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Local and Landscape-Level Environmental Conditions Drive Habitat Selection Across Terrestrial Mammal Species

Björn H. Franke[1] | Aafke M. Schipper[1,2] | Tal Avgar[3,4] | Luca Börger[5,6] | Nilanjan Chatterjee[7,8] | Thomas Müller[7,9] | Brian J. Smith[10] | Briana Abrahms[11,12] | Abdullahi H. Ali[13] | Nina Attias[14] | Hattie L. A. Bartlam-Brooks[15] | Floris M. van Beest[16] | Jerrold L. Belant[17] | Dean E. Beyer Jr.[17] | Niels Blaum[18] | Michael B. Brown[19] | Bayarbaatar Buuveibaatar[20] | Francesca Cagnacci[21,22] | Simon Chamaillé-Jammes[23,24] | Nandintsetseg Dejid[7] | Jasja Dekker[25] | Arnaud L. J. Desbiez[14,26] | Julian Fennessy[19,27] | Christina Fischer[28] | Ilya Fischhoff[29] | Adam T. Ford[3] | Benedikt Gehr[30,31] | Jacob R. Goheen[32] | Ronaldo Gonçalves Morato[33] | Mark Hebblewhite[34] | Robert Hering[35] | Marco Heurich[36,37] | A. J. Mark Hewison[38,39] | Lynne A. Isbell[40] | Matthew Kauffman[41,42] | Andrew Jakes[42] | René Janssen[43] | Paul F. Jones[44] | Bob Jonge Poerink[45] | Clayton Lamb[4] | John D. C. Linnell[46,47] | A. Catherine Markham[48] | Courtney J. Marneweck[19,49] | Jenny Mattisson[50] | John McEvoy[51] | Erling Meisingset[52] | Evelyn Merrill[53] | Guilherme de Miranda Mourão[54] | Bram Van Moorter[55] | Nicolas Morellet[38,39] | Atle Mysterud[56] | John Odden[55] | Kirk A. Olson[57] | Agustín Paviolo[58,59] | Tyler Petroelje[60] | Kelly M. Proffitt[61] | Kasim Rafiq[11,12] | Nathan Ranc[38,39] | Christer Moe Rolandsen[50] | Daniel I. Rubenstein[62] | Sonia Saïd[63] | Hall Sawyer[64] | Niels Martin Schmidt[16] | Nuria Selva[65,66] | Agnieszka Sergiel[66] | Erling Johan Solberg[50] | Melissa Songer[57] | Jonas Stiegler[67] | Olav Strand[50] | Siva Sundaresan[62] | Jeffrey J. Thompson[68,69] | Wiebke Ullmann[18] | Dorj Usukhjargal[70] | Ulrich Voigt[71] | Filip Zięba[72] | Tomasz Zwijacz-Kozica[72] | Mark A. J. Huijbregts[1] | Marlee A. Tucker[1]

Correspondence: Björn H. Franke (bjoern.franke@ru.nl)

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ABSTRACT

Aim: Animal movements are a fundamental process affecting communities and ecosystems. Quantifying habitat selection across species and habitats is key for understanding how animals respond to environmental change. Currently, we lack comparative studies that examine how habitat selection varies across species traits and landscapes. We aim to quantify global patterns of habitat selection to help understand the fundamental drivers of movement behaviour.

Location: Global.

Time Period: Contemporary.

Major Taxa Studied: Terrestrial mammals.

Methods: We estimated selection coefficients for terrain ruggedness, vegetation productivity, human population density and distance to roads of individual terrestrial mammals through step-selection analysis of 1344 GPS tracks across 48 species. We quantified intra- and interspecific variation and tested whether selection coefficients were associated with species traits and habitat availability.

Results: We observe an overall avoidance of roads and areas of high human population density as well as rugged terrain, with a large proportion of individuals selecting for areas of intermediate NDVI. However, we also found large intraspecific variation in habitat selection and show that this variation is predicted by local and landscape-level environmental conditions rather than species traits. Individuals in more remote areas exhibited weaker functional responses to human presence than those in more disturbed areas. Avoidance of rugged terrain is also context-dependent, with stronger avoidance when local

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ruggedness is high. The only exception to the observed intraspecific variability is consistent species-level responses to road proximity.

Main Conclusions: Our findings contribute to the understanding of habitat selection by terrestrial mammals, showing that selection is largely shaped by environmental conditions and that animals exhibit high plasticity in their responses. Our results also provide further evidence for the significant impact of roads on animal movement. These insights can help us to understand the potential effects of environmental change on the behaviour of mammal species around the world.

1 | Introduction

Global environmental change has wide-ranging effects on animal behaviour (Doherty et al. 2021), which may generate human-wildlife conflicts and alter ecosystem functioning (Wilson et al. 2020). Human-modified landscapes have particularly strong impacts on the movement of animals (Tucker et al. 2018; Doherty et al. 2021), which in turn affects processes such as seed dispersal (Tucker et al. 2021), biomass and nutrient flows within and between ecosystems (Bauer and Hoye 2014), disease transmission (Omondi et al. 2020) and habitat modification (Martin et al. 2018; Maher et al. 2023). The disruption of animal movement can have wide-ranging consequences for communities and ecosystems (Wilson et al. 2020). To mitigate these impacts, it is essential to understand the fundamental ecological processes underlying movement not only within single species and populations, but also across species through comparative studies (Tucker et al. 2018, 2023).

Comparative movement studies have so far focused on descriptive measures of space use and movement patterns. For example, existing studies have found differences in movement distances and home range sizes between trophic levels, with carnivores generally utilising larger areas than herbivores (Tucker et al. 2014, 2018; Fauvelle et al. 2017; Noonan et al. 2020). Human activities are associated with an increase in displacement across several taxonomic groups (Doherty et al. 2021), a decrease in the median and long-movement distances of terrestrial mammals (Tucker et al. 2018) and a reduction in home range size and the proportion of available habitat (Hirt et al. 2021). These studies demonstrate that there are considerable generalities in species' responses to human activities around the globe and that species traits can be key in understanding how animals react to environmental change. Habitat selection—the preference or avoidance of certain environmental features or resources—is another fundamental aspect of animal behaviour that emerges from encountering habitats due to movement (Nathan et al. 2008; Van Moorter et al. 2016). However, generalities in what influences habitat selection across species have not been investigated, despite it being a crucial part of an individual's movement process. Investigating generalities in habitat selection across species requires a unified approach in which selection responses are directly comparable.

Here, we present the first comparative study of habitat selection patterns using GPS data from 48 medium to large-bodied terrestrial mammal species and 34 countries. We used an integrated step-selection approach (Avgar et al. 2016) to quantify selection patterns for 1344 individuals and to examine inter- and intraspecific variation in selection. We then related habitat selection to species traits (body size, relative brain size, trophic level) as well as environmental availability to explore functional responses across species, i.e., the extent to which animals change their selection depending on the environmental conditions, such as the availability of a certain resource or habitat type (Mysterud and Ims 1998; Mason and Fortin 2017) or the degree of human activity (Burton et al. 2024). We defined environmental availability at two levels: step-level availability and track-level availability. Step-level availability reflects the local conditions at an animal's given location, which affects its next movement decision at a point in time. Track-level availability represents the environmental conditions that the animal moves in along the entirety of its track, reflecting the landscape it lives in.

We quantified habitat based on a few key characteristics relevant to many species. Vegetation productivity, quantified by the Normalised Difference Vegetation Index (NDVI), is often used as a proxy for resource availability across ecological studies (Pettorelli et al. 2011). The Terrain Ruggedness Index (TRI) is commonly used to quantify elevational differences in a landscape (Nellemann and Fry 1995), as it affects the energy that animals need to expend in order to move around their habitat (Shepard et al. 2013). We included distance to roads and human population density as previous studies revealed significant avoidance responses to roads (Barry et al. 2020; Bastianelli et al. 2024) as well as areas with high human population density (Dellinger et al. 2013). We expected that animals will generally avoid areas of higher TRI (Shepard et al. 2013), with larger-bodied species showing stronger avoidance due to the higher energetic costs of moving across terrain (Taylor et al. 1972). We expected that many animals would select for intermediate values of NDVI, because it has been shown that high-NDVI areas such as closed-canopy forests can provide less foraging resources below the canopy than more open areas (e.g., Prokopenko et al. 2017; Jones et al. 2019). We also expected animals to avoid roads and areas with high human population density, in line with previous studies (Tucker et al. 2018, 2023; Barry et al. 2020; Bastianelli et al. 2024; Dellinger et al. 2013), with the possible exception of species that are well-adapted to human landscapes (e.g., agricultural areas). The impacts of roads are strongest in their immediate vicinity (de Jonge et al. 2022), resulting in a functional response, where animals will increasingly avoid roads and areas with high human population density when in areas of higher human impact (i.e., low average distance to roads and high human population density). Finally, we analysed whether habitat selection is related to species' traits, as we expected potential differences in selection between species in relation to trophic level (Rosenheim 2004), body size

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(Gil-Sánchez et al. 2025), as well as relative brain size, where larger relative brain size is related to better spatial memory and more efficient navigation capacity (Nathan et al. 2008; Fagan et al. 2013).

