

## LETTER

# Density-dependent habitat selection alters drivers of population distribution in northern Yellowstone elk

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**Abstract**

Although it is well established that density dependence drives changes in organismal abundance over time, relatively little is known about how density dependence affects variation in abundance over space. We tested the hypothesis that spatial trade-offs between food and safety can change the drivers of population distribution, caused by opposing patterns of density-dependent habitat selection (DDHS) that are predicted by the multidimensional ideal free distribution. We addressed this using winter aerial survey data of northern Yellowstone elk (*Cervus canadensis*) spanning four decades. Supporting our hypothesis, we found positive DDHS for food (herbaceous biomass) and negative DDHS for safety (openness and roughness), such that the primary driver of habitat selection switched from food to safety as elk density decreased from 9.3 to 2.0 elk/km<sup>2</sup>. Our results demonstrate how population density can drive landscape-level shifts in population distribution, confounding habitat selection inference and prediction and potentially affecting community-level interactions.

**KEYWORDS**

cougar, density dependence, food-safety tradeoff, habitat selection, ideal free distribution, predation risk, predator-prey interactions, RSF, spatial distribution, wolf

## INTRODUCTION

Density dependence is a pervasive ecological process, and incorporating it into models of population abundance is critical for understanding population dynamics and informing management (Abadi et al., 2012; Guthery & Shaw, 2013). Whereas much is known about how density dependence affects variation in abundance over time, relatively little is known about how it affects abundance over space. This is a particular problem for the study of habitat selection, where density-dependent habitat selection (DDHS) is a foundational assumption (Rosenzweig, 1981) that is rarely tested and often ignored (Avgar et al., 2020). This gap is significant because unmeasured density-dependent variation in habitat selection may limit the accuracy of empirical models

for inferring drivers of fitness (e.g. food vs. safety) and predicting spatial distribution and abundance (Boyce & McDonald, 1999; Matthiopoulos et al., 2015, 2019).

The expectation of DDHS arises from optimal foraging theory (MacArthur & Pianka, 1966) via the ideal free distribution (IFD; Fretwell & Lucas, 1969). The IFD postulates that a population's density influences the fitness benefits that individuals receive from a habitat (Morris, 1987), and that individuals use habitats in a way that equalises fitness across occupied habitats (Fretwell & Lucas, 1969; Křivan et al., 2008). According to IFD, as population density increases, individuals occupy progressively lower-quality habitats ('spillover'), resulting in 'negative DDHS'—the strength of selection for high-quality habitat decreases with density (Morris, 2003; Rosenzweig, 1991). Alternatively, fitness

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in certain habitats can increase with population density (Stephens & Sutherland, 1999), leading to an increase in selection strength for these habitats—‘positive DDHS’ (Morris, 2002). Positive DDHS manifests as habitat switching, where individuals leave habitats associated with high fitness at a low density, shifting into habitats associated with high fitness at a high density (Greene & Stamps, 2001).

Fitness is never determined by a single environmental driver; thus, habitat selection reflects a balancing act along multiple dimensions and scales, each with its own context-dependent relative contribution to overall fitness (multidimensional IFD sensu Avgar et al., 2020). Population density is one of these contexts, and whether fitness in a habitat decreases or increases with density varies across different habitat dimensions. For example, fitness typically decreases with density due to reduced per-capita food acquisition (Le Bourlot et al., 2014), whereas it typically increases with density due to increased safety (i.e. reduced per-capita predation risk; reviewed by Lehtonen & Jaatinen, 2016). If food and safety are spatially independent, we expect negative DDHS along both dimensions: at low density, individuals select habitats with more food and safety, but as density increases, individuals spill into habitats with less food or safety. Conversely, if food and safety are negatively correlated in space, individuals select habitats with more food *or* safety. Thus, we expect negative DDHS along the safety dimension and positive DDHS along the food dimension; as density increases, safety in numbers increases and simultaneously, increasing intraspecific competition makes food more limiting to fitness, hence a stronger driver of habitat selection. (Avgar et al., 2020).

Despite the theoretical and practical importance of DDHS, empirical understanding of DDHS and its effects on inference and prediction from habitat selection models is underdeveloped (Avgar et al., 2020). This is especially true in free-living systems (McLoughlin et al., 2010), which involve complex trade-offs (e.g. food for safety) that are often missing in experimental systems (Lima & Dill, 1990), habitat selection at multiple scales (Johnson, 1980) and multiple interacting species. To fill this gap, we tested the hypothesis that trade-offs between food and safety generate positive DDHS for food resources and negative DDHS for safe habitats, such that the drivers of habitat selection switch from food to safety as density decreases. We did so by constructing and applying a population-level habitat selection model to winter aerial-survey data of northern Yellowstone elk collected over 16 years spanning 4 decades. Our findings demonstrate how ignoring DDHS can confound both ecological inference and prediction. We provide novel evidence of multidimensional IFD and of DDHS as an important driver of habitat selection and spatial distribution in a free-living system.

## METHODS

### Study area

Our study occurred in the winter range of the northern Yellowstone elk population (Houston, 1982; Lemke & Mack, 1998). We expanded the area previously used to define the winter range (e.g. Tallian et al., 2017) to include adjacent areas where elk were also occasionally counted (Figure S1). We believe the modified polygon better captures the full extent used by this population. Our study area encompassed 1900 km<sup>2</sup>, compared with the 1520 km<sup>2</sup> previous authors have cited. Approximately two-thirds of the winter range falls within the boundaries of Yellowstone National Park (YNP), with the remaining one-third to the north in the state of Montana. Elevations range between 1500 and 3000 m, and the area experiences long, cold winters (Houston, 1982). Northern Yellowstone elk migrate from high-elevation summer ranges, often in the interior of YNP, to the lower elevation winter range, where they are found from December to April (Houston, 1982; White et al., 2010).

