conclusions

As anthropogenic development and climate change drive rapid environmental shifts, effective conservation requires that resource managers understand how habitat selection behavior varies over space and time to predict how organisms will respond to future change. Our proposed VP-SHAA workflow is a spatially explicit and transparent model framework that partitions individual variation in habitat selection behavior to draw population-level inference and prediction. We controlled population-level selection coefficients by systematically considering individual variability, availability and extent dependence, and temporal shifts in environmental space. This approach overcomes limitations researchers face drawing inferences across populations spanning an environmental gradient that could otherwise constrain our ability to make predictions in novel places or times. The flexibility of this workflow further enables customization of the model to match specific systems or research questions by incorporating different sources of variability in habitat selection behavior. The application of the VP-SHAA workflow for pronghorn in Utah sheds light on previous unknown drivers of habitat selection and established a baseline understanding of behavior that will motivate



future pronghorn research. Overall, our results demonstrate the inferential and predictive capabilities of the VP-SHAA workflow, an adaptable approach controlling for variation that otherwise confound habitat selection analyses.

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