2 | Methods

2.1 | Individual Step-Selection Responses

2.1.1 | Movement Data

We compiled GPS tracking data for 1344 individuals from 48 terrestrial mammal species, collected by co-authors during 1998–2023 across 34 countries (Table S1). Due to the inherent constraints of GPS tracking, our dataset is limited to medium to large-bodied mammal species. We removed unrealistic movements using a threshold speed of >4 m/s (Tucker et al. 2018, 2023), and removed the first seven days of tracking to eliminate potential effects from capturing (Stiegler et al. 2024). We used the R package *amt* (Signer et al. 2019) to resample all trajectories to 6-h steps (the finest temporal grain that allowed us to retain most individuals of most species) with a 15% (54 min) tolerance interval. The final tracks had a median length of 1129 steps at 6-h time steps (mean: 1372.4 steps; 25th percentile: 544.5 steps; 75th percentile: 1675.2 steps). A median length of 1129 consecutive 6-h steps would correspond to a median track length of 282 days, yet tracks can contain gaps and thus cover slightly longer periods than implied by their number of steps. For an overview of the number of individuals per species see Table S1. To assess whether 6-h steps are appropriate for capturing independent movement decisions, we measured autocorrelation in the absolute headings of each individual track using correlograms (see Supporting Information Methods 1), which showed near zero autocorrelation across individuals and species at 6-h intervals (Figures S3 and S4).

2.1.2 | Environmental Data

For our analysis, we included MOD13Q1 V6.1 16-day NDVI obtained through the Env-DATA system (Dodge et al. 2013) at 250-m resolution using inverse-distance interpolation, TRI as calculated using the *terra* R package based on SRTM elevation data accessed via *elevatr* (Hollister et al. 2017) at zoom level 11 and resampled to 250-m resolution, 5-year human population density from the European Commission Joint Research Centre Data Catalogue (GHS-POP R2023A) resampled from native 100-m resolution to 250-m resolution, and distance to the nearest major road (up to and including tertiary roads following the OpenStreetMap classification system) based on 2016 OpenStreetMap data accessed through WorldPop (WorldPop, 2018) and resampled from 100-m resolution to 250-m resolution because this was the finest resolution at which NDVI data was available. For the time-varying covariates NDVI and human population density, we always used the temporally closest available data layer. We transformed all variables except for NDVI using log $(X+0.01)$ transformation because of their positively skewed distributions including true zero values. We then standardised all covariates using z-transformation based on their respective mean and standard deviation values across the entire dataset.

2.1.3 | Integrated Step-Selection Model

Step-selection analyses (SSA) quantify the relative importance of environmental heterogeneity in an individual's movement decisions at a fine spatial grain. SSA uses movement data to compare steps taken relative to alternative steps that were available to the individual, but which were not selected at the time. A conditional logistic regression model is then used to estimate selection coefficients for each environmental variable included in the analysis. These selection coefficients indicate an individual's preference for the respective environmental variable and, crucially, are simultaneously estimated with the movement parameters, accounting for the fact that movement and resource selection are not independent (Avgar et al. 2016).

We generated 20 alternative steps for each "used" step using the *amt* R package (Signer et al. 2019), based on step lengths and turning angles sampled from gamma and von Mises distributions fitted to each individual track, respectively. We annotated the endpoints of all used and available steps with the environmental covariates outlined above. We then fitted a single step-selection model to each individual track (Equation 1). We included the log-transformed TRI, human population density and distance to the nearest major road in the model, as well as the linear and quadratic term for NDVI to allow for selection of intermediate NDVI. To test for a functional response in habitat selection, we calculated the step-level availability of each covariate as the average covariate value across each cluster (i.e., each set of one used and its corresponding 20 available steps). We included an interaction of each covariate term with its respective step-level availability in the model (Equation 1):

$$\begin{aligned}\hat{w}(x) = \exp\big(&\beta_1\,\mathrm{TRI} + \beta_2\,\mathrm{roadD} + \beta_3\,\mathrm{popdens} + \beta_4\,\mathrm{NDVI} \\ &+ \beta_5\,\mathrm{NDVI}^2 + \beta_6 \log(\mathrm{SL}) + \beta_7 \cos(\mathrm{TA}) + \beta_8(\log(\mathrm{SL}) * \cos(\mathrm{TA})) \\ &+ \beta_9\big(\mathrm{TRI} * \overline{\mathrm{TRI}}\big) + \beta_{10}\big(\mathrm{roadD} * \overline{\mathrm{roadD}}\big) + \beta_{11}\big(\mathrm{popdens} * \overline{\mathrm{popdens}}\big) \\ &+ \beta_{12}\big(\big(\mathrm{NDVI} + \mathrm{NDVI}^2\big) * \overline{\mathrm{NDVI}}\big)\big)\end{aligned} \tag{1}$$

where $\hat{w}(x)$ is the estimated step-selection function, TRI is the TRI, roadD is the distance to the nearest road, NDVI is NDVI, popdens is the human population density, SL is the step length, TA is the turning angle and covariate terms with overlines indicate cluster-level mean values.

For some individuals, the annotated covariate data had large gaps or showed zero variance. This was due to gaps in the NDVI data ($n=20$ individuals, 1.5% of the dataset), lack of variance in distance to roads ($n=121$ individuals, 9.0%, including all individuals of *Ovibos moschatus*, for which the nearest major road was located across the ocean), or individuals in remote areas with zero human population density along their entire track ($n=226$ individuals, 16.8%). In those cases, we fitted a simpler model without the covariate of concern and the associated interactions. Given the overall size of the dataset, we did not expect these slight reductions in sample size to affect the modelling outcomes. Additionally,

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the respective coefficients for the removed variables and their standard errors were set to NA before proceeding with further analysis. We further conducted a sensitivity analysis with an additional *time of day* term to account for different behaviours during daytime and nighttime. While there were some differences in daytime and nighttime selection within individuals (Figures S6 and S7), this distinction did not result in differences in the cross-species analyses we conducted, and we do not include it here.

2.1.4 | Processing Selection Coefficients

We extracted all selection coefficients and their associated standard errors from each individual step-selection model (Equation 1). We excluded one individual of *Martes foina* from further analysis as its model produced a negative adjusted shape parameter, an indicator of poor model fit. Four individual models (0.3% of the dataset) returned non-numeric standard errors for the quadratic or linear NDVI coefficient. For these individuals, we excluded all NDVI-related coefficients from further analysis. To test for a functional response at the step level, we used the individual models to calculate selection coefficients at six fixed step-level availability levels (see Table 1). These coefficients can be interpreted as the individual's selection response to the respective variable when it finds itself in an environment with the given step-level availability value. For example, the human population density selection coefficient at a step-level availability of 100 people/km^2 describes the selection of that animal when the average of the human population density values across the end points of its theoretically available next steps is 100 people/km^2.

