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

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Abstract

Predicting future space use by animals requires models that consider both habitat availability and individual differences in habitat selection. The functional response in habitat selection posits animals adjust their habitat selection to availability, but population-level responses to availability may differ from individual responses. Generalized functional response (GFR) models account for functional responses by including fixed effect interactions between habitat availability and selection. Population-level resource selection functions instead account for individual selection responses to availability with random effects. We compared predictive performance of both approaches using a functional response in elk (*Cervus canadensis*) selection for mixed forest in response to road proximity, and avoidance of roads in response to mixed forest availability. We also investigated how performance changed when individuals responded differently to availability from the rest of the population. Individual variation in road avoidance decreased performance of both models (random effects: $\beta = 0.69$, 95% CI 0.47, 0.91; GFR: $\beta = 0.38$, 95% CI 0.05, 0.71). Changes in individual road and forest availability affected performance of neither model, suggesting individual responses to availability different from the functional response mediated performance. We also found that overall, both models performed similarly for predicting mixed forest selection ($F_{1,58} = 0.14$, $p = 0.71$) and road avoidance ($F_{1,58} = 0.28$, $p = 0.60$). GFR estimates were slightly better, but its larger number of covariates produced greater variance than the random effects model. Given this bias-variance trade-off, we conclude that neither model performs better for future space use predictions.

Introduction

We conserve and manage landscapes in ways we assume make them most profitable for use by wildlife populations (Gaillard et al. 2010). The profitability of landscapes depends on which habitats individuals within those populations are best adapted to use (Merrick and Koprowski 2017). Individuals select habitats to which they are adapted, and when changing environments produce gradients of habitat availability, their selection changes (Mysterud and Ims 1998). 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). Thus, our approaches to forecasting population distributions must be robust to the influences of both individual variation and habitat availability on space use. However, habitat selection models that account for availability are typically agnostic individual differences in habitat selection, 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; McCabe et al. 2021). Indeed, variation in space use among individuals provides behavioural redundancy that can maintain population-level fitness, i.e., population growth, when environmental change imposes selection pressure (Edelaar and Bolnick 2019). Given our understanding of functional responses to habitat selection and the adaptive importance of individual differences in habitat selection,

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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.

Habitat selection is an individual's behavioral response to the environment that nests within the functional response framework. 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). The ratio of resident to migratory individuals and demographic characteristics should affect how larger populations select habitat in response to changing availability. Thus, even if models account for habitat availability, not accounting for individual variation in habitat selection may lead to model error and 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, more active and exploratory southern red-backed voles (*Myodes gapperi*) and deer mice (*Peromyscus maniculatus*) selected forests with higher ground cover and light levels than their less active conspecifics (Brehm and Mortelliti 2021). However, all individuals need not follow the same patterns of habitat use when the environment changes. Instead, different personalities may respond with different plasticity to changes in habitat availability. In the previous example, active and exploratory voles and mice converged on the same habitat selection strategies as their less active conspecifics after silvicultural changes to the forest structure (Brehm and Mortelliti 2021), indicating they

responded more strongly to the change in habitat availability. These variable responses to availability by individuals are analogous to behavioural reaction norms (BRNs; Dingemanse et al. 2010). BRNs may be correlated with the functional response in habitat selection. However, if the slope of an individual's BRN differs from that of the functional response, then its future habitat selection will not agree with the population-level model used to predict it (Box 1).

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 (Carlson et al. 2021). 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). Like the slope of a BRN, random slopes account for plasticity, or the magnitude of the change in habitat selection across contexts (Gillies et al. 2006). They can be regressed against mean availability to estimate the functional response, similar to fitting a separate logistic regression model for each individual (Holbrook et al. 2017) without having to explicitly account for availability as in the GFR. 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, 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 variation among individuals 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. 2017a, b; Montgomery et al. 2018). We first measured the relative strength of selection for two habitat covariates by individuals during two consecutive time periods. We then compared the ability of the population-level GFR and random effects models, fit with data from the earlier period, to predict selection strength by individuals in the later period. The GFR model makes predictions based on the context of current habitat availability, and thus we expected its predictions to agree with future habitat selection effect sizes if individual selection follows the same functional response in both periods (Box 1: Fig. 7A). Since the random effects model fits a single selection coefficient for the population and thus does not assume individuals also follow a functional response, we expected it to perform best if the functional response changes between periods (Box 1: Fig. 7B). To investigate how agreement with the functional response affects performance, we

compared the extent to which the performance of each population-level model depended on how much availability and individual selection strength for covariates differed from the population-level response. Because its predictions are based on population-level responses, we expected the GFR model to perform worse for individuals whose response to changing availability between the two periods differed most from the population response, while this would not affect performance of the random effects model.

