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Research article

Forecasting animal distribution through individual habitat selection: insights for population inference and transferable predictions

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Habitat selection models frequently use data collected from a small geographic area over a short window of time to extrapolate patterns of relative abundance into unobserved areas or periods of time. However, such models often poorly predict the distribution of animal space-use intensity beyond the place and time of data collection, presumably because space-use behaviors vary between individuals and environmental contexts. Similarly, ecological inference based on habitat selection models could be muddled or biased due to unaccounted individual and context dependencies. Here, we present a modeling workflow designed to allow transparent variance-decomposition of habitat-selection patterns, and consequently improved inferential and predictive capacities. Using global positioning system (GPS) data collected from 238 individual pronghorn, *Antilocapra americana*, across three 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 30×30 m resolution but an extent of 220 000 km². We believe our transferable workflow can provide managers and researchers alike a way to



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turn limitations of traditional habitat selection models – variability in habitat selection – into a tool to understand and predict species-habitat associations across space and time.

Keywords: *Antilocapra americana*, context dependence, habitat selection functions, model transferability, scale, species distribution models

Introduction

One of the central aims of ecology is to understand why species have their observed spatio-temporal distributions (Yates et al. 2018). 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 et al. 2020). SHAAs include species distribution models (SDMs), occupancy models, 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 et al. 2015, 2020, Fieberg 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 et al. 2015). While part of the allure of SHAAs and their prevalence in ecological literature stems from their capacity for inference, there is also the promise of their predictive capabilities (Matthiopoulos et al. 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 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 (Johnson et al. 2004), prioritizing translocations (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 (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 et al. 2022, Gantchoff et al. 2022, Heit et al. 2023).

The transferability of SHAAs is often limited by availability dependence, and 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 (Fieberg et al. 2010, Bastille-Rousseau et al. 2015, Fieberg et al. 2018, Bowersock et al. 2023). 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 et al. 2010, Matthiopoulos 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 (Fieberg et al. 2010, Bastille-Rousseau 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.) 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 be adequately accounted for.

Recent improvements have been made to SHAAs to increase their predictive performance. Matthiopoulos 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 have termed ‘variance partitioning species-habitat association analysis’ (VP-SHAA). This workflow consists of data preparation, modeling, and the generation of inferential and/or predictive 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 from our mixed models to predict habitat selection coefficients across space and time, and demonstrate both how to quantify transferability and generate predictive maps. Our goal is to improve the transferability of SHAAs 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. Pronghorn are North America’s only extant endemic ungulate and are considered habitat specialists, yet are wide-ranging, and relatively understudied compared to other game species in the American West (Berger 2004). Data on pronghorn ecology to support scientifically informed conservation decisions are scarce. While knowledge of present drivers of pronghorn habitat selection is an important contribution to our understanding of pronghorn biology, it will likely be inadequate for future management given the rapidly changing global climate. The necessity of protecting America’s endemic ungulate and present dearth of information make pronghorn an ideal species to test the

inferential and predictive capabilities of the VP-SHAA workflow to aid in present and future management. Our goal is to use our VP-SHAA workflow to infer present drivers of pronghorn habitat selection and predict their space use in areas where pronghorn were not monitored, to assist resource managers with future-focused conservation efforts.

Material and methods

Methodological approach

Before discussing our specific methods for pronghorn in Utah, we provide a concise overview of how our VP-SHAA workflow (Fig. 1) differs from existing methods. In this work, we analyze individual habitat selection in each season-year using exponential habitat selection functions (eHSF) with a use-available design. To standardize what is considered ‘available’ across our individuals we chose to define available habitats as those occurring within a fixed square spatial extent centered on the animal’s location mid-season. We note that our approach is one of several approaches to delineating availability when fitting habitat selection functions (e.g. using a minimum convex polygon around observed locations), all of which assume that availability does not vary across ‘used’ points within some discrete spatial and temporal extents. None of these approaches is ‘right’ or ‘wrong’; each involves discretizing time and space, and each provides a different scope of inference and reflects a different set of assumptions (Northrup et al. 2013, 2022, Prokopenko et al. 2017). An arguably more objective approach is to use information about the animal’s movement capacity to define what is available to it at any point in space and time (e.g. using integrated step-selection analysis, Avgar et al. 2016). Powerful as these dynamic-availability approaches are, their application to predicting animal space-use distributions is involved and is still beyond the reach of many practitioners (see the Supporting information for further details and discussion).