The linear and quadratic coefficients for NDVI are not independent as they together describe a single parabolic response curve. To interpret these coefficients, we translated the coefficients into two independent and more ecologically relevant descriptors of the quadratic response curve: the NDVI value at which the parabolic response reaches its vertex point (from hereon *vertex coordinate*), and the distance between the vertex point and the focus point of the parabola along the y-axis (from hereon *focal length*). This is similar to the characterisation of environmental niches as Gaussian curves by Panzacchi et al. (2015), but also allows for non-Gaussian responses, such as selection for either high or low, and selection for both extreme high and low values. For example, for an individual that selects for intermediate NDVI values while avoiding areas of very low and very high NDVI, the vertex coordinate indicates the highest-selected NDVI value, whereas the focal length describes the width of the quadratic response—a large focal length indicates more generalist behaviour, while a small focal length would indicate more specialist behaviour (Figure S1). Further, the sign of the focal length indicates whether the parabola opens upwards (selection for extremes) or downwards (intermediate selection). Following the numbering of coefficients in Equation (1), we calculated the vertex coordinate as follows:

$$V_{\text{NDVI}} = -\frac{\beta_4}{2\beta_5} \tag{2}$$

and the focal length as follows:

$$\text{FL}_{\text{NDVI}} = \frac{1}{4\beta_5} \tag{3}$$

Since all covariates were standardised before running iSSA, we back-transformed the NDVI vertex coordinates from standardised NDVI to regular NDVI units. We grouped response curves into six classes (convex, concave, accelerated increase, accelerated decrease, decelerated increase, decelerated decrease) based on the sign of their focal length and whether their vertex points were within or outside the [0.1] interval.

2.2 | Interspecies Habitat Selection Analysis

2.2.1 | Predictor Variables

We annotated each individual selection coefficient with mean species body mass (grams), brain mass (grams), and trophic level (herbivore, omnivore, carnivore) from the COMBINE database (Soria et al. 2021). The dataset covered a body mass range from 1.3 (*Martes martes*) to 4565 kg (*Loxodonta africana*), and included 26 herbivores, 12 omnivores, and 10 carnivores. The focus on medium to large-bodied mammal species reflects the body size constraints of GPS tracking devices. To account for the allometric relationship between body mass and brain mass, we conducted a phylogenetic least squares regression analysis between log-transformed species brain mass and log-transformed body mass for all species present in both the COMBINE database and the mammalian phylogeny published by Upham et al. (2019). We then extracted the normalised residuals from this model for the species present in our dataset as a measure of relative brain size (Benson-Amram et al. 2016), with negative values indicating a below-average brain-to-body mass ratio. These residuals ranged from −1.613 (*Procyon lotor*) to 3.150 (*Lycaon pictus*). To test for a functional response at the individual track level, we also calculated track-level availability for each individual as the mean covariate value across all used and available steps. This is similar to taking the average covariate value across a species' home range, yet gives increased weight to areas that an animal moves in more frequently.

2.3 | Statistical Analysis

We fitted linear mixed-effects models, using selection coefficients (or, in case of NDVI, derived selection metrics) at each step-level availability level as response variables. As predictors, we used the species traits described above (log body mass, relative brain mass, trophic level) as well as the individual's track-level availability. Since most species in our dataset are herbivorous, we used the 'herbivore' level as reference level for the trophic level factor. In all linear mixed-effects models, we accounted for the data structure using species as a random intercept.

We used a model selection approach to identify the most parsimonious models, fitting and comparing all possible candidate models—including a null model—based on maximum likelihood estimation using the *lme4* package (Bates et al. 2015) and

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TABLE 1 | The explanatory variables included in the best-supported models explaining variability in selection coefficients (or descriptors, for NDVI) for environmental and anthropogenic variables included in the models.

Variable (units)	Step-level availability	Terms of best model	ICC	Selection coefficient	Step-level availability	Terms of best model	ICC
Road distance (m)	0	Track-level availability	0.781	NDVI focal length	0	Track-level availability	0.000
	250	Track-level availability	0.257		0.2	Track-level availability + log (bodymass)	0.000
	500	Track-level availability	0.184		0.4	Track-level availability	0.000
	1000	Track-level availability	0.109		0.6	(intercept-only)	0.000
	2000	Track-level availability	0.058		0.8	(intercept-only)	0.000
	5000	Track-level availability	0.044		1	(intercept-only)	0.000
Pop. density (people/km^2)	0	Track-level availability	0.008	NDVI vertex	0	(intercept-only)	0.007
	50	Track-level availability	0.077		0.2	Track-level availability	0.002
	100	Track-level availability	0.099		0.4	(intercept-only)	0.000
	200	Track-level availability	0.122		0.6	(intercept-only)	0.011
	400	Track-level availability	0.146		0.8	(intercept-only)	0.041
	800	Track-level availability	0.170		1	(intercept-only)	0.043
Terrain ruggedness (TRI)	0	Track-level availability	0.299				
	0.2	Track-level availability	0.060				
	0.4	(intercept-only)	0.083				
	0.6	(intercept-only)	0.094				
	0.8	(intercept-only)	0.103				
	1	(intercept-only)	0.111				

Note: Step-level availability indicates the average local environmental value for each variable in its associated units. All models include random intercepts for species. ICC = interclass correlation coefficient of the best model, where 0 indicates that all variation lies within species (no effect of species identity on habitat selection) and 1 indicates no within-species variation (habitat selection determined by species identity). For all slopes and intercepts, see Table S1.

dredge() from the *MuMIn* package (Barton and Barton 2015). We identified the best-supported models using the Bayesian information criterion (BIC), as BIC reduces the risk of overfitting compared to other methods such as the Akaike information criterion (Raffalovich et al. 2008). We then refitted the best-supported models using restricted maximum likelihood (REML) and the Nelder–Mead optimisation algorithm (Nelder and Mead 1965), since the default BOBYQA algorithm used by *lmer*() caused convergence issues in some models. Due to non-normality in the data, we transformed all response variables using the log-modulus transformation (John and Draper 1980), defined as $\text{logmod}(y) = \text{sign}(y) * \log(|y| + 1)$. This

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transformation allows for the logarithmic yet continuous scaling of approximately symmetric data, which includes both positive and negative values with long tails. In all cases, we included the coefficients' inverse squared SEs as regression weights to give higher weights to coefficients that were estimated with higher confidence. For the calculations of the standard errors of linear combinations of selection coefficients, see Supporting Information Methods 2. To assess the relative contribution of intraspecific and interspecific variability to the variability observed across the individual coefficients, we calculated the intraclass correlation coefficient (ICC) as outlined by Nakagawa and Schielzeth (2010). ICC ranges between 0 and 1 and in our case estimates the proportion of variance in the model explained by the random effect *species*.

3 | Results

3.1 | Individual Step-Selection Responses

The extracted selection coefficients were variable across species (Figure 1A–F); however, we did find general patterns of avoidance of roads, high human population density, and rugged terrain and a tendency of preference for intermediate NDVI values. Specifically, we observed that most animals avoided roads, as indicated by positive coefficients reflecting that animals are selecting for distances further away from the nearest road (Figure 1A,B). This avoidance was stronger when closer to a road (Figure 1A), but still persisted at larger distances for many species (Figure 1B). For human population density, we observed very weak selection at low step-level population density (Figure 1C) and more avoidance at higher step-level population density (Figure 1D), although the variation was considerable and only in a few species all individuals consistently avoided areas with higher human population density (Figure 1C,D). Selection coefficients for terrain ruggedness indicated preference for more rugged terrain only at low step-level ruggedness (Figure 1E), and only a few species, such as *Lynx lynx* and *Gulo gulo*, showed consistent selection for more rugged terrain across all individuals (Figure 1E,F).

Individuals in environments with high productivity (high track-level NDVI) tended to be slightly more specialised (i.e., showing a larger focal length) in their NDVI responses than individuals in low-productivity environments. This difference in specialisation was slightly stronger when local productivity was low, meaning that animals in an overall highly productive environment show more specialised selection when they find themselves in a local gap in productivity. Individuals in high-productivity areas also tended to have higher NDVI vertices. As for most individuals the response curve was concave (Figure 2), the vertices mostly represent the NDVI selection optima, meaning that at higher landscape productivity, animals also select for areas of higher productivity. For examples of how individual NDVI responses change with changing step-level availability, see Figure S2.

3.2 | Interspecies Habitat Selection Analysis

For most selection coefficients, BIC-based model selection identified either the model containing track-level availability or the intercept-only model as the best-supported model (Table 1), and the species traits considered in our analysis were not included. The only exception to this was the NDVI focal length model at step-level NDVI of 0.2, where a weak signal of body size was retained in the best candidate model. Interspecific variation as quantified by ICC was generally very low (Table 1). As the ICC metric represents the proportion of variance in the model that is explained by the random effect, in this case *species*, this finding indicates high intraspecific variability in selection. The only exception was road selection at zero distance from the nearest road (Table 1), that is, when an animal is on a road, where 78.1% of the variation in the data could be explained by differences among species, indicating that all individuals of a given species show very similar responses to roads.

