Individual differences in habitat selection mediate landscape level predictions of a functional response

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Highlighted Student Paper statement: Changing habitat availability affects habitat selection, but individuals vary. We found this variation is best modelled by not assuming all individuals modify selection with availability.

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Abstract

Context
Conserving and managing habitat for animals requires robust models to predict their space use.
The functional response in habitat selection posits that animals adjust their habitat selection
according to availability.

Objectives
Habitat availability can change over short time periods and small spatial distances, and thus
failing to account for changes in habitat availability while modelling may not produce reliable
predictions in the near-term or future. However, because individuals may respond to habitat
availability differently, the functional response is also limited for predicting habitat selection by
individuals.

Methods
Using a functional response in elk (Cervus canadensis) selection for mixed forest in response to
road proximity, we compared habitat selection predictions made by population-level resource
selection functions (RSFs) with random effects to incorporate individual differences in selection,
to generalized functional response (GFR) RSFs.

Results
We found that since not all individuals followed the road-dependent functional response, the
random effects model both predicted the distributions of individuals more accurately ($R^2 = 0.62$
vs. $R^2 = 0.51$) and produced coefficient estimates that matched their selection for mixed forest
and distance from roads better than the GFR model (RMSE = 0.25 vs. RMSE = 0.29 and 0.37 vs. 0.46).

Conclusions

Individual habitat selection often varies within populations, and revealing those differences shows how individuals help populations respond to environmental change. We suggest that evaluating individual differences using multiple predictive approaches is necessary to forecast long–term habitat selection.

Keywords: Species distribution models, behavioural reaction norms, Cervus canadensis, resource selection, space use, habitat availability
Introduction

We conserve and manage landscapes in ways we assume make them most profitable for wildlife populations (Gaillard et al. 2010). However, the profitability of landscapes change when the individual animals within populations have different habitat preferences (Merrick and Koprowski 2017) and as those habitats become more or less common on the landscape (McLoughlin et al. 2010). Thus, our approaches to forecasting animal distributions must be similarly robust to the influences of individual variation and habitat availability on space use. The relationship between use and availability of habitat often changes over gradients of availability, and this idea — known as the functional response in habitat selection (Mysterud and Ims 1998) — is becoming central to forecasting the distributions of populations in new environments (Clark et al. 2019; Muhly et al. 2019; Wilber et al. 2020). However, population-level space use is underpinned by individuals that do not necessarily respond uniformly to environments with different habitat availability (Leclerc et al. 2016). Habitat selection models are typically agnostic to these individual differences, even while a number of recent studies have explicitly highlighted their importance (e.g., Lesmerises and St-Laurent 2017; Montgomery et al. 2018; Schirmer et al. 2019; Perrig et al. 2020). Given our understanding of functional responses to habitat selection and the importance of individual differences in habitat selection, we suggest there is a need to ascertain whether models based on the functional response should indeed improve our ability to forecast the distributions individual animals when they are faced with environmental change.

The functional response framework is affected by the fact that habitat selection is an individual’s behavioral response to the environment. Resource selection functions (RSFs) model selection as the relative probability that an animal will select a location based on the availability
of habitat at that location (Matthiopoulos et al. 2020). Methods like the RSF-based generalized functional response (GFR) further incorporate the functional response by allowing habitat selection coefficients to vary with local habitat availability (Matthiopoulos et al. 2011). Thus, based on the environment alone, a GFR model should be better able to forecast distributions outside of the context in which it is developed. As a result, the GFR approach has garnered use in models aimed at understanding how to best manage habitat to preserve its use by animal populations facing large scale disturbances (Morato et al. 2018; Mumma et al. 2019). However, the compositions of populations change over time and space, and these changes may have implications for habitat selection independent of the environment. For example, female black bears (Ursus americanus) avoid males in spring to protect their cubs, resulting in different habitat selection between the sexes (Lesmerises and St-Laurent 2017). At a larger scale, conspecific density in elk (Cervus canadensis) motivates some individuals to migrate while others remain resident (Eggeman et al. 2016). Thus, even if habitat availability is considered, not accounting for individual variation in habitat selection may lead to misleading forecasts of distribution.