Wolves (*Canis lupus*) and cougars (*Puma concolor*) are the two main predators of northern Yellowstone elk during winter (Kohl et al., 2019). Elk comprised 96% of the wolf diet in winter from 1995 to 2009 (Metz et al., 2012) and 75% of the cougar diet from 1998 to 2005 (Ruth et al., 2019). Alternative prey for wolves and cougars in the system include bison (*Bison bison*), deer (*Odocoileus hemionus*, *O. virginianus*), moose (*Alces alces*), pronghorn (*Antilocapra americana*) and bighorn sheep (*Ovis canadensis*) (Metz et al., 2012; Ruth et al., 2019).

### Data collection

A timeseries of winter counts of northern Yellowstone elk extends to the 1920s, and the population has fluctuated with various management practices and climatic conditions throughout it (MacNulty et al., 2020). Since 1988, these data have included georeferenced locations of elk groups in many years, allowing us to estimate habitat selection. Elk were counted via aerial, fixed-wing surveys designed to provide a full population census. Surveys took place mainly between 08:00 and 12:00 over 1 and 4 days between late December and March of each winter (Appendix S1). In some years, the count did not occur or georeferenced group data were only available within YNP. We used a state-space model (see Appendix S1 in Tallian et al., 2017) to interpolate total abundance in years with incomplete data so that we could predict using our fitted habitat selection model. We used the partial georeferenced data for validation (see *Model evaluation*). Counts reached an all-time high in 1994 near 20,000 elk and a low of less than 4000 in 2013 (MacNulty et al., 2020). Thus, this timeseries of georeferenced counts provided information about elk

distribution across a wide range of population densities, ideal for measuring DDHS.

During the study period (1988–2020), densities of wolves and cougars also varied in the study area. Wolves were reintroduced to YNP during 1995–1997 (Bangs & Fritts, 1996), and their population increased to a maximum in 2003 and declined thereafter (Smith et al., 2020). Cougar densities generally increased across the study period (Marcus et al., 2022; Ruth et al., 2019). Consequently, the risk of predation by each of these predators has varied substantially across the timeseries of elk distribution analysed here.

## Model structure

We modelled elk counts ( $n_{i,t}$ ) within a pixel ( $i$ ) in a year ( $t$ ) using a Bayesian generalised linear mixed model (GLMM). We used 1 km<sup>2</sup> pixels to average over elk daily movements (Appendix S1). We did not have data to directly account for imperfect detection, but we found our results were insensitive to it (Appendix S2). We used a negative-binomial likelihood to accommodate overdispersion in our count data, a distribution commonly used to model animal group sizes (Ma et al., 2011). Factors other than habitat, for example, sex-specific social interactions, are at least partially responsible for group size distributions (Gerard et al., 2002), which results in overdispersion that should be modelled to avoid overfitting. Elk group sizes in our dataset range from 1 to over 1000 individuals, as seen with elk in other areas (Brennan et al., 2015; Proffitt et al., 2012).

We modelled the expected count ( $\lambda_{i,t} = E[n_{i,t}]$ ) in each pixel and year as a function of 22 covariates (indexed by  $k$ ; Table S1), a time-varying offset ( $\alpha_t$ ), a temporal random effect ( $\eta_{i,t}$ ) and a spatial random effect ( $s_i$ , equation 1), all of which we describe in detail in Appendix S3. We used the natural logarithm (hereafter, log) as the link function.

$$\log(\lambda_{i,t}) = \alpha_t + \eta_{i,t} + s_i + \sum_{k=1}^K \beta_k x_{i,t,k} \quad (1)$$

We estimated the size parameter of the negative binomial distribution as a single free parameter ( $r$ ) such that:  $n_{i,t} \sim \text{NegBin}\left(\frac{r}{r+\lambda_{i,t}}, r\right)$ .

Because we set the area of each pixel to 1.0 km<sup>2</sup>, we can interpret  $\lambda_{i,t}$  as expected density in elk/km<sup>2</sup>. Note that ‘expected density’ refers to the expected value of our response variable. Contrast this with ‘(log) average range-wide density’, which is a predictor variable, hereafter  $\log(\text{Dens})$ .

## Habitat variables

We treated habitat variables as fixed effects representing food, safety, or other conditions. The slope of each

variable measures habitat selection (see Appendix S4). We rasterised all count data and variables on a 1-km grid, retaining only pixels falling within the study area ( $N = 1978$ ). We describe processing for all variables in Appendix S5. Variables describing conditions—snow-water equivalent (SWE), elevation and cosine and sine of aspect (northing and easting respectively; Table S1)—were included to control for important known drivers of elk density but were not the target of inference.

Because northern Yellowstone elk are primarily grazers (Houston, 1982), we measured food using total herbaceous biomass from the Rangeland Analysis Platform (RAP) annual biomass (v2.0) layer (Jones et al., 2021; Robinson et al., 2019). This layer combines information about total growth from 16-day NDVI data with plant functional type estimates to calculate growth of grasses and forbs (the annual layer sums all 16-day layers). For each winter, we used the layer corresponding to the preceding growing season to measure potential forage availability for elk that winter. We log-transformed this covariate to reduce the influence of very high values from agriculture outside YNP. We refer to this as the food variable.

We measured predation risk using the risky places approach such that habitat covariates indexed predation risk (Moll et al., 2017). Previous research has shown that risk to elk from wolves and cougars varies with tree canopy openness and terrain roughness. The wolf habitat domain is characterised by high openness and low roughness, whereas the cougar habitat domain is characterised by lower openness and high roughness (Kohl et al., 2019). On a fine temporal (5 h) and spatial scale (30 m), Kohl et al. (2019) showed that individual elk manage risk from wolves and cougars by moving into each predator's habitat domain at the time when that predator is least active. At the coarser scale of our analysis, we expected elk to select 1-km<sup>2</sup> pixels with a mixture of intermediate levels of openness and roughness that facilitate efficient switching between wolf and cougar habitat domains across the diel cycle. Thus, we expected elk density to be greatest at intermediate values of these variables, which indicate high heterogeneity in the pixel (Appendix S1; Figure S4). To test this, we included linear and quadratic terms for openness and roughness to parameterise a parabola that quantified how elk select for safety at the 1-km<sup>2</sup> scale. Hereafter, we refer to these as the safety variables. To check the raw data for a negative correlation between food and safety, we created a composite safety variable by taking the product of the openness and roughness rasters. We used Spearman's correlation to check this assumption. All other food-safety comparisons were model based (see *Quantifying DDHS*).