Animals in less disturbed areas such as remote parts of Canada and Brazil (large track-level mean distance to roads and low human population density) tend to show consistent avoidance of roads, with little influence of step-level availability on selection coefficients (Figure 3A). They also avoid areas of high human population density, although this avoidance depends on the step-level conditions and becomes less strong as the step-level human population density decreases (Figure 3B). Animals in areas with higher road density show strong availability-dependence in road selection, with strong avoidance when close to roads but a strong tendency to move towards a road when they are further away (Figure 3A). Their response to human population density is consistently positive and less dependent on step-level conditions (Figure 3B). For terrain ruggedness selection, we observed availability dependence only at low step-level ruggedness, where animals living in overall more rugged areas showed selection for areas of higher ruggedness. Animals living in largely flat environments always avoid rugged terrain, although more strongly at high step-level ruggedness (Figure 3C).

4 | Discussion

In this study, we found significant intraspecific variation in habitat selection and reinforced the importance of environmental conditions at both local and landscape-level in determining movement. Differences in selection between individuals of the same species generally surpass differences between species. Our results suggest that mammals exhibit an inherently high degree of behavioural plasticity in their habitat selection and exhibit a functional response to environmental conditions. We show that some behaviours, such as the avoidance of areas with high human impact, can be observed across species and continents. These findings are in line with observations made previously in species-level studies, such as the general avoidance of roads and densely populated areas (Prokopenko et al. 2017; Doherty et al. 2021; Bastianelli et al. 2024). We also show that animals generally exhibit a slight preference for flatter terrain likely to reduce energy expenditure (Shepard et al. 2013), although there is considerable variation in the dataset. Species outside of these trends generally are adapted to living in rugged terrain (e.g., *L. lynx, G. gulo*), or use human landscape features such as fields and plantations for food and shelter (e.g., *Lepus europaeus*, *Vulpes vulpes*, *Capreolus capreolus*). The dominating selection

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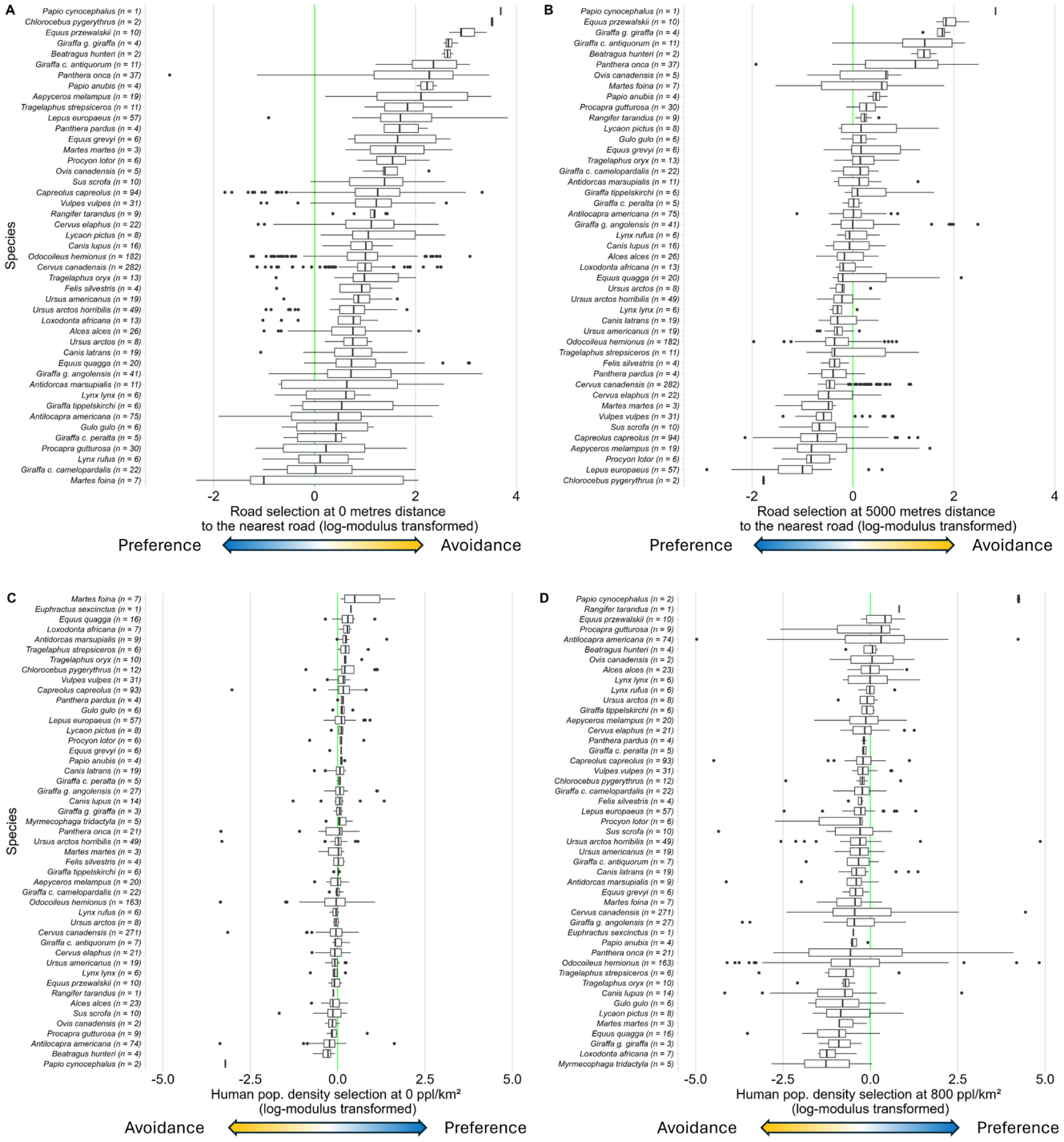

FIGURE 1 | Habitat selection coefficients for distance to the nearest road (A, B), human population density (C, D), and Terrain Ruggedness Index (TRI) (E, F) at low and high step-level availability values for the different species analysed. The number of individuals sampled per species differs between covariates due to gaps in data. The green line indicates a selection coefficient of zero (equivalent to no preference for higher or lower values). Species are ordered by median selection coefficient.

for intermediate NDVI is also in line with previous studies, particularly for herbivores, which often select for areas of intermediate vegetation cover (Prokopenko et al. 2017; Jones et al. 2019).

Further, we show that the species traits included here are not informative for predicting habitat selection at the step-selection scale, likely due to the large amount of intraspecific variation in selection. Instead, we demonstrate that the environmental conditions along the entire track predict habitat selection better than the species traits we included, while the functional response to the track-level environment changes depending on the immediate step-level availability and the habitat variable