Individuals within populations also exhibit consistent differences in habitat selection even when faced with the same changes in the environment. These differences in habitat selection are often not correlated with sex or population density, but instead depend on personality traits that are more difficult to measure in wildlife populations. For example, bolder bank voles (Myodes glareolus) occupied larger home ranges with lower vegetation height than their shyer conspecifics (Schirmer et al. 2019). When individual animals use different habitat selection strategies to respond to the same changes in availability (Bastille-Rousseau et al. 2020), individual habitat selection-environment interactions may not follow a predictable pattern. These
individual-level responses to habitat availability are analogous to behavioural reaction norms (BRNs; Dingemanse et al. 2010). While BRNs may mirror the functional response in habitat selection, consistent individual differences could also manifest in a lack of agreement between individual- and population-level models (Box 1). The potential for variation among BRNs may make it difficult to predict even near-term habitat selection by individuals using population-level models, compounding the challenge of forecasting animal distributions following large-scale and long-term changes in the environment.

One approach to deal with individual differences is to challenge the assumption that all individuals sharing a common environment will also make similar habitat selection decisions. An alternative model construction approach is to include random coefficients for selection of habitat by individuals. This allows habitat selection models to accommodate both individual differences and the functional response (Muff et al. 2020). Random intercepts account for average individual differences from the mean selection response, and random slopes account for plasticity, or the magnitude of the change in habitat selection across contexts (Gillies et al. 2006). Together, these random effects are analogous to BRNs, which are regressed against the mean availability to arrive at an estimate of habitat selection for the population (Holbrook et al. 2017). Random effects can also be incorporated into a GFR framework to account for the effects of individual differences on population-level estimates (Muhly et al. 2019). However, individual differences in habitat selection are still obscured when a habitat selection-environment interaction is assumed at the population level (Leclerc et al. 2016). Models with only random effects instead make a single estimate of habitat selection for the population, potentially reducing the variance between individual-level and population-level models when among-individual variation is high.

Ultimately, the ability of a habitat selection model to forecast animal distributions when the
environment changes depends on its ability to reconcile individual differences with population-level patterns.

Here, we tested whether the GFR model or the random effects model better predicts habitat selection by individual elk (*Cervus canadensis*), an animal with demonstrated individual differences in habitat selection (Eggeman et al. 2016, Prokopenko et al. 2017, Montgomery et al. 2018). We evaluated selection in two ways. First, we predicted the spatial distribution of individuals within their home ranges based on their selection for the combination of habitat characteristics at each spatial location. Second, we individually measured the relative strength of selection for each habitat by individuals in environmental space. We then compared spatial distribution predictions and habitat selection strength according to the GFR and random effects models, with those of individual-level models as a benchmark for their performance. The GFR model makes predictions based on the context of habitat availability, and thus we expected it to best predict spatial distributions and agree with habitat selection effect sizes in case of low variation among individuals (Box 1: Fig. IA). However, since the random effects model fits a single mean selection coefficient for the population and thus does not assume individuals also follow the population-level functional response, we expected it to perform best when individuals select habitat differently in response to the same environmental changes (Box 1: Fig. IB).
Methods

Study Area

Our study area (Fig. 1) is located in Riding Mountain National Park (50.83 N, 100.20 W), a protected area at the interface of the Boreal Plains and Prairie ecozones in Manitoba, Canada. The region is characterized by long, cold winters, and precipitation falls primarily as snow between November and April. The park is located within Treaty 2 Territory, the original lands of the Anishinaabeg people and the homeland of the Métis Nation. The underlying Manitoba Escarpment consists of rugged terrain, natural habitats, and elevations from 333 to 757 m. The largely agricultural land surrounding the park imposes a distinct boundary: deciduous (43%), coniferous (4%), mixed coniferous-deciduous forests (32%), wetlands (13%), and fescue grassland (1%) within the park give way to open farmland and communities outside the park connected by a dense road network. We recognize the continued relationships between the people of the Tootinaowaziibeeng, Ebb and Flow, Sandy Bay, Rolling River, Keeseekoowenin, Waywayseecappo, and Gambler First Nations from Treaties 1, 2, and 4, and the land and wildlife within and surrounding the park, including the elk population in this study.