To support our assertion that the safety variables reflect how elk perceive risk, we included interactions between wolf and cougar densities and each of the safety variables. If the safety variables were good metrics of safe and risky places, we expected predator densities

to alter the strength of selection for the safety variable or shift the parabola vertex (most preferred openness/roughness). We predicted increasing wolf density would decrease selection strength or push the vertex away from open and smooth (i.e. away from the wolf and into the cougar habitat domain). Conversely, we predicted increasing cougar density would increase selection strength or push the vertex towards open and smooth habitat. Whereas aerial surveys occurred mostly during daylight hours before noon when wolves were more active than cougars (Kohl et al., 2019), we did not expect an effect of survey timing due to our coarse spatial scale (Appendix S1).

To measure DDHS, we included an interaction between the food/safety variables and  $\log(\text{Dens})$ . These interactions allowed for flexibility in the patterns of DDHS, but due to the linear and quadratic terms involved in the formulation, interpretation of the effects is most easily accomplished graphically (see *Quantifying DDHS*). Note that we assume that DDHS occurs as a function of the current density, not a time-lagged density. Whereas time lags are important for density dependence to operate on population growth rates (Turchin, 1990), we assume that the mechanisms for DDHS (competition for resources, safety in numbers) operate more instantaneously than their fitness consequences.

## Model fitting

We created all quadratic and interaction terms and separately scaled and centered them before fitting. We did not transform the log-density offset or the sine and cosine of aspect, but we z-transformed all other variables to facilitate model fitting. We performed all data preparation and analyses in R (v. 4.1.1), and we fitted the GLMM via MCMC using R package NIMBLE v. 0.11.1 (de Valpine et al., 2017, 2021). We used Laplace priors with mean 0 on all regression parameters, referred to as the ‘Bayesian lasso’, to prevent overfitting (Hooten & Hobbs, 2015). We ran the model for 100,000 iterations across three chains, discarded the first 20,000 as burn-in (including adaptation) and thinned by 20 to obtain 4000 posterior samples/chain for inference. All analysis code and data are available on GitHub and published through Zenodo (doi:10.5281/zenodo.6687904).

## Model evaluation

We used the Gelman–Rubin statistic to evaluate MCMC convergence (Gelman & Rubin, 1992). We then used out-of-sample data to validate our model. Counts outside of YNP in the Montana portion of the study area were unavailable in 1994, 2002 or 2004, so we withheld the YNP data for these years from model fitting and used them to validate our model. Additionally, we withheld data from

2020, which were available for the entire study area, as an additional year of validation data.

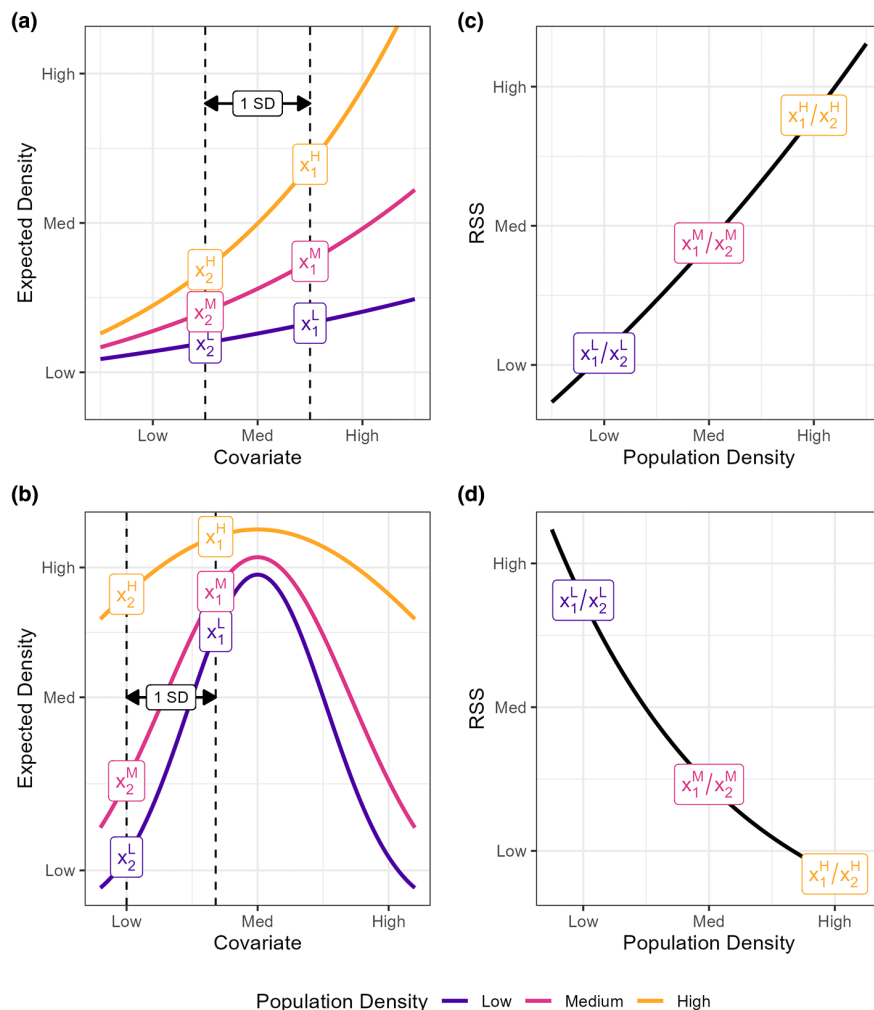
To perform validation, we used our fitted model to predict expected elk densities for each year, including all fixed and random effects. We compared expected elk densities under the model to observed densities from the count by calculating ordinary residuals ( $n_{i,t} - \lambda_{i,t}$ ), Pearson residuals ( $\frac{n_{i,t} - \lambda_{i,t}}{\sqrt{\text{var}(\lambda_{i,t})}}$ ) and Spearman's correlation coefficient between predicted and observed densities. We compared ordinary residuals and Spearman's correlation between the training and testing years. We used Pearson residuals to check for residual spatial autocorrelation by fitting non-parametric spline correlograms to these residuals (Bjørnstad & Falck, 2001).