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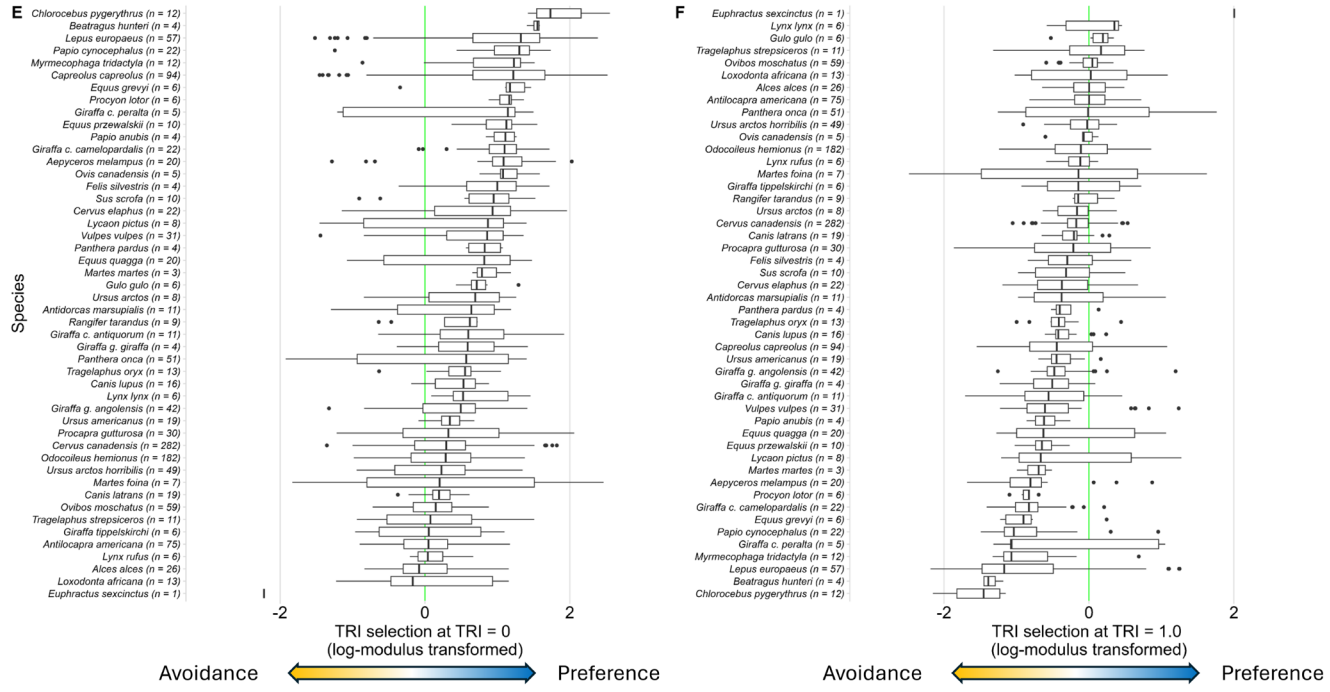

FIGURE 1 | (Continued)

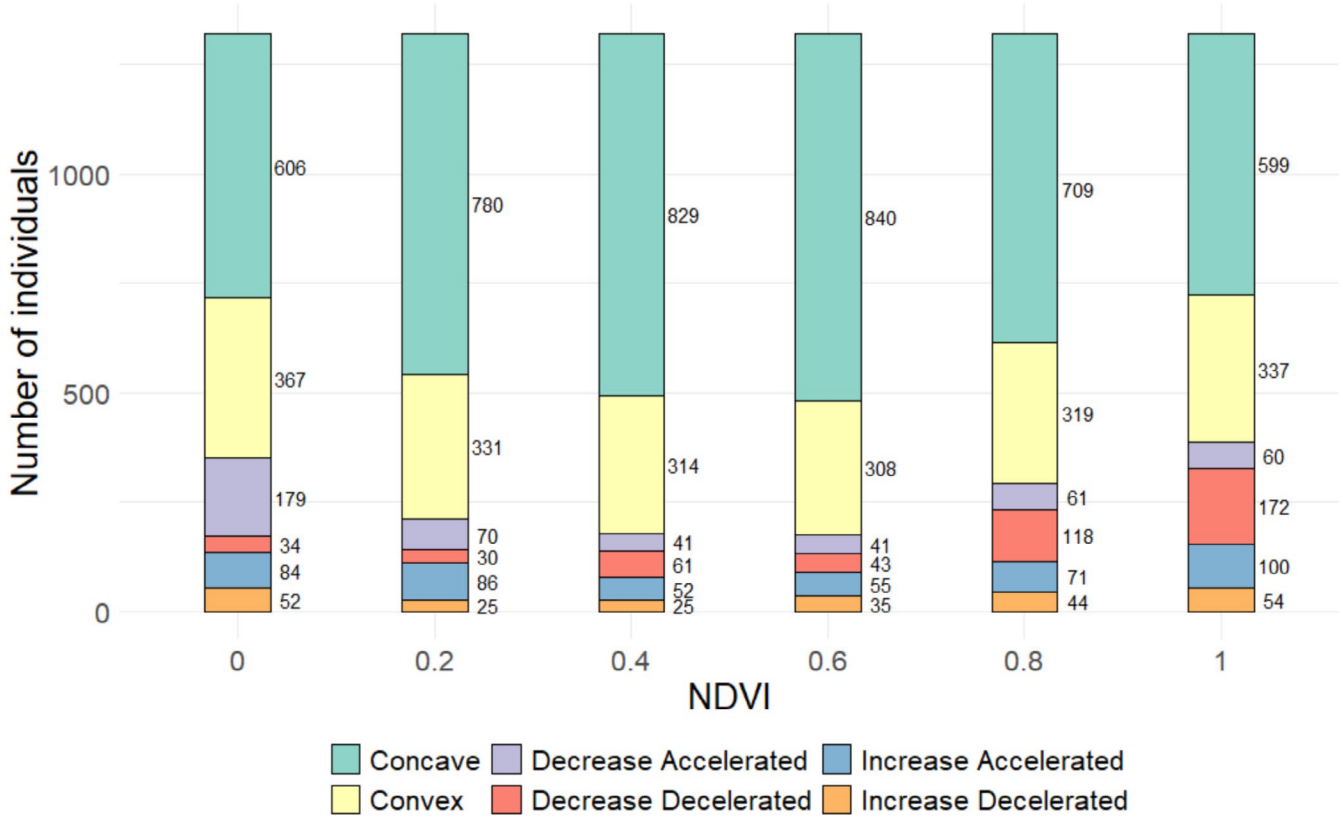

FIGURE 2 | Distribution of Normalised Difference Vegetation Index (NDVI) response curve shapes depending on local (step-level) conditions. Numbers next to the bars indicate the number of individuals with the given response curve shape. Concave curves indicate intermediate selection, convex curves indicate extreme selection, decreasing curves indicate selection for lower NDVI, increasing curves indicate selection for higher NDVI. Total $n = 1322$ individuals with NDVI coefficients. For 21 individuals, NDVI was removed from the step-selection model due to large data gaps or lack of variance (see Section 2).

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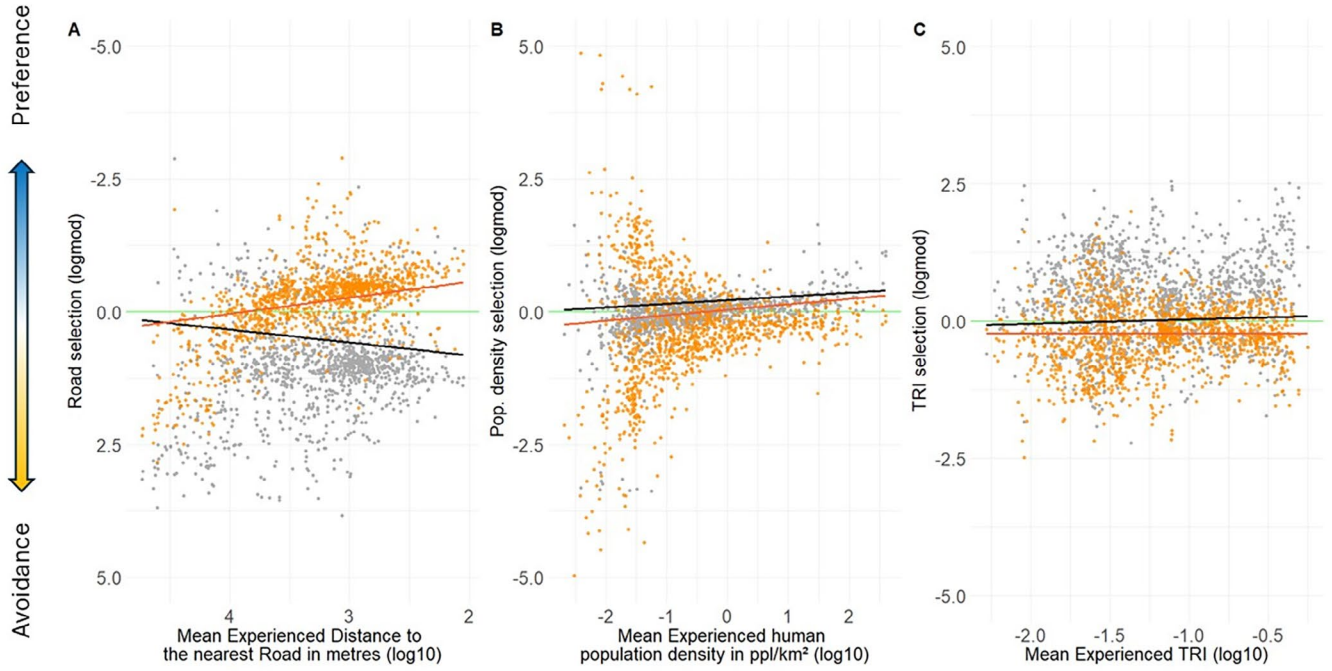