Elk Data

Global Positioning System (GPS) collars were deployed on elk in northwest Riding Mountain National Park from 2003 to 2016. Elk were captured between late January and early February during three periods in 2003–2005, 2011–2012, and 2015–2016 using a net gun fired from a helicopter. To prevent sex-related and seasonal differences in habitat selection behaviour from influencing our models, we included only data from female elk within the winter season. Collaring was part of a federal and provincial elk management program, and culling meant that
some collars collected as little as one week of data. We removed any individual with fewer than 84 location points over the study period — the equivalent of one week of data collected at 2–15 hour relocation frequencies — to exclude these individuals from the analysis. We also screened the data for two-dimensional fixes, step lengths longer than could be travelled by the animal within a time step, and spikes in movement between duplicate points (Bjørneraas et al. 2010). After cleaning, our data included 24 individuals with between 84 and 735 GPS points per individual.

Fitting Resource Selection Functions with Functional Responses

RSFs are a suite of widely used methods to quantify habitat selection, or the relative probability of habitat use by an individual or population compared to that available (Matthiopoulos et al. 2020). We estimated habitat selection \( w(x) \) by elk using exponential form logistic regression RSFs (Manly et al. 2002):

\[
 w(x_i) = \exp[\beta_1 \cdot h_1(x_i) + \beta_2 \cdot h_2(x_i) + \cdots + \beta_n \cdot h_n(x_i)] 
\]

Which describes the selection of a location \( x_i \) in habitats \( h_1 \) to \( h_n \), where \( \beta \) denotes selection coefficients for habitats. Many use-availability resource selection functions model selection at the third order (Johnson 1980), drawing a sample of availability from within the home range of an individual to compare to observations of use.

To test the performance of the GFR and random effects models, we needed to use an existing functional response. We based this functional response on inferences from previous work on elk space use. The Riding Mountain elk population frequently uses mixed forest because it provides both forage and cover from predators (van Beest et al. 2016). Other
populations of elk are known to avoid roads because they are associated with risk from humans (Prokopenko et al. 2017). Particularly in areas of higher human use where roads are difficult to avoid entirely, elk also cope by using denser vegetation cover (Dugal et al. 2013). Thus, we modelled selection coefficients for mixed forest as a function of average distance to road during elk rifle season — approximately December 1st to January 31st — during which time we expected the strongest response to risk from humans. We detected a functional response trade-off in which individuals that were closer to roads on average selected mixed forest more strongly (Supplementary Fig. S1). Importantly, we did not detect a strong response for the opposite: individual selection for distance to road did not depend on mixed forest cover (Supplementary Fig. S2).

We used the GFR model to test whether the functional response improved predictions of individual habitat selection. We modelled the functional response by including four pair-wise fixed effect interactions between selection for the natural log of distance to road and mixed forest, and the mean availability of each variable in the home ranges of individuals (Matthiopoulos et al. 2011):

\[
w(x_i) = \exp[\beta_0 + \beta_1 \cdot h_1(x_i) + h_{11k}(x_i) + h_{12k}(x_i) + \gamma_{1k} \cdot h_1(x_i)] \quad \text{eqn 2}
\]

Where \(\beta_0\) is the individual intercept, \(h_{1,1k}\) is the coefficient for \(h_1\) given the mean proportion of \(h_1\) for individual \(k\) in its home range, \(h_{1,2k}\) is the coefficient for \(h_1\) given the proportion of \(h_2\), and \(\gamma_{1k}\) is the random coefficient of \(h_1\) for individual \(k\). Random coefficients are used to incorporate individual differences in habitat selection resulting from differences in availability (Muff et al. 2020), including GFR models (Muhly et al. 2019). We also included
random coefficients for both covariates in the random effects model, allowing the model to accommodate individual differences in selection without modelling the functional response as a fixed effect:

\[ w(x_i) = \exp[\beta_0 + \beta_1 \cdot h_1(x_i) + \gamma_{1k} \cdot h_1(x_i)] \quad \text{eqn 3} \]