Methods

Study area

Our study area is 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 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 during 8 weeks in the winter season from December 1 to January 29. All collars collected relocations at either 1- or 2-h frequencies.

We divided the 8-week study period into four 2-week blocks to test the performance of the GFR and random effects models for predicting selection by individuals. Individual collars collected data either during the first two blocks (blocks 1 and 2) from December 1 to 15 and December 16 to 30, or during the second two blocks (blocks 3 and 4) from December 31 to January 14 and January 15 to January 29. Thus, data were available for all individuals only during two consecutive blocks. In all cases, we used models fit using data from the earlier period to predict selection by individuals during the later period (i.e., block 1 used to predict block 2, block 3 used to predict block 4). To facilitate model convergence, we excluded any individual with fewer than 60% of the minimum expected location points in either of its 2-week blocks (the equivalent of 100 relocations for collars with 2-h relocation frequencies). 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 35 individuals with between 109 and 343 GPS points per 2-week block.

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):

$$w(x_i) = \exp\left[\beta_1 h_1(x_i) + \beta_2 h_2(x_i) + \dots \beta_n h_n(x_i)\right], \tag{1}$$

which describes the selection of a location x_i in habitats h_1 to h_n, where β 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. We drew a separate sample of available points from a 100% minimum convex polygon (MCP) surrounding the used points in each individual 2-week block home range. We confirmed the entire home range was available by comparing the mean home range diameter (3.1 km, 95% CI 0.9, 7.9) with the largest distance travelled by elk from our population within 1 h (3.9 km). We then generated ten 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).

To test the performance of the GFR and random effects models, we conducted a preliminary analysis to identify where a functional response was likely to occur. We targeted our efforts based 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. 2017a, b). 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, in addition to individual selection for mixed forest as a function of mixed forest availability, we were interested in selection for mixed forest as a function of their average distance to road. We expected the strongest response from Riding Mountain elk during our study period because it coincides with rifle season—approximately December 1st to January 31st. Based on our preliminary analysis, we detected a weak functional response trade-off in which individuals that were closer to roads on average selected mixed forest more strongly. The relationship between distance to road and selection for mixed forest was similar between blocks 1 and 2 and blocks 3 and 4 (Fig. 1), suggesting individual BRNs followed the same functional response. We also expected elk with more available mixed forest—those within the park that do not use human-modified habitat (Brook 2010)—to avoid roads more strongly. Thus, in addition to a functional response for road avoidance as a function of average distance to roads, we also modelled a functional response for road avoidance as a function of mixed forest availability. However, unlike selection for mixed forest, road avoidance by some individuals differed between their blocks. Individuals with more mixed forest in their home ranges did avoid roads more strongly, but only in the fourth block. The same individuals did not change their response to roads in the previous third block, suggesting their BRNs did not follow the same functional response as individuals with data in blocks 1 and 2 (Fig. 1).

We tested whether modelling the functional response improved predictions of individual selection for mixed forest and distance to road by comparing predictions made by the GFR and random effects models. We fit two individual-level RSF models per individual using data from its earlier and later blocks, and a single population-level GFR and random effects model per individual using data from the remaining individuals collected during its earlier block. We fit the GFR and random effects models 200 times per individual to obtain a bootstrapped set of models, each time sampling the remaining individuals with replacement. All models included the same fixed effect covariates: distance to road as a continuous variable and mixed forest habitat as a categorical variable. We centred and scaled both covariates to facilitate convergence. We obtained roads data from Manitoba Conservation (1994, 2006) and land cover data from Agriculture and Agri-Food Canada Annual Crop Inventory (2019), both at 30 m resolutions.

Random coefficients are used to incorporate individual differences in habitat selection resulting from differences in availability (Muff et al. 2020), including in GFR models (Muhly et al. 2019). We 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 as follows:

$$w(x_{ik}) = \exp\big[(\beta_0 + \gamma_{0k}) + \beta_1 h_1(x_{ik}) + \gamma_{1k} h_1(x_{ik}) + \beta_2 h_2(x_{ik}) + \gamma_{2k} h_2(x_{ik})\big], \tag{2}$$
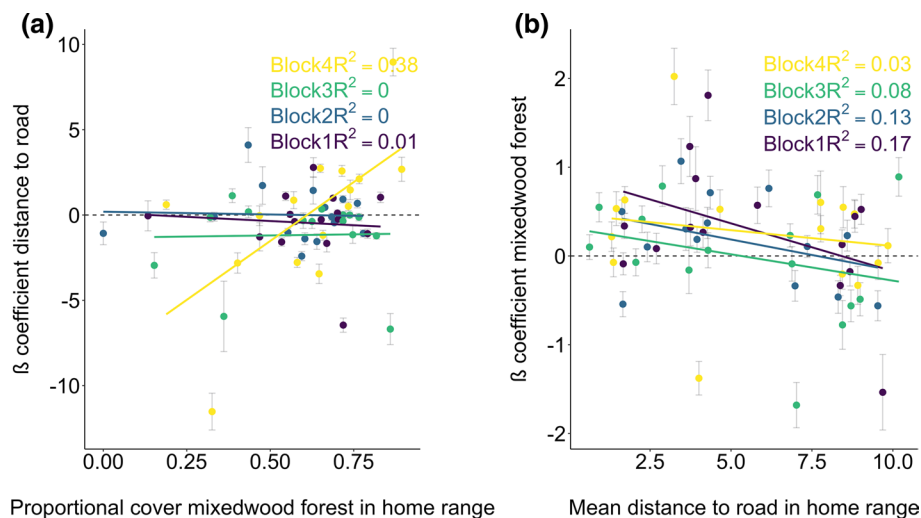
Fig. 1 Change in selection for distance to road (a) or mixed forest (b) as the availability of the other covariate changes in individual home ranges. Points represent selection coefficients ± SE from individual resource selection functions, and solid lines represent the population-level functional response in each of four blocks: (1) December 1–15, (2) December 16–30, (3) December 31–January 14, and (4) January 15–January 29. Functional responses are based on preliminary analysis to target models for comparing the generalized functional response and random effects models

where γ_0 is the individual intercept, β_n is the coefficient for habitat h_n, γ_{nk} is the random coefficient for habitat h_n for individual k, and x_{ik} is the ith location for individual k. We included random intercepts to control for uneven sample sizes among individuals, which were uncorrelated with random coefficients (Gillies et al. 2006).

We modelled the functional response by including four pair-wise fixed effect interactions between selection for habitat covariates and the mean availability of each covariate for individuals in the GFR model (Matthiopoulos et al. 2011) as follows:

$$w(x_{ik}) = \exp\big[(\beta_0 + \gamma_{0k}) + (\beta_1 + \gamma_{1k})h_1(x_{ik}) + (\beta_2 + \gamma_{2k})h_2(x_{ik})$$
$$+ \beta_{11k}h_{11}(x_{ik}) + \beta_{12k}h_{12}(x_{ik}) + \beta_{22k}h_{22}(x_{ik}) + \beta_{21k}h_{21}(x_{ik})\big],$$
$$(3)$$

where β_{n1k} is the coefficient for habitat h_n given the mean proportion of habitat h_1 in the home range of individual k, β_{n2k} is the coefficient for habitat h_n given the mean proportion of habitat h_2 in the home range of individual k. Finally, we assigned weights of 1000 to the set of available points in Eqs. 2 and 3 to ensure our logistic regression models approximated an inhomogenous Poisson point process model (Fithian and Hastie 2013).

Evaluating performance of 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. RSS is the ratio of selection estimates between two locations, x_i and x_j, i.e., $\mathrm{RSS}(x_i, x_j) = w(x_i)/w(x_j)$ (Avgar et al. 2017). If values of habitat covariates differ between the two locations, RSS can be used to understand how habitat characteristics influence selection. RSS can also be used to compare how the relative direction and magnitude of selection for a habitat changes across a gradient of availability when the model includes interactions between covariates (Box 1; Prokopenko et al. 2017a, b). This provides a means to assess how closely individual selection coefficients follow the functional response, or in our example how selection of mixed forest is influenced by average distance to road, or vice-versa, in the GFR model.

We first calculated log-RSS by each individual in the latter of their two blocks. We then calculated the log-RSS from each bootstrapped random effects, GFR, and individual model from the individual's earlier block. We made comparisons between the earlier and later blocks by setting the values of distance to road and mixed forest at locations x_i and x_j to different values. We calculated log-RSS for distance to road by setting distance to road at location x_i to the 0.05 quantile of the population, distance to road at location x_j to the 0.5 quantile of the population, and mixed forest at both locations x_i and x_j to zero. We calculated log-RSS for

mixed forest by setting distance to road at both locations x_i and x_j to the 0.95 quantile of the population, and mixed forest at locations x_i and x_j to zero and 1. We set the values of h_{2nk} and h_{1nk} in the GFR model—which includes fixed effect interactions between selection and availability—to the mean distance to road or mean mixed forest availability from the individual's later block.