FIGURE 3 | Relationships between track-level availability (mean experienced availability) and unweighted selection coefficients for (A) distance to the nearest road, (B) human population density (C) terrain ruggedness index. Data points are unweighted individual selection coefficients. Coefficients at lowest step-level availability level in dark grey, coefficients at highest step-level availability level in orange. Regression lines show intercept and slope from the best-supported weighted linear mixed-effects model (Table 1). Note that the axes are reversed in (A), where 'high availability' represents large distance to roads, thus the orange line represents selection when far away from a road (i.e., high step-level distance to road), while the black line represents selection when close to a road (i.e., low step-level distance to road).

in question. Interestingly, the role of roads appears to be an exception to this overall finding. Our results show that when animals are in the immediate vicinity of a major road (i.e., at a step-level availability of zero), 78.1% of the variation in selection coefficients is explained. This indicates that immediate barrier effects are very similar across individuals of the same species. These findings support the previously found strong effect of roads on animal behaviour (Barry et al. 2020; Bastianelli et al. 2024) and suggest that the avoidance of human impacts can outweigh all other selection behaviour, which may ultimately affect population survival (Moore et al. 2023). This may be amplified by the frequent association between roads and other types of linear infrastructure, such as fencing, which have been shown to affect populations in similar ways (Jones et al. 2019, 2022).

Our results underline the importance of spatial grain in movement studies. While species traits clearly determine large-scale space use such as home range size and displacement distance (Tucker et al. 2014, 2018; Fauvelle et al. 2017; Noonan et al. 2020), they do not predict habitat selection. Since step-selection coefficients are strongly dependent on the spatial and temporal resolution of the analysis (Avgar et al. 2016; Signer et al. 2017), the patterns identified here may not be observed consistently across all spatiotemporal resolutions. Fisher et al. (2011) demonstrated that there is variation in the spatial grain that best explains habitat selection among species, with the "characteristic" grain being determined by a species' body size. To ensure interspecies comparability, we chose a consistent spatial resolution of the covariates and the step duration interval and tested for autocorrelation in headings to assess whether the overall spatial structure still has an impact on the independence assumptions of the model. While we did not identify major autocorrelation issues, prioritising comparability across species may still play a role in estimating very large coefficients with high uncertainties observed in a few species (e.g., for *Papio cynocephalus*, *Martes foina*). Nevertheless, we are confident that our inverse variance weighting approach has prevented significant influence of these outlier cases on our results, and that the patterns observed across species are robust. We further note that not all levels of step-level availability were experienced by all individuals, so coefficients were extrapolated especially at the higher end of step-level availability values for human population density and distance to the nearest road.

While we show that variation in habitat selection within the covered range is overall more strongly functionally dependent on the immediate environment than species identity, we note that there are additional drivers that will also shape animal movement and selection (also see Shaw 2020). For example, interactions with other organisms affect movements and selection (Ellison et al. 2024), although these are difficult to quantify based on GPS data alone (Potts et al. 2022). Additional traits that may affect habitat selection but could not be included due to limited data availability, include dispersal behaviour, territoriality, sex- or age-based information or more detailed dietary preferences and strategies (see e.g., Esmaeili et al. 2021). These additional factors may contribute to habitat selection on the individual level, making it an emergent property that is shaped by the individual's characteristics and context-dependent decisions, rather than species-level differences in preferences. There could also be additional environmental variables that may better

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capture species-specific ecological niches that we were unable to include here (e.g., microhabitats). Therefore, we do not believe that our findings should be interpreted as a fundamental rejection of the concept of species-level habitat selection, but rather highlight the importance of individual responses to environmental context.

We did not include interactions between different environmental variables as this would inflate the number of parameters to be estimated by the step-selection models beyond the limits of the data. This topic could be explored in future studies, for example, by investigating whether animals select for different NDVI (vegetation productivity) values in areas of higher human pressure, as observed in elk (Prokopenko et al. 2017). Future studies also could address the individual variation that remains unexplained by our modelling approach by focusing on several species tracked simultaneously within the same environment, or comparing different populations of the same species across an environmental gradient. While there is plenty of research on the drivers of intraspecific variation, conducting such studies for a range of species at the same time may confirm and shed further light onto how differences between individuals arise and whether the underlying processes are similar across species.

In conclusion, our results suggest that habitat selection is largely driven by the environment, with considerable intraspecific variation, while generalities such as the avoidance of areas in close proximity of roads can be seen across species. We show that habitat selection changes based on both step-level (local) and track-level (landscape) availability, while species traits alone are not suitable for predicting habitat selection. Overall, our findings shed light on how the environment itself, but also environmental change and anthropogenic activity, may affect the behaviour of species across the globe. Given the current rate of ecological change the world is facing, it is crucial to be able to predict how animals may react (Gomez et al. 2025). The findings presented here show that if data on a particular species are lacking, the environmental variation present in a landscape could still inform possible habitat selection behaviour. Given that step-selection functions parametrise an underlying movement model, which can be applied to simulate animal movement or landscape connectivity in different or changing environments (Avgar et al. 2016; Signer et al. 2017), our findings have the potential to contribute to improved movement modelling approaches that account for environmental availability. In turn, this may help to refine ecosystem models and conservation scenarios for species that lack the required empirical data. Understanding the habitat selection responses of a broader range of species will further strengthen our ability to understand and predict ecological responses to global change as well as aid our efforts to mitigate its adverse effects.

Author Contributions

B.H.F., A.M.S., M.A.J.H. and M.A.T. conceived the manuscript; B.H.F. conducted the analyses; and B.H.F., A.M.S., M.A.J.H. and M.A.T. wrote the first manuscript draft. T.A., L.B., N.C., T.M. and B.J.S. provided additional input on methodology. All authors contributed datasets, key input on the analyses and writing, and gave final approval for publication.