Our focus here is thus on exponential habitat selection functions (with static availability domains) which can be directly applied to a given landscape to predict animal space-use distribution at a given scale. DeCesare et al. (2012) introduced a nested scale structure for SHAA, accounting for the conditional availability at first, second, and third order of selection. These orders of selection are inherently nested, and thus estimates are conditional (i.e. third-order selection is conditional on second-order selection). However, implementation hurdles arise, especially for wide-ranging species, where it is often difficult to obtain range-wide data, given populations cross state and federal boundaries. In our workflow, we have attempted to account for the challenges associated with scaling and scale dependence that limit the inferential and predictive capabilities of SHAA models in several aspects. First, we standardize the extent for our availability domains for our individual HSFs across season and years. Second, we take care to match the scale of our covariates to the scale at

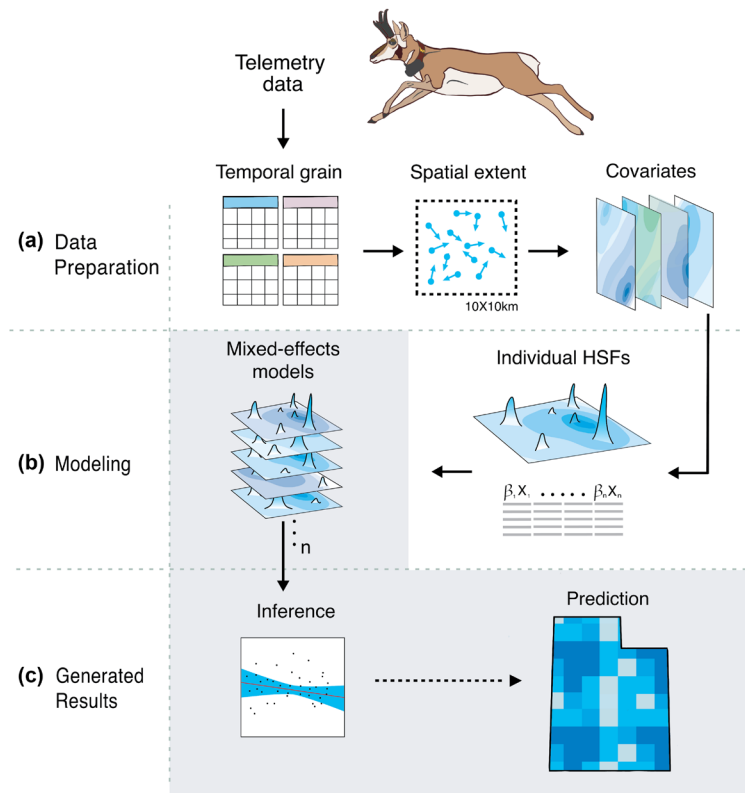


Figure 1. Variance partitioning species-habitat association analysis(VP-SHAA) workflow with three stages; (a) data preparation, (b) modeling, and (c) results (see ‘Methodological approach’). White and gray background denotes individual- and population-level inference, respectively.

which animals are responding to them. Third, when scaling from individual to population-level inference, we carefully partition our individual variation using a two-stage framework to generate inference at the population-level.

Addressing the challenges of scale is a complex task. Our objective is to develop predictive models of the probability of use based on remotely sensed landscape data and GPS telemetry data that consider multiple scales of selection (Johnson 1980, DeCesare et al. 2012, Buderman et al. 2023). We integrate second- and third-order selection to account for temporally varying landscape characteristics available for use during movements within the home range (third-order selection), while also considering individual home range selection (second-order selection) during biologically relevant periods of the year. In the Supporting information we describe our workflow for creating our second-order projections, which closely followed the workflow described here but defined the entire state of Utah as ‘available’. Finally, we calculated the pixel-by-pixel product of the second- and third-order projections for each season, status, and sex combination in our dataset (Supporting information). This process created ‘unconditional third-order’ probability of use maps, which 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 a flexible method to evaluate population-level habitat selection by considering individual habitat-selection behaviors while also accounting for scale and availability dependencies.

Data preparation

Pronghorn captures

The Utah Division of Wildland Resources (UDWR) captured pronghorn across the state from 2017 to 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.

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. 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 migratory (April), summer ranging (July), and fall migratory (November) behavior. Individuals were considered to be 'ranging' when on their winter range and were not assigned a movement status (Supporting information).

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 et al. 2002, Van Beest et al. 2010, Prokopenko et al. 2017).