We considered models from the earlier block to be better predictors when their log-RSS was closer to that of individual log-RSS from the second block. To compare individual with random effects and GFR log-RSS between blocks, we calculated the Z-score of the individual log-RSS on the bootstrapped distribution of the population-level model log-RSS. We considered individuals with a lower absolute value of their Z-score to be better predicted by their population-level model. We also compared individual selection between their earlier and later blocks by calculating the difference in log-RSS between the two periods. We used these comparisons to test the prediction that the performance of the GFR model depends on either within-individual variation in habitat selection or availability. Specifically, we fit a linear regression with Z-score as the response variable and the difference in availability and individual selection between blocks as predictor variables, weighted by the inverse of the variance of the bootstrapped distributions of the GFR and random effects models.

Results

Variation in selection and availability

Individuals varied more in availability of mixed forest than distance to road. Between blocks, individual home ranges differed in availability of mixed forest by a median of 4.82% cover (95% CI 0.28, 22.17). Individual distances to roads varied between blocks by a median of 0.41 m km^{-1} (95% CI 0.04, 1.64). Individuals varied in their responses to mixed forest and distance to road, with some selecting and others avoiding (Supplementary Fig. S1).

Model performance

Though the population-level models predicted future selection for distance to road (Fig. 2) and mixed forest (Fig. 3) for some individuals better than others, we detected no overall difference in predictive performance between the random effects and GFR models. The GFR model performed slightly better than the random effects model; Z-scores comparing individual log-RSS for mixed forest in the later block with population-level mixed forest log-RSS distributions were closer to zero in the case of the GFR model than the random effects model (Fig. 4). However, when we weighted the
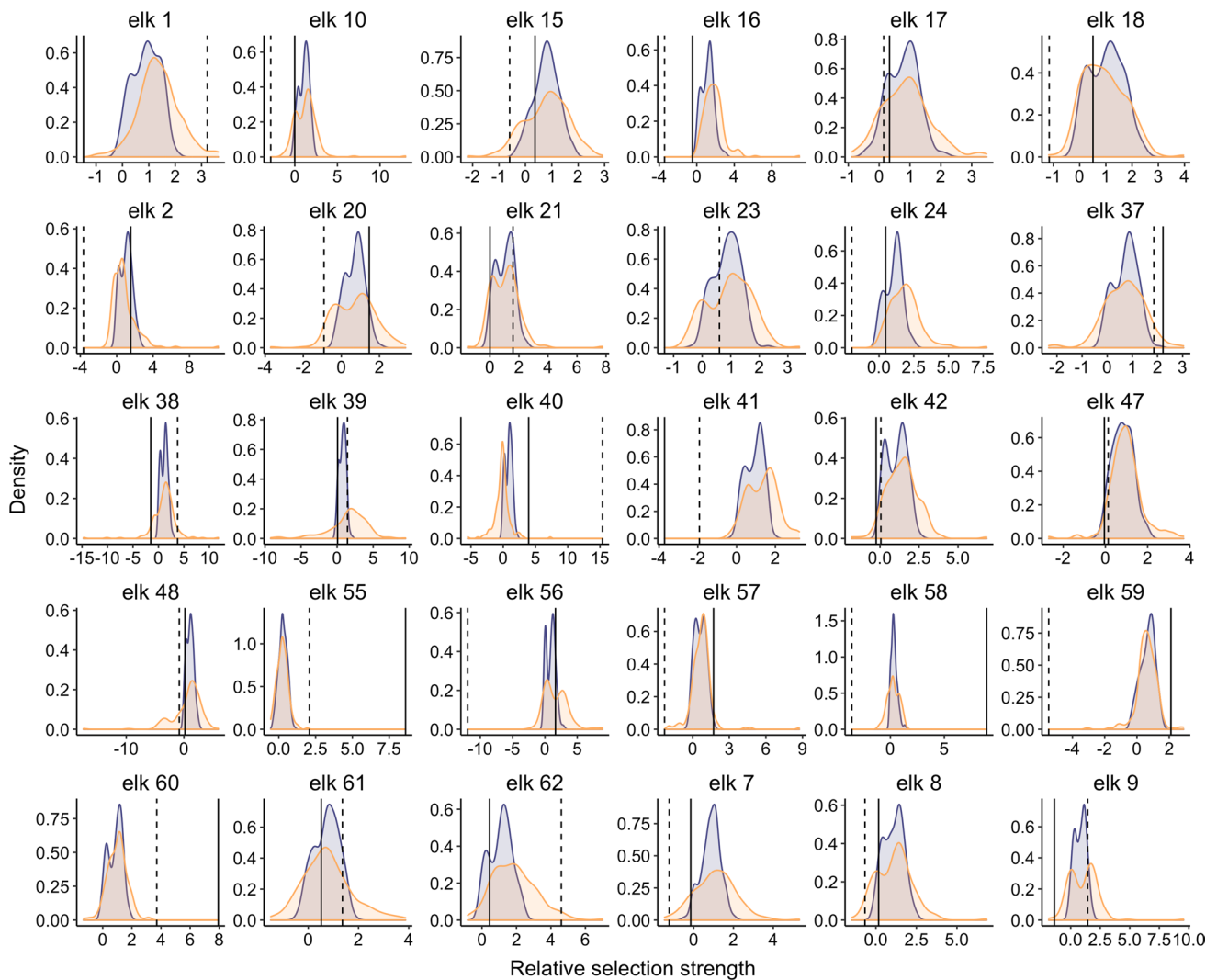
Fig. 2 Relative selection strength (RSS) for a location in mixed forest 300 m from the nearest road versus a location in mixed forest 5 km from the nearest road, compared among the generalized functional response model (orange distributions), random effects model (purple distributions), and individual models from an earlier period (dashed vertical lines). True RSS from later-period individual models (solid ver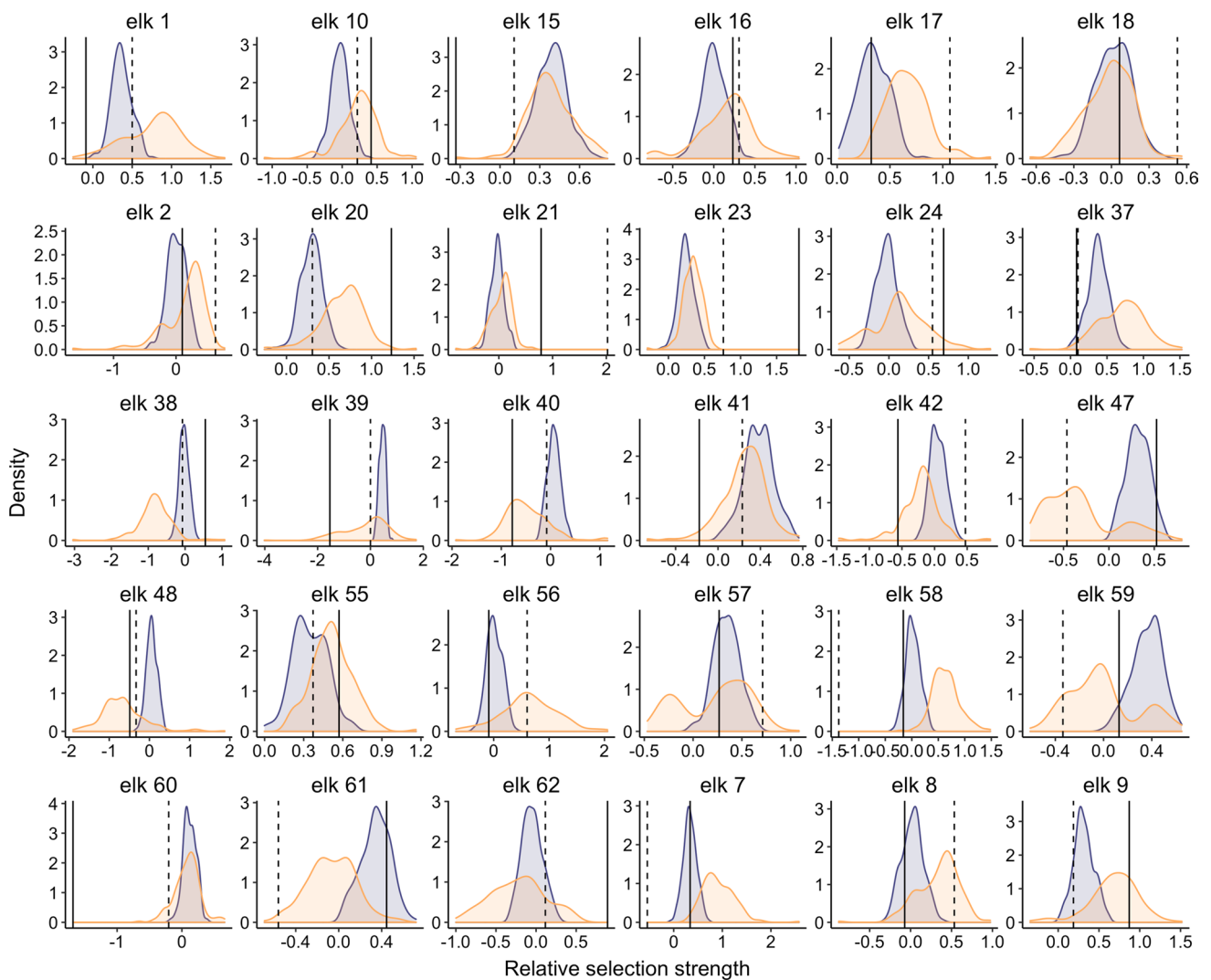tical lines) are shown to contextualize predictive model performance. Population-level models are considered better predictors when their distributions overlap the individual model lines. Arabic numerals above plots represent individual identifications. Distributions are comprised of RSS calculated from 200 bootstrapped models per individual, using data collected from the remaining individuals in the earlier period