To estimate model goodness-of-fit, we calculated a likelihood-based pseudo- $R^2$  for each posterior sample from the MCMC, yielding a distribution of pseudo- $R^2$ . We calculated our pseudo- $R^2$  using the method of Nagelkerke (1991), which compares the likelihood of the data under the fitted model to a null model. For our null model, we fitted a model where expected elk density was a function of only the time-varying offset ( $\alpha_t$ ), and the only other parameter estimated by the model was the size parameter of the negative binomial distribution,  $r$ .

## Quantifying DDHS

We quantified DDHS by measuring relative selection strength (RSS), the ratio of expected densities in two habitats (Avgar et al., 2017; Fieberg et al., 2021).  $\text{RSS}(x_1, x_2)$  is how many times more elk we expect at the habitat in the numerator ( $x_1$ ) compared to the habitat in the denominator ( $x_2$ ). The effect sizes of the habitat variable–density interactions indicate the strength of the DDHS, but because (1) this is on the scale of the link function, and (2) multiple variables are involved in the safety interaction, it is easier to visualise DDHS via RSS. Credible intervals around our RSS predictions account for the uncertainty in parameter estimates and their covariance, which clarifies inference on the quantity of interest (DDHS). Figure 1 provides a hypothetical example of how RSS indicates DDHS. Our model estimates expected density using linear (food; Figure 1a) or quadratic (safety; Figure 1b) formulations. A plot of RSS as a function of density reveals the pattern of DDHS: positive slopes show positive DDHS (Figure 1c), negative slopes show negative DDHS (Figure 1d) and a horizontal line shows no DDHS. We calculated RSS for the food and safety variables by comparing habitats that differ by one standard deviation (SD) in the focal variable (with all other variables held at their mean), which makes the magnitude of RSS comparable between variables. For safety, we altered openness and roughness by 0.5 SD each (1 SD total). The habitat we chose for the numerator ( $x_1$ ) always had the higher expected elk density. For the food variable,





**FIGURE 1** Conceptual figure depicting density-dependent habitat selection (DDHS). Left column (a, b) shows how expected density could change with a habitat covariate and average population density (colour). Right column (c, d) recasts the patterns in (a) and (b) in terms of relative selection strength (RSS), the ratio of expected densities in different habitats. We calculated  $RSS(x_1, x_2)$  as the ratio of expected densities for a 1-SD change in the covariate (dashed vertical lines). For our purposes, the numerator ( $x_1$ ) is always larger than the denominator ( $x_2$ ). ‘H’, ‘M’ and ‘L’ in superscript refer to high, medium and low population density. Calculating RSS across a range of average population densities (e.g.  $x_1^H/x_2^H, x_1^M/x_2^M, x_1^L/x_2^L$ ) yields the RSS curve, which more clearly demonstrates DDHS. In (a), expected density is modelled with just a linear term for the covariate, and expected density increases monotonically with an increase in the covariate (positive habitat selection). In this example, RSS (slope of each line) increases with population density; this is positive DDHS (c). Alternatively, if RSS decreased with population density, this would be negative DDHS (not shown). In (b), expected density is modelled with linear and quadratic terms such that expected density peaks at an intermediate value. A narrow parabola at low density indicates stronger selection, whereas a wider parabola at high density indicates weaker selection. This example demonstrates negative DDHS but note that positive DDHS is also possible. We calculated RSS as the ratio of expected densities when the covariate is near the vertex of the parabola ( $x_1$ ) that is, when the habitat covariate is lower ( $x_2$ ). Calculating RSS across a range of population densities yields the RSS curve (d), which in this case demonstrates negative DDHS. In summary, whether a habitat covariate is modelled with solely a linear term or also includes a quadratic term, the slope of the RSS curve plotted against population density shows the pattern of DDHS.

$x_1 = 661$  kg/ha and  $x_2 = 376$  kg/ha (Figure 1a). For the safety variables, we chose values that did not span the vertex (Figure 1b). Under our hypothesis of a trade-off between food and safety, we predicted positive DDHS for food and negative DDHS for safety.

To understand the relative drivers of habitat selection, we compared the magnitude of RSS between our habitat variables. Together with our predictions of positive DDHS for food and negative DDHS for safety, we predicted that habitat selection was driven by safety at low densities and food at high densities; that is, we predicted

that the two RSS curves with opposite slopes would cross.

To understand the impact of density on predicted elk distribution, we created a map of the study area showing the change in RSS from high (9.3 elk/km<sup>2</sup>) to low (2.0 elk/km<sup>2</sup>) density which approximated the observed decrease over time. We fixed all spatial covariates and predator densities to their value in 2008, then we calculated RSS where  $x_1$  was each observed pixel and  $x_2$  was a habitat with mean values for all covariates. We took the log of RSS so that relative to mean conditions, positive values

represent selection, zero represents no preference and negative values represent avoidance. We repeated this at low and high elk density. For each pixel, we subtracted the high-density log-RSS from the low-density log-RSS, which we term  $\Delta \log\text{-RSS}$ . Positive values indicate that selection for the pixel increased as elk density decreased, whereas negative values indicate that selection decreased with elk density.