We delineated a 10×10 km square availability domain centered on the pronghorn's position mid-month for each individual-month-year data subdivision. We chose to use a 100 km^2 extent based on typical monthly home range size (Supporting information) to align with the scale of our covariates for prediction. This choice was made to ensure consistency, especially in cases where we lack information about the home range of uncollared individuals or those that have not entered the population. The decision to use a square shape was influenced by logistical considerations, enabling predictive mapping that matches the raster size of covariates to the selection scale of individuals. It is worth noting that the choice of this domain is system and question specific, and other research questions or motivations might lead to a different choice of availability domain.

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 HSF models. It is good practice to standardize covariates to the same spatio-temporal resolution to account for scale dependence in the analysis. After reviewing the primary literature, we selected a suite of environmental covariates representing known drivers of ungulate space-use (Supporting information). Since habitat selection is, in part, a behavioral response to environmental variation, the spatiotemporal grain used to measure environmental attributes will affect our inference. We recommend using the temporal grain chosen above and a single spatial grain for all covariates. For pronghorn, we extracted covariate values from remotely sensed products at a

30×30 m 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.

Modeling

Accounting for individual behavioral variability in habitat selection functions

With standardized habitat covariates, we can begin analyzing individual and temporal variations in habitat selection behavior by estimating selection coefficients for each study organism based on temporal data subdivision. We used logistic regression to estimate the parameters of the eHSF that are fitted to each data subdivision independently. Our eHSFs take the form:

$$\begin{aligned} w(x) = & \exp(\beta_0 + \beta_{\text{elevation}} \times \text{elevation}(x) \\ & + \beta_{\text{roughness}} \times \text{roughness}(x) + \beta_{\text{herbaceous}} \times \text{herbaceous}(x) \\ & + \beta_{\text{shrub}} \times \text{shrub}(x) + \beta_{\text{tree}} \times \text{tree}(x) \\ & + \beta_{\text{eastings}} \times \text{eastings}(x) + \beta_{\text{northings}} \times \text{northings}(x)) \end{aligned}$$

where $w(x)$ is the space-use intensity at position x in geographical space, β_0 is the baseline log space-use intensity at x (i.e. space use intensity where all other predictors are 0; inestimable under the 'use-available' design used here), and the other β s are habitat-selection coefficients (Supporting information).

Habitat-selection coefficients can be interpreted in terms of relative selection strength (RSS; Avgar et al. 2017); the ratio between the use intensity of two alternative positions assuming that the two positions are equally available (in geographical space) and environmentally identical but differ in the value of a single habitat covariate (i.e. along a single environmental axis). For standardized continuous predictors, such as $\text{elevation}(x)$ in our model, the eHSF coefficients $\exp(\beta_{\text{elevation}})$ is the RSS for two positions differing by one SD unit of elevation, while all other predictor variables remain constant.

Since each 30×30 m pixel within our availability domain had the same covariate values, we assigned one available point per pixel. The used points consisted of the GPS points per individual in that specific season. We assigned a weight of 1 to the used points and a weight of 5000 to the available points, following the guidance of Fieberg et al. (2021).

Mixed-effect model structure for variance decomposition

To gain a better understanding of the factors influencing habitat selection, we used a covariate-specific linear mixed-effects model. We constructed separate models for each estimated eHSF selection coefficient. This approach allowed us to investigate the contributions of individual, temporal, availability-dependence, and environmental factors to the variation in habitat selection. Our models, constructed for each covariate, took on the following form:

$$\begin{aligned}
\beta_{\text{elevation}_i} = & \beta_1 \times \text{biomass}_i + \beta_2 \times \text{snow}_i + \beta_3 \times \text{road}_i \\
& + \beta_4 \times \text{elevation}_i + \beta_5 \times \text{is.Winter}_i \\
& + \beta_6 \times (\text{is.Winter}_i \times \text{is.Male}_i) \\
& + \beta_7 \times (\text{is.Winter}_i \times \text{precipitation}_i) + \beta_8 \times \text{is.Spring}_i \\
& + \beta_9 \times (\text{is.Spring}_i \times \text{is.resident}_i) \\
& + \beta_{10} \times (\text{is.Spring}_i \times \text{precipitation}_i) + \beta_{11} \times \text{is.Summer}_i \\
& + \beta_{12} \times (\text{is.Summer}_i \times \text{is.resident}_i) \\
& + \beta_{13} \times (\text{is.Summer}_i \times \text{precipitation}_i) + \beta_{14} \times \text{is.Fall}_i \\
& + \beta_{15} \times (\text{is.Fall}_i \times \text{is.resident}_i) \\
& + \beta_{16} \times (\text{is.Fall}_i \times \text{precipitation}_i) \\
& + u_{\text{unit:year}(i)} + v_{\text{ID}(i)} + \varepsilon_i \\
u_{\text{unit:year}(i)} \sim & N(0, \sigma_{\text{unit:year}}^2) \\
v_{\text{ID}(i)} \sim & N(0, \sigma_{\text{ID}}^2) \\
\varepsilon_i \sim & N(0, \sigma^2)
\end{aligned}$$