Z-score comparisons between models by the inverse of the variance of the log-RSS distributions, there was no difference in their abilities to predict selection for either distance to road ($F_{1, 58} = 0.28$, $p = 0.60$) or mixed forest ($F_{1, 58} = 0.14$, $p = 0.71$). The variance of the GFR model log-RSS distributions was generally higher than the random effects distributions (Figs. 3, 4). The variance of the individual slopes from the GFR model (Supplementary Fig. S2) was higher than that of the individual slopes from the random effects model (Supplementary Fig. S3). Fixed effect coefficients and

variance of random effects from all bootstrapped models are summarized in Supplementary Figs. S2 and S3.

Effects of variation in availability and selection on model performance

Changes in habitat selection by individuals affected the performance of both the GFR and random effects models. Z-scores comparing individual log-RSS for distance to road in the later block with distance to road log-RSS

Fig. 3 Relative selection strength (RSS) for a location in mixed forest versus outside mixed forest and located 5 km from the nearest road, compared among the generalized functional response model (orange distributions), random effects model (purple distributions), and individual models from an earlier period (dashed vertical lines). True RSS from later-period individual models (solid vertical lines) are shown to contextualize predictive model performance. Population-level models are considered better predictors when their distributions overlap the individual model lines. Arabic numerals above plots represent individual identifications. Distributions are comprised of RSS calculated from 200 bootstrapped models, using data collected from the remaining individuals in the earlier period

distributions increased with individual differences in selection for distance to road between the earlier and later blocks (random effects: $\beta = 0.69$, 95% CI 0.47, 0.91; GFR: $\beta = 0.38$, 95% CI 0.05, 0.71; Fig. 5b). In contrast, individual differences in selection for mixed forest between blocks did not affect Z-scores (random effects: $\beta = 0.61$, 95% CI -0.37, 1.59; GFR: $\beta = 0.08$, 95% CI -0.25, 0.41; Fig. 5a). Similarly, changes in habitat availability between the earlier and later blocks did not affect Z-scores comparing either individual log-RSS with log-RSS for mixed forest (random effects $\beta = -0.44$, 95% CI -2.78, 1.90; GFR $\beta = 0.17$, 95% CI 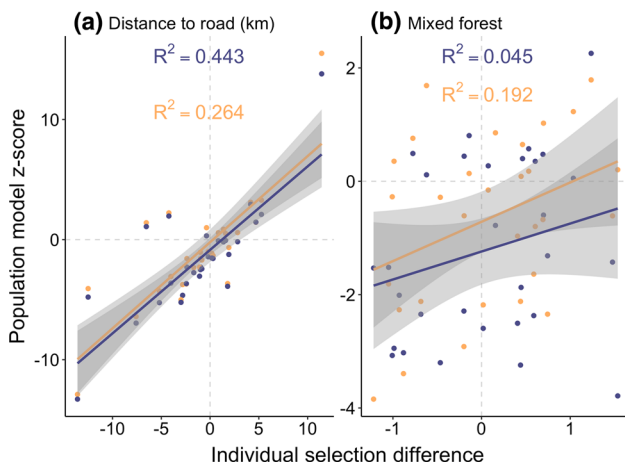-1.52, 1.86; Fig. 6a) or distance to road (random effects $\beta = 0.69$, 95% CI -1.92, 3.30; GFR $\beta = 0.69$, 95% CI -1.59, 0.41; Fig. 6b).