## RESULTS

### Model overview & assessment of key assumptions

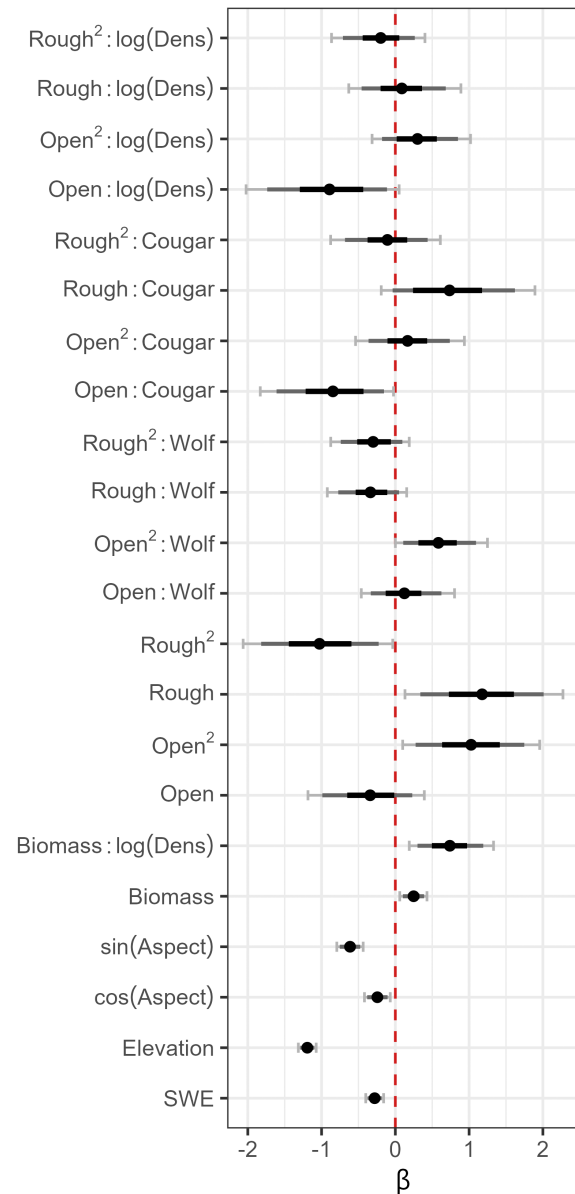
Our model indicated that elk selected for southwest-facing, low-elevation slopes with minimal snow cover. This is indicated by negative coefficients for  $\cos(\text{Asp})$  [aspect northing],  $\sin(\text{Asp})$  [aspect easting], Elevation and SWE (Figure 2, Figure S6).

Expected elk density increased with herbaceous biomass (Figure S7a), consistent with our assertion that herbaceous biomass reflects elk forage availability. Contrary to our prediction that elk would most prefer an intermediate openness, expected elk density was greatest at 100% openness, and the relationship between openness and elk density was largely monotonic for the observed range of openness (Figure S7b). Expected elk density was greatest for a roughness of 23.5 m (intermediate, as expected) with all other covariates held at their mean (Figure S7c). Spearman's correlation between biomass and the product of openness and roughness was  $-0.18$ , supporting our assumption that food and safety are negatively correlated.

Elk altered selection for safety variables with increasing predator densities in a manner that indicated openness and roughness were valid indices of spatial variation in predation risk. As wolf density increased, RSS for openness decreased (Figure 3a), whereas it increased as cougar density increased (Figure 3b), consistent with our predictions. Wolf density increased RSS for roughness, but the effect of cougars was negligible (Figure S8). Wolf density shifted the vertex of the parabola in the expected direction (from wolf to cougar habitat domains): at low wolf density (0 wolves/100 km<sup>2</sup>), the vertex was 22.3 m (90% credible interval [CI]: 20.1–25.0), and at high wolf density (10 wolves/100 km<sup>2</sup>), the vertex was 26.1 m (90% CI: 22.1–32.1; Figure 3c). Cougar density did not shift the vertex (Figure 3d).