where $\beta_{\text{elevation}_i}$ is the selection coefficients from the individual HSFs for observation i . The β terms are the fixed effect component of the model that accounted for individual-level characteristics, including sex, season, age, reproductive status, and movement strategy (i.e. whether the individual was a ‘mover’ or a ‘resident’ in a given season-year; Supporting information). We incorporated interactions between precipitation covariates, sex, movement strategy, and season to account for additional temporal variability. Additionally, we included the availability of the habitat covariate that corresponded to the modeled eHSF coefficient as a fixed effect. By considering availability, we were able to differentiate between the selection of a specific habitat and its actual availability (availability dependence), which facilitated the identification of the underlying mechanisms driving variation in habitat selection. To address residual unexplained individual variation, we included random effects for individual and WMU-year combinations, where $v_{\text{ID}(i)}$ is the random effect for individual, $u_{\text{unit:year}(i)}$ is the random effect on year and wildlife management unit, and ε_i is the residual error term. Finally, the response variables were weighted using their respective inverse variance. This weighting approach assigned less influence to the coefficient estimates associated with higher uncertainty (DeCesare et al. 2012, Holbrook et al. 2019, Dickie et al. 2020).

We note that one limitation of the approach we have taken here is that it assumes independence among the different eHSF coefficients (although some covariation may be captured by the random effects). It is theoretically possible to overcome this limitation by fitting a single multivariate-response model.

However, appropriately including availability dependencies, random effects, and inverse-variance weights in such a multivariate model is far from trivial and is likely inaccessible to most practitioners. We have thus opted to keep our workflow as simple and interpretable as possible.

Generated results

Drawing habitat selection inference

Functional responses (also known as availability dependence) in habitat selection refer to the oft-observed phenomenon of shifts in the relative use of habitats or resources following shifts in the availability of habitat or resources (across space or time) (Mysterud et al. 1999, Holbrook et al. 2019, Avgar et al. 2020a). 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 the population-level selection coefficients derived from the fixed effects of the variance-partitioning models described above, against the overall availability of that covariate to assess availability dependence (Fieberg et al. 2010, DeCesare et al. 2012, Holbrook et al. 2019). In our system, we used the selection coefficients from our fitted mixed-effects models to assess how, in each season, pronghorn may respond to a change in availability at the population level, and how this change may differ by sex and movement classification (Supporting information).

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

Making spatial predictions

Our aim was 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.

Using standardized parameters from our mixed-effects models, 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 dataset. To ensure that our predictions were made at the same scale the model was fit, we overlaid a grid of 10×10 km pixels across Utah, corresponding to the size of the pronghorn availability domain.

For mapping third-order selection, we used the fixed effects from the mixed-effects models to predict habitat selection within each 10×10 km pixel during each season. To estimate the relative probability of pronghorn use, we down-scaled our predictions to 30×30 m by substituting our expected coefficient values into our eHSFs within each $10 \times$

10 km pixel. We normalized our third-order habitat selection rasters so that they sum to 1 within each 10×10 km pixel (McLoughlin et al. 2010).

Unconditional third-order mapping

In our methodology, we incorporated the concept of nestedness across selection orders (DeCesare et al. 2012, 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; 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 using the covariates from our eHSF models and the estimated selection coefficients from our mixed-effect models. 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’ (Supporting information).

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 (Morris et al. 2016, Buderman et al. 2023).

Validation

Transferable models are needed to accurately predict space-use in environments that differ greatly from those used during model training (Fieberg et al. 2018, Aldossari et al. 2022). Properly evaluating predictive model performance is therefore critical when developing conservation strategies that account for future environmental change (Yates et al. 2018). There have been many methods suggested for validating model predictive performance in the literature (Boyce et al. 2002, Roberts et al. 2017, Aldossari et al. 2022). We validated our model using a year of data that was not used for model training (293 individuals, 77 of which were new to the study, monitored in 2021). Additionally, pronghorn differ from other ungulates, such as elk and mule deer, in that they have low site fidelity and are facultative migrants, in which their behavioral tactics vary within or across years (Jakes et al. 2018, Morrison et al. 2021), supporting the relative independence of the training and testing datasets. Our workflow, applied here to forecast new animals in the future on the same landscape, holds potential for application to different animals and landscapes, depending on data availability.