We included random intercepts in both models to control for uneven sample sizes among individuals, which were uncorrelated with random coefficients (Gillies et al. 2006). We also assigned weights of 1,000 to the set of available points in each model to ensure our logistic regression models approximated an IPP model (Muff et al. 2020). Finally, to prevent bias associated with shrinkage of the random intercepts toward zero, we fixed the variance of the random intercepts to the large value $10^6$ as recommended by Muff et al. (2020). All models included the same fixed covariates: the natural log of distance to road as a continuous variable, and mixed forest as a categorical variable. We obtained both land cover and roads data from Manitoba Conservation (1994, 2006).

**Predictive Performance of Resource Selection Functions**

Mapping RSF outputs is a common practice for predicting the utilization distributions of animals, where the selection for each location in a spatial raster is calculated based on the RSF coefficients and the habitat characteristics of the pixel (Morris et al. 2016). We used the mapping approach to compare how well the random effects and GFR models approximated the distributions of individual habitat selection. Unlike most RSF models that draw a single sample of used and available locations for the entire study period, we wanted to account for individual variability in habitat selection over the 2–month study period from December 1st to January 31st.
Thus, we compared individual selection within a moving window of 30–day home ranges, to individual selection as predicted by the population-level GFR and random effects model including data from all individuals, and an individual-level “training” model built from the surrounding 90 days of data from the individual in the comparison. We compared 33 date windows in total, shifting the temporal and spatial location of the home range at increments of one day.

We drew a separate sample of available points from a minimum convex polygon (MCP) surrounding the used points in each moving window comparison, using the mean distance to road and mean availability of mixed forest cover within each MCP for the GFR interaction. We generated 10 available points per used point as a compromise between minimizing time required for model convergence and limiting the bias that can be introduced in RSFs when the landscape is not represented by a large availability sample (Northrup et al. 2013). We used linear regression to compare each individual’s relative selection for locations on the raster as predicted by the 30–day home range, to its selection for those locations as predicted by the GFR, random effects, and individual-level training models. We evaluated fit using the $R^2$ of each individual comparison averaged across the population.

Calculating Effect Sizes for Resource Selection Functions

We used relative selection strength (RSS) to evaluate individual differences in selection for mixed forest and distance to road from population-level responses. Because presence-availability RSFs do not compare used locations to true absences, their coefficients only represent the relative probability of selection given the covariates in the model. RSS estimates selection between two locations, $x_i$ and $x_j$, given a difference in the value of a covariate $h_1$, while holding the value of other habitats constant (Avgar et al. 2017). RSS can also be used to
compare how the relative direction and magnitude of selection for $h_1$ changes at different levels of $h_2$ when the model includes an interaction between the covariates (Box 1; Prokopenko et al. 2017). This provides a means to assess how closely individual selection coefficients follow the functional response, or in our example how selection of mixed forest ($h_1$) is influenced by average distance to road ($h_2$), or vice-versa. We calculated the RSS for each $x_i$ using the equation $\log RSS = \Delta h_1 \cdot (\beta_1 + \beta_{1,2} \cdot h_2(x_j))$, where $\beta_1$ and $\beta_{1,2}$ are the selection coefficients for $h_1$, and $h_1$ given availability of $h_2$ at $x_j$, respectively, and $\Delta h_1$ is the change in $h_1$ between $x_i$ and $x_j$.