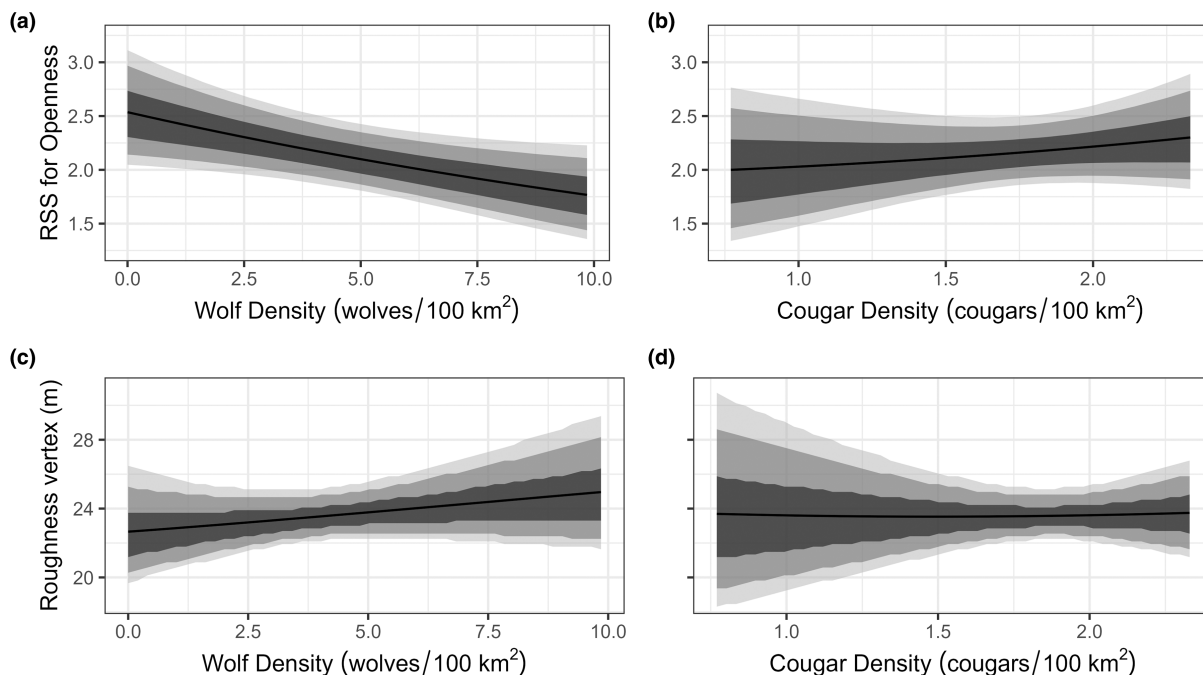
### Density-dependent habitat selection

Elk exhibited positive DDHS with respect to food, demonstrated by the positive  $\text{Biomass}:\log(\text{Dens})$  coefficient (Figure 2) and the positive slope of the RSS curve (Figure 4). Elk exhibited negative DDHS for openness,

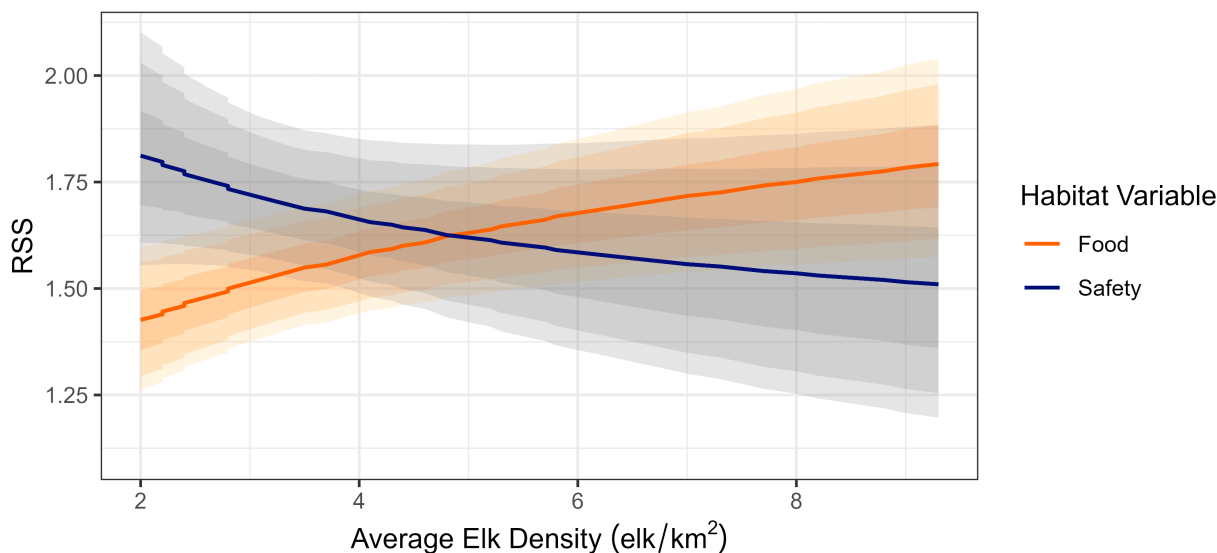


**FIGURE 2** Fitted model coefficients. Points are posterior means and bars are credible intervals (black bars: 50% credible intervals; dark grey bars: 80% credible intervals; light grey bars with end caps: 90% credible intervals). Red dashed line indicates 0 (no effect).

shown by the negative  $\text{Open}:\log(\text{Dens})$  coefficient (Figure 2) and the negative slope of the RSS curve (Figure 4). Since the  $\text{Open}^2:\log(\text{Dens})$  coefficient was estimated near 0 (Figure 2), the linear coefficient drove the pattern (Figure 4). These patterns are consistent with a trade-off between food and safety, expected under the multidimensional IFD (Avgar et al., 2020), supporting our main hypothesis. By contrast, elk exhibited no DDHS with respect to roughness. The 50% CIs for the  $\text{Rough}:\log(\text{Dens})$  and the  $\text{Rough}^2:\log(\text{Dens})$  terms overlapped 0 (Figure 2). Although the mean trend in RSS for roughness with increasing elk density was slightly positive, high uncertainty indicated this effect was negligible (Figure S9).