Predictive model validation

To assess the predictive performance of our workflow, we fit the model using the selection coefficients output from the three years of pronghorn data for the withheld dataset to obtain ‘true’ selection coefficients. We compared the 2021 predicted coefficients to the ‘true’ selection coefficients obtained using inverse variance weighted Pearson’s correlation coefficients. To evaluate the improvement in model transferability, we compared the VP-SHAA full model predictions to predictions from season-only and null (intercept-only) models. We quantified the difference using a goodness-of-prediction metric (Burzykowski and Biecek 2020). Specifically, we subtracted the null model’s weighted correlation estimates from the full model’s correlation estimates and divided by two for each mixed-effects model.

Spatial predictive validation

We calculated the out-of-sample Boyce index (BI) for the predicted third-order and unconditional projections (Boyce et al. 2002). This assessment was conducted using the 10×10 km pixels, where GPS points were available for each season and year. We only used 10×10 km 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, five 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 30×30 m pixels within a 10×10 km pixel for each season-status-sex classification. To measure model transferability, we applied Spearman’s rank correlation (Nielsen et al. 2010) for each 10×10 km cell and calculated the mean and SD for each season-status-sex classification as a metric of model transferability.

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 10×10 km 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).

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.

Results

Habitat selection inference

A visualization of the distributions of the seven eHSF coefficients shows tremendous variability, with coefficients encompassing both positive (selection) and negative (avoidance) values across data subdivisions (Fig. 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 of our mixed-effects models demonstrates 42 of the 56 population-level averages had confidence bounds that overlapped 0, indicating a lack of significance (Fig. 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 females in winter ($\beta = -1.15$). Winter females ($\beta = -0.108$) and spring movers ($\beta = -0.139$) selected against north-facing slopes.

The predictive habitat selection maps demonstrate differences in relative probability of selection for each season-status-sex classification (Supporting information). Here, third-order (Fig. 3a), second-order (Fig. 3b), and unconditional third-order mapping (Fig. 3c) indicate predicted habitat selection

in each 30×30 m pixel within the 100 km pixels across the study area for female movers and residents in summer. Although Fig. 3a, c look visually similar, Fig. 3c selection has greater variation and definition at the 30 m 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 (Fig. 3a).

Spatial predictions

Transferability

We assessed model transferability for our predicted selection coefficients in our mixed effects models as well as our spatial predictions using an additional year of monitoring data collected in 2021. 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 1).

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 (Table 2). The BI correlation values varied between resident and mover individuals for each season-status-sex category. During winter, ranging females exhibited higher rank correlation estimates in the

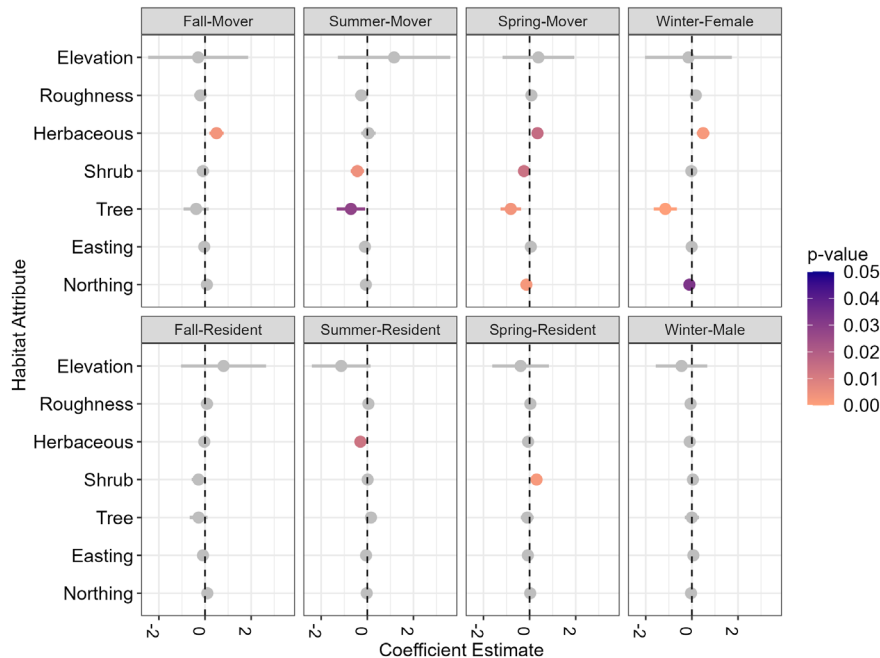


Figure 2. Estimates and 95% confidence intervals for relative habitat selection strength in pronghorn *Antilocapra americana*, 2018–2020 (Utah, USA), based on seven covariates. Significance is a color-coded gradient, with lighter shades indicating lower significance, darker shades indicating higher significance,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