Affiliations

[1]Department of Environmental Science, Radboud Institute of Biological and Environmental Sciences, Radboud University, Nijmegen, the Netherlands | [2]PBL Netherlands Environmental Assessment Agency, The Hague, the Netherlands | [3]Department of Biology, University of British Columbia, Kelowna, British Columbia, Canada | [4]Wildlife Science Center, Biodiversity Pathways Ltd, Edmonton, Alberta, Canada | [5]Department of Biosciences, Swansea University, Swansea, UK | [6]Centre for Biomathematics, Faculty of Sciences and Engineering, Swansea University, Swansea, UK | [7]Senckenberg Biodiversity and Climate Research Centre, Frankfurt am Main, Germany | [8]Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St. Paul, Minnesota, USA | [9]Department of Biological Sciences, Goethe University Frankfurt, Frankfurt, Germany | [10]Department of Wildland Resources and Ecology Center, Utah State University, Logan, Utah, USA | [11]Department of Biology, Center for Ecosystem Sentinels, University of Washington, Seattle, Washington, USA | [12]Botswana Predator Conservation, Wild Entrust, Maun, Botswana | [13]Hirola Conservation Program, Garissa, Kenya | [14]Instituto de Conservação de Animais Silvestres, Campo Grande, Mato Grosso do Sul, Brazil | [15]Structure and Motion Lab, Royal Veterinary College, London, UK | [16]Department of Ecoscience, Aarhus University, Roskilde, Denmark | [17]Department of Fisheries and WIldlife, Michigan State University, East Lansing, Michigan, USA | [18]Department of Plant Ecology and Nature Conservation, University of Potsdam, Potsdam, Germany | [19]Giraffe Conservation Foundation, Windhoek, Namibia | [20]Mongolia Program, Wildlife Conservation Society, Ulaanbaatar, Mongolia | [21]Animal Ecology Unit, Research and Innovation Centre, Fondazione Edmund Mach, Trento, Italy | [22]National Biodiversity Future Centre, Palermo, Italy | [23]CEFE, CNRS, Univ Montpellier, EPHE, IRD, Montpellier, France | [24]LTSER France, Zone Atelier Hwange, Dete, Zimbabwe | [25]Jasja Dekker Dierecologie BV, Arnhem, the Netherlands | [26]Instituto de Pesquisas Ecológicas, IPÊ, São Paulo, Brazil | [27]School of Biology and Environmental Science, University College Dublin, Dublin, Ireland | [28]Faunistics and Wildlife Conservation, Department of Agriculture, Ecotrophology, and Landscape Development, Anhalt University of Applied Sciences, Bernburg, Germany | [29]Compassionate Dude Dog Training, Los Angeles, California, USA | [30]Wildtier Schweiz, Zürich, Switzerland | [31]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland | [32]Department Natural Resource Ecology and Management, Iowa State University, Ames, Iowa, USA | [33]Panthera, New York, New York, USA | [34]Wildlife Biology Program, Franke College of Forestry and Conservation, University of Montana, Missoula, Montana, USA | [35]Ecology/Macroecology, Institute of Biochemistry and Biology, University of Potsdam, Potsdam, Germany | [36]Department of National Park Monitoring and Animal Management, Bavarian Forest National Park, Grafenau, Germany | [37]Faculty of Natural Resources, University of Freiburg, Freiburg, Germany | [38]Université de Toulouse, INRAE, CEFS, Castanet-Tolosan, France | [39]LTSER ZA PYRénées GARonne, Auzeville Tolosane, France | [40]Department of Anthropology and Animal Behavior Graduate Group, University of California, Davis, California, USA | [41]U.S. Geological Survey, Reston, Virginia, USA | [42]Wyoming Migration Initiative and Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, Wyoming, USA | [43]Bionet Natuuronderzoek, Stein, the Netherlands | [44]Alberta Conservation Association, Lethbridge, Alberta, Canada | [45]Ecosensys, Zuurdijk, the Netherlands | [46]Norwegian Institute for Nature Research, Lillehammer, Norway | [47]University of Inland Norway, Koppang, Norway | [48]Department of Anthropology, Stony Brook University, Stony Brook, New York, USA | [49]Applied Behavioural Ecology and Ecosystem Research Unit (ABEERU), Department of Environmental Sciences, University of South Africa, Johannesburg, South Africa | [50]Norwegian Institute for Nature Research, Trondheim, Norway | [51]Commonwealth Scientific and Industrial Research Organisation (CSIRO) Land and Water, Australian Tropical Science and Innovation Precinct, Townsville, Queensland, Australia | [52]Division of Forest and Forest Resources, Norwegian Institute of Bioeconomy

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Research, Tingvoll, Norway | [53]Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada | [54]Embrapa Pantanal, Corumbá, Mato Grosso do Sul, Brazil | [55]Norwegian Institute for Nature Research, Oslo, Norway | [56]Department of Biosciences, Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo, Oslo, Norway | [57]Conservation Ecology Center, Smithsonian National Zoo and Conservation Biology Institute, Front Royal, Virginia, USA | [58]Instituto de Biología Subtropical (IBS), Universidad Nacional de Misiones (UNaM) – CONICET, Puerto Iguazú, Argentina | [59]Asociación Civil Centro de Investigaciones del Bosque Atlántico, Puerto Iguazú, Argentina | [60]Michigan Department of Natural Resources, Marquette, Michigan, USA | [61]Montana Fish, Wildlife & Parks, Bozeman, Montana, USA | [62]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey, USA | [63]Office Français de la Biodiversité, Direction de la Recherche et de L'appui Scientifique, "Montfort", France | [64]Western Ecosystems Technology, Laramie, Wyoming, USA | [65]Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas (CSIC), Sevilla, Spain | [66]Institute of Nature Conservation, Polish Academy of Sciences, Kraków, Poland | [67]Department of Animal Ecology, University of Potsdam, Potsdam, Germany | [68]Guyra Paraguay - CONACYT, Asunción, Paraguay | [69]Instituto Saite, Asunción, Paraguay | [70]Department of Biology, National University of Mongolia, Ulaanbaatar, Mongolia | [71]Institute for Terrestrial and Aquatic Wildlife Research, University of Veterinary Medicine Hannover, Foundation, Hannover, Germany | [72]Tatra National Park, Zakopane, Poland

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Disclosure

Statement of inclusion: This study draws on existing datasets collected from a wide range of global regions. All data providers are included as co-authors and were given the opportunity to contribute their perspectives and contextual knowledge. Our author team includes researchers from both Global South and Global North institutions, reflecting the diverse origins of the data and promoting equitable collaboration. We recognise that ecological research conducted in the Global South is often disproportionately led by Global North institutions, and we are committed to acknowledging and addressing such structural biases in future research.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data reported in this paper is available at Zenodo, https://zenodo.org/records/15756163. This includes the iSSA input data and the analysis code.

References

Avgar, T., J. R. Potts, M. A. Lewis, M. S. Boyce, and L. Börger. 2016. "Integrated Step Selection Analysis: Bridging the Gap Between Resource Selection and Animal Movement." *Methods in Ecology and Evolution* 7, no. 5: 619–630. https://doi.org/10.1111/2041-210x.12528.

Barry, T., E. Gurarie, F. Cheraghi, I. Kojola, and W. F. Fagan. 2020. "Does Dispersal Make the Heart Grow Bolder? Avoidance of Anthropogenic Habitat Elements Across Wolf Life History." *Animal Behaviour* 166: 219–231. https://doi.org/10.1016/j.anbehav.2020.06.015.

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Barton, K., and M. K. Barton. 2015. "Package 'Mumin'." Version, 1(18), 439.

Bastianelli, M. L., C. von Hoermann, K. Kirchner, et al. 2024. "Risk Response Towards Roads Is Consistent Across Multiple Species in a Temperate Forest Ecosystem." *Oikos* 2024, no. 7: e10433. https://doi.org/10.1111/oik.10433.

Bates, D., M. Maechler, B. Bolker, et al. 2015. "Package 'lme4'." Convergence, 12(1), 2.

Bauer, S., and B. J. Hoye. 2014. "Migratory Animals Couple Biodiversity and Ecosystem Functioning Worldwide." *Science* 344, no. 6179: 1242552. https://doi.org/10.1126/science.1242552.

Benson-Amram, S., B. Dantzer, G. Stricker, E. M. Swanson, and K. E. Holekamp. 2016. "Brain Size Predicts Problem-Solving Ability in Mammalian Carnivores." *Proceedings of the National Academy of Sciences of the United States of America* 113, no. 9: 2532–2537.

Burton, A. C., C. Beirne, K. M. Gaynor, et al. 2024. "Mammal Responses to Global Changes in Human Activity Vary by Trophic Group and Landscape." *Nature Ecology & Evolution* 8, no. 5: 924–935. https://doi.org/10.1038/s41559-024-02363-2.

de Jonge, M. M. J., J. Gallego-Zamorano, M. A. J. Huijbregts, A. M. Schipper, and A. Benítez-López. 2022. "The Impacts of Linear Infrastructure on Terrestrial Vertebrate Populations: A Trait-Based Approach." *Global Change Biology* 28, no. 24: 7217–7233. https://doi.org/10.1111/gcb.16450.

Dellinger, J. A., C. Proctor, T. D. Steury, M. J. Kelly, and M. R. Vaughan. 2013. "Habitat Selection of a Large Carnivore, the Red Wolf, in a Human-Altered Landscape." *Biological Conservation* 157: 324–330. https://doi.org/10.1016/j.biocon.2012.09.004.

Dodge, S., G. Bohrer, R. Weinzierl, et al. 2013. "The Environmental-Data Automated Track Annotation (Env-DATA) System: Linking Animal Tracks With Environmental Data." *Movement Ecology* 1: 1–14.

Doherty, T. S., G. C. Hays, and D. A. Driscoll. 2021. "Human Disturbance Causes Widespread Disruption of Animal Movement." *Nature Ecology & Evolution* 5, no. 4: 513–519. https://doi.org/10.1038/s41559-020-01380-1.

Ellison, N., J. R. Potts, M. R. Boudreau, L. Börger, B. K. Strickland, and G. M. Street. 2024. "Social Interactions and Habitat Structure in Understanding the Dynamic Space Use of Invasive Wild Pigs." *Wildlife Biology* 2024, no. 5: e01247.