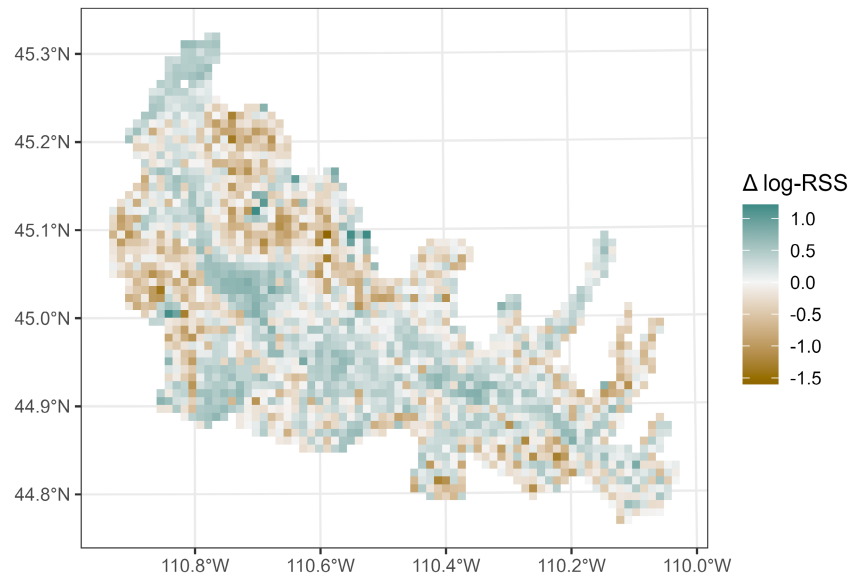
**FIGURE 3** Changing elk selection for risk variables with predator density. Openness and roughness describe important dimensions of the wolf and cougar habitat domains, that is, those habitats where they are most likely to kill elk. The wolf habitat domain is open and smooth, whereas the cougar habitat domain is rough and more forested. Relative selection strength (RSS) for openness (top row) is the ratio of expected density when openness is 100% versus when openness is 82%, a 1 SD change in openness. (a) RSS for openness decreases with wolf density (less selection for the wolf habitat domain), whereas (b) it increases with cougar density (less selection for the cougar habitat domain). The roughness vertex (bottom row) is the value of roughness that is most strongly selected by elk, that is, the vertex of the parabola describing selection. (c) The roughness vertex shifts to rougher habitat as wolf density increases (away from the wolf habitat domain); however, (d) elk did not shift the roughness vertex in response to cougar density. In all panels, predictions were made using samples from the entire posterior distribution. Solid black lines are mean effects and shaded grey envelopes are 50%, 80% and 90% credible intervals.



**FIGURE 4** Density-dependent habitat selection for food and safety. At low density (x-axis), relative selection strength (RSS) for a one standard deviation (1 SD) change in safety (0.5 SD of openness and 0.5 SD of roughness) is greater than the RSS for a 1 SD change in food (herbaceous biomass). At high density, this relationship flips, with a greater RSS for food than for safety. Changing average range-wide elk density alters the main driver of elk habitat selection from safety at low density to food at high density. Solid lines are posterior mean estimates and shaded envelopes are 50%, 80% and 90% credible intervals.

The stronger driver of elk habitat selection was safety at low elk density and food at high elk density (Figure 4), matching our prediction. At low elk density

(2.0 elk/km<sup>2</sup>), the RSS for a one-SD change in food was 1.43 (90% CI = 1.26–1.60) and the RSS for a one-SD change in safety was 1.81 (90% CI = 1.55–2.10). At high



**FIGURE 5** Change in log-RSS from high elk density to low elk density. Relative selection strength (RSS) is the ratio of expected density in each pixel of the landscape to the expected density in a habitat with all habitat variables held at their mean. The natural logarithm of RSS (log-RSS) is a measure of habitat selection, with positive values indicating preference versus the mean conditions, zero indicating no preference versus the mean conditions, and negative values indicating avoidance versus the mean conditions. Here, we plot  $\Delta \log\text{-RSS}$ , the difference between log-RSS when average range-wide elk density is high (9.3 elk/km<sup>2</sup>) versus when average range-wide elk density is low (2.0 elk/km<sup>2</sup>). Positive values (blue-green pixels) indicate that selection for the pixel increased as elk density decreased (the observed pattern over time), whereas negative values (brown pixels) indicate that selection for the pixel decreased as elk density decreased. All habitat variables and predator densities are held at their 2008 levels for demonstration.

elk density (9.3 elk/km<sup>2</sup>), the RSS for a one-SD change in food was 1.79 (90% CI = 1.57–2.04) and the RSS for a one-SD change in safety was 1.51 (90% CI = 1.20–1.88).

Posterior mean  $\Delta \log\text{-RSS}$  varied from  $-1.6$  to  $3.0$  with a mean of  $0.0$  across all pixels, indicating that changing selection resulted in habitat switching across space—the selection strength for some habitats decreased while the selection for other habitats increased, resulting in a redistribution of the population. Figure 5 illustrates the spatial pattern in  $\Delta \log\text{-RSS}$ .

## Model evaluation

The Gelman–Rubin statistics indicated MCMC convergence for all top-level parameters (Appendix S6). Ordinary residuals and Spearman's correlations were similar between in-sample and out-of-sample predictions (Figure S10). Residuals had mean near 0, indicating good model accuracy. Mean pseudo- $R^2$  for our model was 0.065 (90% CI = 0.064–0.066), indicating low precision (to be expected under the negative binomial distribution). We found little to no residual spatial autocorrelation in all years (Figure S11).

## DISCUSSION

Density dependence is a fundamental concept in ecology, and its importance for a species' abundance over time is

well understood (Berryman & Turchin, 2001; Brook & Bradshaw, 2006; Dennis & Taper, 1994). Although theory establishes that density dependence should also act on abundance in space (Morris, 2003; Rosenzweig, 1991), comparatively little empirical work has demonstrated the role of density dependence in shaping population distribution. In this study, we provide rare empirical evidence that density alters drivers of habitat selection and population distribution in a free-living system, consistent with theoretical expectations under the multidimensional IFD (Avgar et al., 2020). This is a broadly important conceptual advance because it links population density to the community-level interactions (i.e. consumer–resource, predator–prey) that determine an organism's distribution in space (Rosenzweig & Abramsky, 1997). Observations of this system at a constant density would lead to erroneous inference on the drivers of habitat selection, biased predictions of population distribution and misunderstanding of community interactions under unobserved densities.

Interactions between predator densities and safety variables indicate that the latter were valid indices of predation risk. RSS for openness decreased with wolf density (Figure 3a) and increased with cougar density (Figure 3b). The effect of predator densities on RSS for roughness was weak; rather, increasing wolf density pushed the most preferred roughness into rougher habitat (Figure 3c). We found no effect of cougar densities on selection for roughness (Figure 3d), and the predator density effects were greater for wolves than for cougars.



Nevertheless, elk avoided densely forested, rough habitats across all elk and predator densities (Figure S7b,c), indicating that risk from cougars was an important driver of elk distribution. Our finding that elk selected for maximum openness (Figure S7b) and that DDHS for safety was primarily driven by openness (Figure S9b) further suggests that elk distribution was more strongly influenced by cougars than wolves. These results independently corroborate the findings of Kohl et al. (2019) that multiple predators (wolves and cougars) influence elk space use.