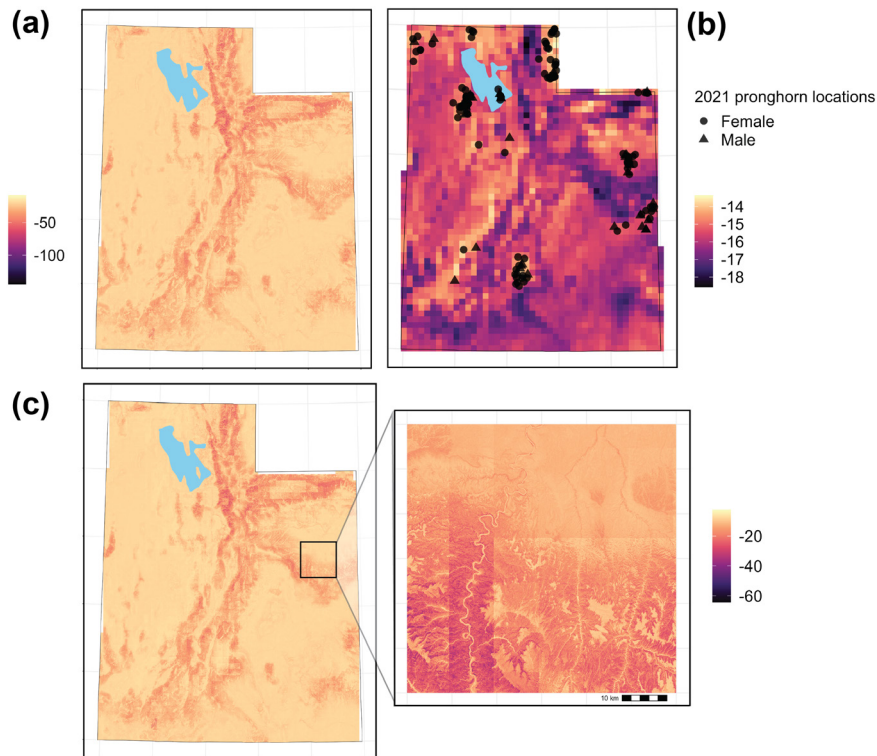


Figure 3. Spatially predictive summer habitat selection maps for female pronghorn across Utah using variance partitioning species-habitat association analysis (VP-SHAA) framework, with exponential habitat selection functions (eHSF) results mapped following [McLoughlin et al. \(2010\)](#). (a–c) display third-order, second-order, and unconditional third-order selection mapping, respectively, with the points in (b) representing the mean GPS location for pronghorn monitored during the summer of 2021. (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 with darker shades indicate lower relative probability of use.

unconditional-order model compared to the null model. Mover status also displayed higher rank correlation estimates than residents across all mapping order-season-sex categories.

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 static habitat components within their seasonal home ranges, such as elevation and roughness ([Fig. 3](#), Supporting information). 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 ([Fig. 3a](#)). Using the VP-SHAA workflow, however, we were able to tease apart the drivers of variability in individual-level habitat-selection to draw

Table 1. Out-of-sample validation using Pearson's weighted correlation to estimate predictive capacity for the full, season-only, and null models. Goodness-of-prediction metric were also estimated for full versus season only and full versus null models. 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 versus predicted selection coefficients	Full	Season	Null	Goodness-of-prediction (Full versus Season)	Goodness-of-prediction (Full versus Null)
Elevation	0.088	−0.103	8.20×10^{-17}	0.095	0.044
Roughness	0.255	0.003	-7.46×10^{-17}	0.126	0.127
Aspect (Easting)	−0.036	0.043	-3.89×10^{-16}	−0.012	−0.017
Aspect (Northing)	0.336	0.360	3.90×10^{-16}	−0.022	0.158
Herbaceous cover	0.040	−0.045	-1.44×10^{-16}	0.043	0.020
Shrub cover	0.156	0.353	4.14×10^{-16}	−0.087	0.078
Tree cover	0.223	0.0293	-2.12×10^{-16}	−0.035	0.112