We used root mean square error (RMSE), to quantify the magnitude with which individual selection for mixed forest and distance to road deviated from the functional response. We calculated mean RSS for $h_1$ by each individual by holding the availability of $h_2$ constant at its average availability in the individual’s home range. We then calculated the population-level RSS for $h_1$ using coefficients from the GFR and random effects models, while holding $h_2$ constant at the availability of each individual. Finally, we compared how well each population model RSS fit the corresponding individual RSS using RMSE, which we averaged over the population.
Results

The number of points per individual differed in each iteration of our model comparisons. Differences resulted from individuals missing data from part of the 30–day testing window or surrounding data, and from variation in fix rates among individuals (n = 21 at 2 hr relocations, n = 3 at 1 hr relocations). We ensured that there was no relationship between the predictive performance of the models and the number of points in the testing data (Supplementary Figs. S3 to S5). We also removed any individual models that failed to converge, or for which either habitat covariate was absent from both used and available samples. These cases produced standard error estimates greater than 30, which we considered implausibly large relative to our coefficient estimates (Field 2009). In total we retained 510 matched sample model comparisons using 24 individuals. All variance inflation factors were less than 1.1, indicating acceptably low multicollinearity among covariates.

Predictive Performance

The random effects model was the best overall model for predicting individual selection of locations within their home ranges ($R^2 = 0.62$; 95% CI = 0.56, 0.68). Next to the random effects model, the individual-level model fit with training data best predicted the distributions of individual selection with $R^2 = 0.57$ (95% CI = 0.49, 0.67). In other words, a model using a single individual’s training data was not as consistent with its own selection of locations within its home range as the random effects model (Fig. 2). The relative performance of the GFR model was lowest with $R^2 = 0.51$ (95% CI = 0.46, 0.57). The three models varied in their performance for predicting habitat selection of individuals a priori identified as deviating from the functional response for mixed forest given distance to road (coloured points, Fig. 2).
Relative Selection Strength

The random effects model also matched individual habitat selection coefficients better than the individual-level and GFR models. Selection coefficients for mixed forest from individual models indicated that elk selected more for locations with higher mixed forest cover than locations further from roads ($\beta = 0.55$, 95% CI = 0.49, 0.61 for mixed forest vs. $\beta = -0.29$, 95% CI = -0.43, -0.15 for distance to road), and many individuals selected for locations with higher mixed forest cover relative to its mean availability (positive sloping coloured lines, Fig. 3a and b). However, many individuals exhibited the opposite pattern, with no clear distinction between individuals based on the average distance to road in their home ranges (lack of gradient pattern, Fig. 3a and b). The random effects model estimated overall stronger selection for locations with higher mixed forest cover (Fig. 3a). The median RMSE between individual-level and random effects model RSS was 0.25 ± 0.009. The GFR model also estimated selection for locations with higher mixed forest cover, with a stronger response the lower the average distance to road in the home range (i.e., a negative functional response for mixed forest with distance to road, black lines, Fig. 3b). However, due to the high individual variation in mixed forest selection, the GFR model overestimated selection for many individuals, resulting in higher RMSE of 0.29 ± 0.011 between the individual-level and GFR models.

Both the GFR and random effects models estimated stronger individual selection for locations further from roads in comparison to the mean distance to road, particularly for locations very close to roads (Fig. 3). However, selection for distance to road was more variable among individuals. Many individuals followed the population-level pattern and selected areas further from roads more strongly than areas closer to roads. A similar number of individuals exhibited the opposite pattern, avoiding areas further from roads in comparison to the mean
(positively sloping coloured lines, Fig. 3 c and d). Individual selection patterns for distance to road also did not depend on mixed forest cover (lack of gradient pattern, Fig. 3 c and d). Correspondingly, there was a weak functional response for distance to road predicted by the GFR model, with selection for the closest distances to roads stronger at lower mixed forest cover (i.e., black lines, Fig. 3 d). In the absence of a strong functional response, the random effects model matched individual RSS better than the GFR model (RMSE 0.37 ± 0.013 vs. 0.46 ± 0.016).
Discussion