We found support for our hypothesis that the food-safety trade-off in our system leads to a switch from safety driving distribution at low density to food driving distribution at high density (Figure 4). We found evidence for positive DDHS for food and negative DDHS for safety, which we would expect when there is a trade-off between food and predation risk. Indeed, biomass and the product of openness and roughness were negatively correlated (Spearman's  $r = -0.18$ ). While this food-safety trade-off is expected to be ubiquitous in nature (Brown & Kotler, 2004), it is difficult to measure, and our approach provides evidence of it. Were there no trade-off, elk at low density could occupy habitats that provided both food and safety, and we would expect spillover from those habitats as density increases (i.e. negative DDHS). The negative correlation between food and safety means that elk cannot satisfy both of these requirements in the same place, thus giving rise to the trade-off and habitat switching as density increases (i.e. positive DDHS; Greene & Stamps, 2001; Avgar et al., 2020). The switch in the relative importance of food and safety leads to some habitats on the landscape becoming less selected while others become more selected; the result is a redistribution of the population (Figure 5). This switch is consistent with theoretical and empirical work on behavioural ecology in predator-prey systems. Organisms should change their risk assessment based on conspecific density (Peacor, 2003), and antipredator behaviours such as vigilance and habitat selection should adjust accordingly (Mooring et al., 2004). This is also consistent with the predation-sensitive food hypothesis, whereby both food and predation limit prey populations (Sinclair & Arcese, 1995); as competition increases and food becomes limiting, prey will increase selection for food and decrease selection for safety. Our work demonstrates how these behaviours manifest in space.

Current empirical understanding of DDHS in free-living vertebrate systems is mostly limited to small mammals (e.g. Morris, 1989; Morris et al., 2000; Rosenzweig & Abramsky, 1985) or domesticated mammals on islands (e.g. Moberg et al., 2009; van Beest et al. 2014b). Previous studies of DDHS in free-living systems, though rare, have also focused on elk (Merrill et al., 2020; van Beest et al. 2014a) or congeneric red deer (*Cervus elaphus*; McLoughlin et al., 2006; Pérez-Barbería et al., 2013); see

Supplemental Discussion for a comparison with our work (Appendix S7). Often, space-use data are collected on short time scales during which population densities are similar (McLoughlin et al., 2010), and the resulting habitat selection models are snapshots of true, DDHS patterns (Boyce et al., 2016; Boyce & McDonald, 1999; Northrup et al., 2022). Our results show that inference or predictions from these snapshots may be unreliable under changing densities.

Space use of organisms can be measured from two perspectives: a population-level (Eulerian) perspective which measures changes in population density at various places over time or an individual-level (Lagrangian) perspective which tracks the locations of individuals over time (Turchin, 1998). Analyses from the Eulerian perspective lend themselves more readily to projection across space at large scales, whereas analyses from the Lagrangian perspective can uncover more detailed mechanism. Individual behaviour scales up to population-level distributions (Mueller & Fagan, 2008), so results from the two perspectives can, in principle, be reconciled. In practice, few studies have compared the Eulerian and Lagrangian approaches to studying population-level space use (but see Phillips et al., 2019; Bassing et al., 2022). In our case, we find both similarities and discrepancies between our work (Eulerian) and previous studies (Lagrangian) of elk habitat selection in northern Yellowstone (Appendix S7). Without the Lagrangian perspective, we could not identify whether DDHS occurred because (1) individuals changed their habitat selection traits (behavioural plasticity), or (2) individuals that exhibited certain habitat selection traits had differential survival and/or reproduction (demographic sorting), although previous research has suggested it is a demographic sorting effect (White et al., 2012). Which perspective provides the best understanding of DDHS is still an open question. Most empirical work on DDHS has made use of isodar theory (Morris, 1988, 2011), which is constructed from the Eulerian perspective and naturally integrates fitness. An important knowledge gap concerns how to connect DDHS to fitness from the Lagrangian perspective, which can reveal more detailed mechanisms of how population regulation plays out in space.

We believe the capacity of DDHS to qualitatively alter community-level interactions is underappreciated and understudied (see Rosenzweig & Abramsky, 1997), especially in predator-prey systems where positive DDHS may lead to landscape-scale habitat switching. For example, the relative importance of consumptive versus non-consumptive effects (Peacor et al., 2013; Sheriff et al., 2020) may critically depend on DDHS (habitat selection is an important antipredator trait; Trussell et al., 2006). If prey only respond to risk by altering their habitat-selection traits at low density (when competition is less costly), the importance of non-consumptive effects may be overstated. Similarly, DDHS may impact competition between prey species. Habitat selection is an

important mechanism for reducing competition between species, which may determine the level of competition (Rosenzweig, 1981), especially when prey species face differential risk. For example, spatial overlap between bison and elk in northern Yellowstone is potentially greater than expected at high elk density if neither species responds strongly to predators.

In conclusion, consistent with theoretical expectations, density dependence alters habitat selection and distribution in free-living systems. Incorporating DDHS into models of distribution is crucial whenever density is variable; ignoring its effects may lead to severely compromised inferential and predictive performance. Our findings underscore that the effects of the food-safety trade-off on prey distribution are dynamic, and that inference and prediction in these systems depends on prey density.

### AUTHOR CONTRIBUTIONS

BJS, DRM and TA conceived and developed the idea. DRS and DWS collected data and supervised the project. BJS performed analyses. All authors contributed to the interpretation of the results. BJS wrote the first draft of the manuscript and all authors contributed substantial edits.

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### DATA AVAILABILITY STATEMENT

All data (and code) are available on GitHub and published through Zenodo (doi:10.5281/zenodo.6687904).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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