Table 2. 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	ranging	F	0.17	0.73	77	0.40	0.35
		M	-0.01	0.69	49	0.22	0.63
Spring	resident	F	0.56	0.55	11	0.70	0.54
		M	-0.48	0.73	7	-0.6	0.80
	mover	F	0.38	0.67	92	0.82	0.85
		M	0.46	0.60	31	0.89	0.76
Summer	resident	F	0.15	0.60	6	0.2	0.61
		M	-0.33	0.65	7	-0.61	-0.13
	mover	F	0.22	0.73	91	0.58	0.95
		M	0.15	0.85	27	0.62	0.61
Fall	resident	F	0.56	0.38	7	0.89	0.86
		M	0.84	0.19	2	0.67	0.87
	mover	F	0.27	0.73	79	0.70	0.62
		M	0.14	0.72	37	0.66	0.83

inference about population-level patterns (Fig. 2, Supporting information). Accounting for availability dependence and differences in sex and movement strategy between individuals were particularly important for drawing accurate inference about habitat selection behavior in our system. To make accurate predictions from fine-scale data across large management regions, our results support the prevailing findings in the literature that correction for scale dependence is necessary and adjustments for availability dependence are useful.

Drivers of pronghorn habitat selection in Utah

To our knowledge, this study is the first to comprehensively analyze pronghorn habitat selection across a wide environmental gradient, considering both static and dynamic habitat factors. Our findings largely support previous research on the environmental factors influencing pronghorn habitat selection. For example, Sawyer et al. (2019) found that pronghorn strongly avoid trees, which is consistent with our findings of females in winter, movers in spring, and residents in fall avoiding tree cover. Similarly, Jacques et al. (2006) discovered that pronghorn prefer grasses over shrubs but show an increased preference for shrubs in the winter, which aligns with our results. Movers during spring and summer, as well as females during winter, avoid shrub cover and instead select herbaceous resources (Fig. 2). Our study also expands on additional environmental factors that may contribute to pronghorn habitat selection. We found no significant evidence of selection for or avoidance of elevation across all seasons and movement types at the third-order. Additionally, we observed selection for rougher terrain by residents during spring and avoidance by movers during fall. Few studies have investigated selection patterns in ungulates, particularly pronghorn, across multiple populations or in an area as diverse in climate and topography as Utah.

Availability dependence, or functional responses in habitat selection, occur when animals change their behavior in response to the availability of suitable habitat and/or the

abundance of resources within these habitats (Mysterud and Ims 1998, Aarts et al. 2013, Avgar et al. 2020b). Animals will therefore adjust their behavior based on the availability of resources, demonstrating that their behavior is influenced by the broader context of their habitat (William et al. 2018, Holbrook et al. 2019). In our study of Utah pronghorn, we found evidence of availability dependence across all seven covariates analyzed. Herbaceous cover, a proxy for forage, showed positive selection, shifting from avoidance to selection as availability increased, across all four seasons at both second- and third-order scales (Supporting information) for both sexes and movement statuses, excluding residents in summer (Supporting information). Hence, pronghorn seem to concatenate their space use in areas of abundant herbaceous cover (forage, at least during the growing season) when in regions with abundant herbaceous cover. This positive functional response is consistent with selection for herbaceous cover being positive at both the 2nd- and 3rd-order scales (Supporting information), reflecting individual variability in habitat selection that transcends scales; individuals that select herbaceous cover at a coarse scale, do so at a fine scale as well ('herbaceous specialist'), and individuals that avoid herbaceous cover do so at both scales ('shrub specialists'). Conversely, shrub selection demonstrated a negative functional response, with selection decreasing as availability increased (Supporting information). This suggests that pronghorn may use shrub habitats only when more preferred habitats or resources are scarce, implying that shrub habitats are less favorable or pose higher risks compared to herbaceous habitats.

Selection of some resources switched depending on the scale observed, indicating that pronghorn adjust their habitat use at different landscape scales in response to changes in availability (Supporting information). At the third order, pronghorn show no selection of elevation, while there is a positive selection at the second order. Similar patterns are observed with east-facing slopes (Aspect Easting) in spring and fall; at the third order, there is no selection or avoidance,

but at the second order, there is avoidance. This could suggest that, at the second order, pronghorn are choosing wetter areas on east-facing slopes and higher elevations, but this selection is not significant within their home range. Conversely, for north-facing slopes (Aspect Northing) in winter and spring, there is no selection at the second order, but negative selection at the third order in winter and spring. This selection could indicate that within their range, pronghorn are choosing warmer slopes with more direct sunlight, but this selection is not considered at the home range scale. These findings highlight how pronghorn respond differently to landscape features at different scales, suggesting varying ecological needs within and across seasonal ranges (Fig. 3). Similar switching behavior has been observed in elk (Prokopenko et al. 2017) and caribou (DeCesare et al. 2012) in response to anthropogenic disturbance. Overall, we have found some evidence that pronghorn adapt their habitat selection differently across scales, providing insights into their habitat selection decisions across environmental gradients.