Forecasting future distributions of animals requires modelling approaches that capture habitat selection in light of near- and long-term environmental changes. We compared the ability of two widely used modelling approaches to predict habitat selection by elk when habitat availability varied in the near term. Random effects models account for individual differences in habitat selection by including random coefficients and intercepts for each habitat. In addition to random effects, the generalized functional response (GFR) model includes fixed effect interactions between habitat selection and availability, allowing coefficient estimates to account for the effect of availability. We found that the random effects model outperformed the GFR model both for predicting near-term spatial distributions (Fig. 2) and for matching the relative strength of selection for habitat by individuals (Fig. 3). Our results demonstrate that accounting for availability does not necessarily improve habitat selection inferences if not all individuals in the population follow the functional response. The link between habitat selection and spatial distributions frames a discussion of which is the most appropriate approach to forecast near- and long-term animal distributions for conservation applications. We submit that the GFR can detect habitat selection patterns that may be useful for forecasting future distributions, but the random effects model is still important for gauging habitat selection by the individuals that do not follow these patterns because they ultimately produce population-level patterns.

When modelling animal distributions, our choice of model should be guided by our interest in either individual- or population-level patterns. Though model performance has traditionally been evaluated by focussing on best practices for parameterization (Brun et al. 2019), structural complexity, and validation method (Gregr et al. 2018), it is also necessary to
evaluate whether models represent the individual mechanisms that produce population-level patterns (Johnston et al. 2019). When all individuals follow the population-level pattern, the functional response model performs well for predicting individual habitat selection (Box 1: Fig. IA). However, when habitat selection by some individuals deviates from the population-level pattern, the functional response is a less reliable predictor for those individuals (Box 1: Fig. IB).

We found the functional response modelled by the GFR did not match individual selection estimates as well as the random effects model because not all individuals responded consistently to availability of mixed forest or average distance to roads (Fig. 3). Similarly, Gillies et al. (2006) found no functional response in grizzly bear (*Ursus arctos horribilis*) selection for elevation due to a large amount of individual variation. Like grizzly bears, elk are also known to exhibit variation in habitat selection both within populations (Montgomery et al. 2018) and across time (Eggeman et al. 2016). Thus, our results suggest the random effects model might be an appropriate approach for predicting the distributions of animals that characteristically exhibit large amounts of individual variation.

Our results also demonstrate that we can reveal individual differences by leveraging the comparative performances of different model evaluation methods. When we predicted selection for locations in home ranges, the RSF output was contingent on the overall availability of both habitats within each home range comparison. In contrast, RSS allowed us to estimate selection for each habitat individually while holding availability of the other habitat constant. Including an interaction between selection for each habitat and the availability of each habitat within the home range further allowed us to determine how closely the GFR and random effects model estimates matched the estimates from individuals with different habitat availability. A subset of individuals drove the functional response for mixed forest by increasing their selection when closer to roads,
and when we compared models using RSS, the GFR provided poorer estimates for individuals that did not follow this pattern (Fig. 3). RSS comparisons can evaluate selection coefficients pertinent to individuals and geographic locations outside the scope of the current model. Thus, the RSS approach may be more informative for forecasting distributions than comparing estimates of selection in geographic space.

Because individual differences underlie population-level patterns, it is important to consider both the functional response (Wittemyer et al. 2019) and individual differences (Merrick and Koprowski 2017) in applied management. GFR model applications attest to its effectiveness for managing wildlife habitat, predicting wolf (*Canis lupus*) distribution in response to anthropogenic disturbance (Muhly et al. 2019) and guiding habitat conservation for lynx (*Lynx canadensis* – Holbrook et al. 2017). However, it is also critical to evaluate its performance for populations with varying degrees of individual differences individual variation in habitat selection. Individual differences in behaviour mediate factors like mortality risk that ultimately determine reproductive success and population-level performance (Ofstad et al. 2020).

Moreover, even when they comprise the minority of behaviours, individual differences in habitat selection can influence effective management and conservation recommendations. For example, by detecting individual differences in Andean condor (*Vultur gryphus*) habitat selection independent of environmental context, Perrig et al. (2020) identified new areas of the species range in need of protection. Their study demonstrates that effective conservation focuses on both individuals and populations. The dual focus on individuals and populations also aligns with our finding that we need to incorporate more than just environmental context to comprehensively predict habitat selection. As we found, the GFR model can detect habitat selection patterns while still masking individual differences in habitat selection. Thus, if we are to make management
recommendations to preserve individual variation in habitat selection, we need to be more judicious in comparing the predictive performance of habitat selection models.