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
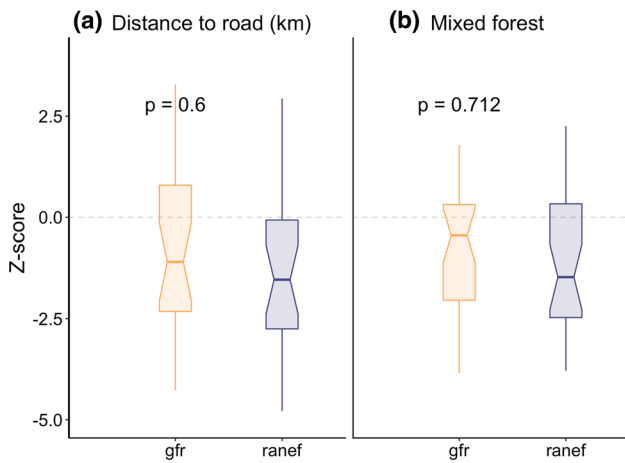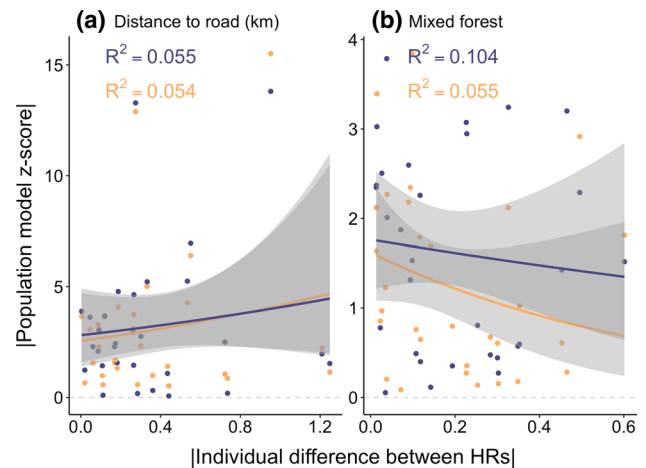
Fig. 4 Comparison of the ability of random effects (ranef) and generalized functional response (gfr) models using data from an earlier time block to predict selection for distance to road (**a**) and mixed forest (**b**) in the next time block. Boxplots measure Z-scores of individual log-RSS on a bootstrapped distribution of log-RSS from each population-level model. P-values are from linear models comparing Z-scores between the gfr and ranef, weighted by the variance of the bootstrapped distribution

Fig. 6 Variation in Z-scores of individual log-RSS on bootstrapped distributions of population model log-RSS as availability of distance to road (**a**) and mixed forest (**b**) changes between an earlier and later time block. Blue points represent individual log-RSS measured along the bootstrapped distribution of the random effects model, and gold points represent individual log-RSS measured along the distribution of the generalized functional response model

Fig. 5 Variation in Z-scores of individual log-RSS on bootstrapped distributions of population model log-RSS as individual selection for distance to road (**a**) and mixed forest (**b**) changes between an earlier and later time block. Blue points represent individual log-RSS measured along the bootstrapped distribution of the random effects model, and gold points represent individual log-RSS measured along the distribution of the generalized functional response model

for individual differences in habitat selection by including random intercepts and random coefficients 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 and GFR models both performed similarly for predicting near-term selection

(Fig. 4); without interactions between selection and availability, random effects in the random effects model accounted for more of the variance in selection (Fig. S2). Performance of neither model declined when availability changed (Fig. 6), but predictions worsened for both models when individual selection changed across time (Fig. 5), suggesting differences from the population response affected performance of both models. Overall, our results suggest the random effects model can perform as well as the GFR model for capturing responses to changing availability, but individual variation in response to availability affects the performance of both models. Though this result poses a difficult problem for prediction, it also frames a fruitful discussion about the most appropriate approach to forecast near- and long-term animal distributions. We submit that the GFR makes use of functional response patterns that may be useful for forecasting future distributions, but consideration should be given to whether or not individuals respond similarly to changes in habitat availability.

Models should be evaluated on whether they represent the individual mechanisms that produce population-level patterns (Johnston et al. 2019). When all individuals follow the population-level pattern, the functional response performs well for predicting individual habitat selection (Box 1: Fig. 7A). 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. 7B). We found the GFR performed well for predicting the functional response for mixed forest as average
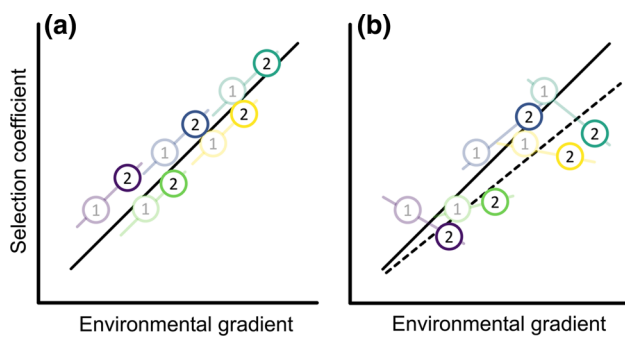
Fig. 7 The effect of individual variation on the ability of the functional response to predict individual habitat selection. Coloured circles show selection for the habitat by individuals measured during an earlier period (1) and later period (2), resulting in behavioural reaction norms (coloured lines) along the environmental gradient to which individuals are exposed. The solid black line shows the population-level functional response for the habitat along the environmental gradient during the earlier period. The dashed black line shows the resulting change in functional response in the second period when individual responses to the environmental gradient vary

distance from roads increased, which was largely consistent between blocks (Fig. 1). However, the performance of both models depended on individual differences in the way in which mixed forest availability affected their road avoidance (Fig. 5), and ultimately the GFR model did not outperform the random effects model. 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). Given the effect of this variation on model performance, our results suggest the random effects model might be just as appropriate as the GFR model for predicting the distributions of animals that characteristically exhibit large amounts of individual variation. Future studies should assess individual variation by quantifying changes in selection between periods of time (e.g., Fig. 1). Individual variation in the functional response could also be captured within the GFR model itself by including random slopes for functional response terms. Application of this approach in other systems may improve the predictive performance of the GFR model over the random effects model.