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 are dependent on their behavioral state (Picardi et al. 2022, Klappstein et al. 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 is important for developing effective conservation strategies for migratory species (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 2). 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 tool for individuals or agencies working to delineate migratory habitat because of its behavioral state-dependent predictive capabilities.

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 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. Moreover, 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.

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 correcting for availability dependence may prove beneficial for certain subpopulations, the value of the correction is not universal. Nonetheless, our VP-SHAA workflow, with or without availability dependence, displayed improved predictive capabilities relative to the null model. 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.

Our work, while constructed in the spirit of DeCesare et al. (2012), differs from this research in several ways. First, we implement a two-stage approach where we decompose the variance from our individual HSFs and use those coefficients in a mixed model framework. Second, we distinguish between preference and availability driven variation, which is necessary for our use of out-of-sample data for prediction. Third, we explicitly accounted for availability dependence in our mixed-models, which allowed us to draw inference on habitat selection and functional responses at the population-level that may have otherwise been overlooked. Researchers can use our workflow to build upon and incorporate first-order selection across a species range, given data availability, into this analysis by multiplying it with the second- and third-order rasters, as we describe in our workflow.

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 habitat selection predictions.

It is important to note that we took every step we could to make a transferable framework, yet, even with a complete year of out of sample data, the predictive results were mixed. Often, researchers employ SHAA models for predicting outcomes relevant to management and conservation efforts. We want to emphasize that we are not suggesting a requirement for a complete validation on an entirely withheld dataset, especially considering that such studies are often data limited. Rather, we demonstrated here that even with available data and meticulous efforts to establish a transferable model, the predictive performance may not align with expectations. Caution is therefore warranted when using these models in a predictive capacity.

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 improves model transferability for pronghorn in this system.

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 flat terrain 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 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.

Without explicitly including availability dependence in our models, we may not have been able to identify differences in selection across an environmental gradient as diverse as Utah, where resources change in availability in both space and time. This exclusion would have restrained our predictive capabilities, leading to ecologically incoherent results. We believe that our findings highlight the importance of

considering both availability and scale dependence in SHAA analyses, as this information provides a more comprehensive approach to habitat selection modeling.

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 allow for population-level inference and predictions. We controlled population-level selection coefficients by systematically considering individual variability, availability dependence, and temporal shifts in environmental space. This approach overcomes limitations researchers often face when 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 the VP-SHAA 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 establishes a baseline understanding of habitat selection behavior that will motivate future pronghorn research. Researchers often have to choose between models that provide strong inferential but poor predictive capabilities, or strong predictive but poor inferential results. Here, we attempted to develop a framework that has both inferential and predictive capabilities, and we have made some progress toward our goal. Testing our workflow on additional species and systems will help to better assess how close we have come. Overall, our results demonstrate the improved inferential and predictive capabilities of the VP-SHAA workflow over traditional SHAA analyses provide a new, flexible approach for controlling for variation that otherwise confounds habitat selection analyses.

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Author contributions

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– review and editing (lead). **Brian J. Smith:** Data curation (equal); Formal analysis (supporting); Methodology (equal); Validation (equal); Visualization (supporting); Writing – review and editing (supporting). **Danielle J. Berger:** Conceptualization (supporting); Writing – original draft (equal); Writing – review and editing (supporting). **Ronan B. Hart:** Data curation (equal); Formal analysis (supporting); Writing – review and editing (supporting). **John Huang:** Data curation (equal); Formal analysis (supporting). **Kezia Manlove:** Formal analysis (supporting); Writing – review and editing (supporting). **Frances E. Buderman:** Formal analysis (supporting); Supervision (supporting); Validation (equal); Writing – review and editing (supporting). **Tal Avgar:** Conceptualization (lead); Formal analysis (supporting); Funding acquisition (lead); Investigation (lead); Methodology (equal); Project administration (lead); Resources (lead); Supervision (lead); Validation (equal); Writing – review and editing (supporting).

Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ecog.07225>.

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.4f4qrfmz> (Winter et al. 2024).

Supporting information

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

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