As an indirect approach to conserving individuals with different habitat selection strategies, habitat conservation efforts could focus on bolstering habitat diversity in addition to preserving those habitats with greatest use. Many habitat selection models make the reasonable assumption that the most important habitats are where individuals best balance resource acquisition with predation risk (Hebblewhite and Merrill 2009; Dupke et al. 2017; Palmer et al. 2017). But ecological processes such as changing population density also alter the availability of resources, and thus the profitability of habitat selection when individuals compete for resources (McLoughlin et al. 2010). Spatially and temporally dynamic resources cause some individuals to adjust how they select habitats over time (Box 1: Fig. IB). An alternative to prioritizing those habitats most profitable in the current ecological context would be to preserve a diversity of habitats. Individual differences are maintained by the unique selective pressures acting on individual fitness in habitats of different conditions and resources (Gaillard et al. 2010). Thus, in addition to ensuring the resilience of populations to environmental change (Sih et al. 2011), a habitat-diversity approach would preserve variation in individuals selecting the habitat. Preserving individual variation in behaviour has demonstrated benefits for ecosystems, maintaining processes like seed dispersal and succession (Brehm et al. 2019).

While many species exhibit individual differences in movement behaviour (Hertel et al. 2020), comparing the predictive performance of the functional response and individual responses may be particularly relevant for social, highly mobile animals like elk. Group sizes of female elk can range from 5 to upwards of 14 or more individuals (Vander Wal et al. 2013), with density shifts depending on local resource availability (McGeachy et al. 2017). Individual elk differ in
their responses to density-dependent resource competition, scaling up to population-level patterns and large geographic extents. For example, in partially migratory populations, density influences the resource abundance in winter ranges, causing some individuals to shift between migratory and resident strategies (Eggeman et al. 2016). Even in our own non-migratory population local selection of habitats with high resource abundance depends on local density (van Beest et al. 2016). Female elk also shift their habitat selection in response to factors like predation risk over their lifetimes (Thurfjell et al. 2017), and thus the demographic effect of individual differences on population distribution may be stronger for elk than for other shorter-lived species. In other species behavioural types are important for determining both local habitat selection (Leclerc et al. 2016) and migration (Harrison et al. 2019). We encourage broader taxonomic comparisons of the GFR with random effects model to evaluate whether the effect of individual differences in habitat selection on model performance is broadly applicable.

Forecasts of animal distributions both in human-modified landscapes (Stjernman et al. 2019) and in the face of climate change (Hein et al. 2013) benefit from the expectation that population-level habitat selection changes across contexts. However, while population distribution patterns might be captured by the functional response, we demonstrated that simpler random effects models are also essential for representing the individuals whose habitat selection deviates from the functional response. Individuals are the units underlying context-dependent habitat selection patterns (Merrick and Koprowski 2017). Recognizing their importance can help prioritize habitat conservation (Perrig et al. 2020) and promote behavioural diversity (Ofstad et al. 2020). Ultimately, we need to consider both habitat availability and individual differences to understand which drives animal distribution patterns and best inform landscape management decisions.
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Declarations

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Availability of data: Data are the property of Parks Canada. We do not have permission to share them.

Code availability: The code is available on GitHub (https://github.com/ljnewediuk/Ind_diff_FR.git)
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Box 1. The link between individual differences and the functional response

The functional response in habitat selection posits that animals adjust their habitat selection as availability changes (Mysterud and Ims 1998). However, agreement between the population-level functional response and individual habitat selection depends on how much individual variation affects the ability of the functional response to predict the selection of individuals when availability changes.