Our results also demonstrate that we can reveal individual differences by leveraging the comparative performances of different model evaluation methods. RSS allowed us to estimate selection for each habitat individually while holding availability of the other constant. Including an interaction between selection for each habitat and the availability of each habitat within home ranges allowed us to determine how the GFR model effect sizes compared to effect sizes

from individual models with different habitat availability. For many individuals that did not follow the functional response, the GFR and random effects models predicted selection for one of the habitats better than the other (e.g., both models accurately predicted road avoidance but not selection for mixed forest by individual 40 in Figs. 2 and 3), decreasing the overall performance of the population-level models. Bootstrapping the models also revealed that for many individuals, the variance in RSS for mixed forest based on GFR model coefficients was larger than the variance in RSS based on random effects coefficients (Fig. 3). The larger variance of the GFR RSS distributions may be the result of it greater number of covariates, which increased the accuracy of its estimates at the expense of greater variance. This bias-variance trade-off ultimately led us to conclude no difference in predictive performance between models. Whether such variance result from meaningful variation in response to availability by the sample of individuals used to fit the models, or uncertainty in GFR coefficient estimates, is likely to impact the predictive performance of the GFR model in any study system.

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 variation in habitat selection in response to availability. 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 requires both an individual and population perspective. The dual focus on individuals and populations also aligns with our finding that we need more than just patterned responses to availability to comprehensively predict habitat selection. As we found, both the GFR and random effects models reveal habitat selection patterns, but added terms may improve their ability to account for individual variation. If we are to make management recommendations to preserve individual variation in habitat selection, we need

to expand our criteria for measuring habitat selection model performance.

As a complementary approach to understanding the effects of individual variation on model performance, future efforts should test how habitat diversity and heterogeneity affect model performance. Many habitat selection models make the reasonable assumption that the most important habitats are where individuals are currently best adapted (Hebblewhite and Merrill 2009; Dupke et al. 2017; Palmer et al. 2017). But population-level habitat selection is adaptive either when different individuals select the habitats to which they are adapted, or the environment changes to suit their adaptations (Edelaar and Bolnick 2019). Past environmental pressure causes some, but not necessarily all, individuals to adjust how they select habitat (Box 1: Fig. 7B), potentially over evolutionary time (Trevail et al. 2021). We found that both population-level models performed worse for individuals whose response to road distance changed most between blocks, but performance did not depend on changes in availability. Depending on the existing capacity of individuals to respond to availability, greater magnitudes of environmental change could induce more or less agreement between individual BRNs and the functional response. We focussed on how small, near-term changes in the environment and individual variation affect the performance of habitat selection models. Future studies could compare model performance between populations having different historic and current exposure to environmental variation. If past exposure to variable environments primes individual capacities to respond in the future, models that account for individual variation may be a particularly important in diverse and heterogeneous environments.

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 populations change their habitat selection across contexts. However, while population-level changes in selection might be captured by the functional response, we demonstrated that simpler random effects models perform just as well when individual 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.

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. 7, each coloured line represents a single individual. Individuals exhibit a behavioural reaction norm for a habitat, the direction and magnitude of which varies along an environmental gradient as an individual's home range changes between two time periods. The functional response for the habitat is positive, i.e., the slope of the increase in selection for the habitat increases along the environmental gradient. Such a response could occur if the environmental gradient measures risk of predation, and the habitat provides cover from that risk. When all individuals respond similarly to the environmental gradient as their positions vary along the environmental gradient, their individual behavioural reaction norms (BRNs) are correlated with the functional response pattern (panel a). In such cases, the functional response is a good predictor of individual selection.

However, if some individuals exhibit a response to the environmental gradient 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 environmental gradient. In such cases, the mean selection by all individuals in the population (dashed line) is likely to be a better predictor than the functional response because it minimizes the variation between all individuals and their predicted selection.

Declarations

Conflict of interest The author declares that they have no conflict of interest.

Ethics approval Data were made available by Riding Mountain National Park and collected in accordance with approved animal care protocols from the University of Saskatchewan (#20060067), University of Manitoba (#F01-037), and Memorial University of Newfoundland (#16-02-EV).

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