In Fig. I, each coloured line represents a single individual. Individuals exhibit functional response for a habitat $h_1$, the direction and magnitude of which varies with the availability of the alternate habitat, $h_2$, within the individual’s home range. When home range availability of habitat $h_2$ is high, the functional response for $h_1$ is more positive, i.e., the slope of the increase in selection for $h_1$ is greater when availability increases (line ‘H’). Such a response could occur if habitat $h_2$ is a risky habitat, and $h_1$ is a safe habitat that provides cover from that risk. The functional response for $h_1$ is weaker when the home range availability of $h_2$ is low (line ‘L’). When all individuals respond similarly to high and low levels of $h_1$ availability, their individual behavioural reaction norms (BRNs) follow the functional response pattern (panel A). In such cases, the functional response for $h_2$ in each $h_1$ context is a good predictor of individual selection.

However, if some individuals exhibit a response to $h_1$ availability that differs from the majority of the population, the functional response is less reliable for predicting individual selection (panel B). Deviation from the functional response could occur if individuals exhibit consistent differences in their habitat selection regardless of the $h_2$ context. In such cases, the mean selection by all individuals in the population (line ‘M’) is likely to be a better predictor
than the functional response because it minimizes the variation between all individuals and their predicted selection.

Fig. I. The effect of individual variation on the ability of the functional response to predict individual habitat selection. The black lines show the population-level functional response for habitat $h_1$ based on the availability of another habitat, $h_2$ ranging from high (H), to mid (M), to low (L) availability. Coloured lines show individual behavioural reaction norms for selection of $h_1$ based on each individual’s availability of $h_2$. In A, the individual-level gradient follows the functional response. In B, individuals deviate from the functional response.
Fig. 1. Study location in northwest Riding Mountain National Park, Manitoba, Canada, with coloured points highlighting GPS location points of individuals that deviate from the expected functional response for mixed forest given their distance to roads, corresponding to highlighted individuals in Supplementary Figs. S1 and S2. The map shows these individuals in the context of GPS locations from all other individuals (grey points), the park boundary (grey polygon), and the road network (grey lines).

Fig. 2. Comparison of the ability of individual-level models fit with training data, random effects model (Ran. Eff.), and the generalized functional response (GFR) model to predict distributions in comparison to individual-level benchmark models, when model coefficients are projected onto a raster surface. Boxplots show adjusted $R^2$ of all model comparisons (1231 in total) between December 1st and January 31st. Points and error bars show adjusted $R^2$ and 95% CI for each individual during the same period, with individuals highlighted that deviate from the functional response for forest given distance to road.

Fig. 3. Comparison between individual selection for mixed forest (A and B) and distance to road (C and D) and population-level selection given low vs. high availability of the other habitat. Coloured lines show the relative selection strength (RSS) for the habitat value at location $x_j$ in comparison to the mean habitat available to the individual (location $x_i$) in each moving window comparison ($n = 510$). Individuals differ in how far they are on average from roads within their home ranges (gradient in A and B) and the proportion of mixed forest in their home ranges (gradient in C and D). Black lines show RSS for the two locations according to each
population-level model with 95% CI (grey ribbon). In panel A, there is a single
selection coefficient for the entire population according to the random effects model
(Ranef; solid line). In panel B, the generalized functional response model (GFR)
selection coefficient depends on the other habitat in the model. The distinctness of the
colour gradient along the y-axis, along with the locations of the coloured lines relative
to the GFR lines, indicates whether individuals follow the functional response. RSS is
shown for the 10th percentile mean distance to road and average mixed forest
availability of individual home ranges (dotted line), and the 90th percentile (dashed
line). Root mean square errors (RMSE) measure the difference between the individual
level model RSS and the population level model RSS, reported as the mean ± SE
RMSE across all individuals (see text for details). Lower RMSE indicates a better fit.
Figure 2
Figure 3

(A) Ranef
RMSE = 0.25 ± 0.0002

(B) GFR
High
Low
RMSE = 0.29 ± 0.011

(C) Ranef
RMSE = 0.37 ± 0.013

(D) GFR
RMSE = 0.46 ± 0.016

Mean distance to road in home range (km)

Mean mixedwood cover in home range

9
6
3

0.8
0.6
0.4
0.2

Distance to road (km) at location $x_j$