Esmaeili, S., B. R. Jesmer, S. E. Albeke, et al. 2021. "Body Size and Digestive System Shape Resource Selection by Ungulates: A Cross-Taxa Test of the Forage Maturation Hypothesis." *Ecology Letters* 24, no. 10: 2178–2191. https://doi.org/10.1111/ele.13848.

Fagan, W. F., M. A. Lewis, M. Auger-Méthé, et al. 2013. "Spatial Memory and Animal Movement." *Ecology Letters* 16, no. 10: 1316–1329. https://doi.org/10.1111/ele.12165.

Fauvelle, C., R. Diepstraten, and T. Jessen. 2017. "A Meta-Analysis of Home Range Studies in the Context of Trophic Levels: Implications for Policy-Based Conservation." *PLoS One* 12, no. 3: e0173361.

Fisher, J. T., B. Anholt, and J. P. Volpe. 2011. "Body Mass Explains Characteristic Scales of Habitat Selection in Terrestrial Mammals." *Ecology and Evolution* 1, no. 4: 517–528.

Gil-Sánchez, J. M., F. J. Herrera-Sánchez, J. Rodríguez-Siles, et al. 2025. "Body Size Rules Habitat Selection and Population Declines After Drought Periods in a Carnivore Community of the Sahara Desert." *Mammalian Biology* 105, no. 1: 69–81. https://doi.org/10.1007/s42991-024-00461-z.

Gomez, S., H. M. English, V. Bejarano Alegre, et al. 2025. "Understanding and Predicting Animal Movements and Distributions in the Anthropocene." *Journal of Animal Ecology* 94: 1146–1164.

Hirt, M. R., A. D. Barnes, A. Gentile, et al. 2021. "Environmental and Anthropogenic Constraints on Animal Space Use Drive Extinction Risk Worldwide." *Ecology Letters* 24, no. 12: 2576–2585.

Hollister, J., T. Shah, A. L. Robitaille, M. W. Beck, and M. Johnson. 2017. "elevatr: Access Elevation Data From Various APIs." R package version 0.1, 3.

John, J., and N. R. Draper. 1980. "An Alternative Family of Transformations." *Applied Statistics* 29, no. 2: 190–197.

Jones, P. F., A. F. Jakes, A. C. Telander, H. Sawyer, B. H. Martin, and M. Hebblewhite. 2019. "Fences Reduce Habitat for a Partially Migratory Ungulate in the Northern Sagebrush Steppe." *Ecosphere* 10, no. 7: e02782.

Jones, P. F., A. F. Jakes, S. E. Vegter, and M. S. Verhage. 2022. "Is It the Road or the Fence? Influence of Linear Anthropogenic Features on the Movement and Distribution of a Partially Migratory Ungulate." *Movement Ecology* 10, no. 1: 37. https://doi.org/10.1186/s40462-022-00336-3.

Maher, S. M., K. J. Barker, K. Kroetz, V. Butsic, B. Leonard, and A. D. Middleton. 2023. "Assessing the Ecosystem Services and Disservices Provided by Migratory Wildlife Across the Greater Yellowstone Ecosystem." *Biological Conservation* 283: 110090.

Martin, J., G. Vourc'h, N. Bonnot, et al. 2018. "Temporal Shifts in Landscape Connectivity for an Ecosystem Engineer, the Roe Deer, Across a Multiple-Use Landscape." *Landscape Ecology* 33: 937–954.

Marneweck, C. J., M. B. Brown, S. Fennessy, et al. 2024. "The Evolution of Tracking Technology for Wild Giraffe (*Giraffa* spp.)." *African Journal of Wildlife Research* 54, no. 1: 46–68.

Mason, T. H., and D. Fortin. 2017. "Functional Responses in Animal Movement Explain Spatial Heterogeneity in Animal–Habitat Relationships." *Journal of Animal Ecology* 86, no. 4: 960–971.

Moore, L. J., S. O. Petrovan, A. J. Bates, et al. 2023. "Demographic Effects of Road Mortality on Mammalian Populations: A Systematic Review." *Biological Reviews* 98, no. 4: 1033–1050. https://doi.org/10.1111/brv.12942.

Mysterud, A., and R. A. Ims. 1998. "Functional Responses in Habitat Use: Availability Influences Relative Use in Trade-Off Situations." *Ecology* 79, no. 4: 1435–1441.

Nakagawa, S., and H. Schielzeth. 2010. "Repeatability for Gaussian and Non-Gaussian Data: A Practical Guide for Biologists." *Biological Reviews* 85, no. 4: 935–956. https://doi.org/10.1111/j.1469-185X.2010.00141.x.

Nathan, R., W. M. Getz, E. Revilla, et al. 2008. "A Movement Ecology Paradigm for Unifying Organismal Movement Research." *Proceedings of the National Academy of Sciences of the United States of America* 105, no. 49: 19052–19059. https://doi.org/10.1073/pnas.0800375105.

Nelder, J. A., and R. Mead. 1965. "A Simplex Method for Function Minimization." *Computer Journal* 7, no. 4: 308–313.

Nellemann, C., and G. Fry. 1995. "Quantitative-Analysis of Terrain Ruggedness in Reindeer Winter Grounds." *Arctic* 48, no. 2: 172–176. <Go to ISI>://WOS:A1995RF80000008.

Noonan, M. J., C. H. Fleming, M. A. Tucker, et al. 2020. "Effects of Body Size on Estimation of Mammalian Area Requirements." *Conservation Biology* 34, no. 4: 1017–1028. https://doi.org/10.1111/cobi.13495.

Omondi, G. P., F. Gakuya, J. Arzt, et al. 2020. "The Role of African Buffalo in the Epidemiology of Foot-and-Mouth Disease in Sympatric Cattle and Buffalo Populations in Kenya." *Transboundary and Emerging Diseases* 67, no. 5: 2206–2221.

Panzacchi, M., B. Van Moorter, O. Strand, L. E. Loe, and E. Reimers. 2015. "Searching for the Fundamental Niche Using Individual-Based Habitat Selection Modelling Across Populations." *Ecography* 38, no. 7: 659–669. https://doi.org/10.1111/ecog.01075.

Pettorelli, N., S. Ryan, T. Mueller, et al. 2011. "The Normalized Difference Vegetation Index (NDVI): Unforeseen Successes in Animal

14668238, 2026, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70212 by University Of California - Davis, Wiley Online Library on [24/03/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Ecology." *Climate Research* 46, no. 1: 15–27. https://doi.org/10.3354/cr00936.

Potts, J. R., L. Börger, B. K. Strickland, and G. M. Street. 2022. "Assessing the Predictive Power of Step Selection Functions: How Social and Environmental Interactions Affect Animal Space Use." *Methods in Ecology and Evolution* 13: 1805–1818. https://doi.org/10.1111/2041-210X.13904.

Prokopenko, C. M., M. S. Boyce, and T. Avgar. 2017. "Characterizing Wildlife Behavioural Responses to Roads Using Integrated Step Selection Analysis." *Journal of Applied Ecology* 54, no. 2: 470–479.

Raffalovich, L. E., G. D. Deane, D. Armstrong, and H.-S. Tsao. 2008. "Model Selection Procedures in Social Research: Monte-Carlo Simulation Results." *Journal of Applied Statistics* 35, no. 10: 1093–1114.

Rosenheim, J. A. 2004. "Top Predators Constrain the Habitat Selection Games Played by Intermediate Predators and Their Prey." *Israel Journal of Zoology* 50, no. 2–3: 129–138. https://doi.org/10.1560/K796-DMB2-546Q-Y4AQ.

Shaw, A. K. 2020. "Causes and Consequences of Individual Variation in Animal Movement." *Movement Ecology* 8, no. 1: 12.

Shepard, E. L., R. P. Wilson, W. G. Rees, E. Grundy, S. A. Lambertucci, and S. B. Vosper. 2013. "Energy Landscapes Shape Animal Movement Ecology." *American Naturalist* 182, no. 3: 298–312.

Signer, J., J. Fieberg, and T. Avgar. 2017. "Estimating Utilization Distributions From Fitted Step-Selection Functions." *Ecosphere* 8, no. 4: e01771. https://doi.org/10.1002/ecs2.1771.

Signer, J., J. Fieberg, and T. Avgar. 2019. "Animal Movement Tools (Amt): R Package for Managing Tracking Data and Conducting Habitat Selection Analyses." *Ecology and Evolution* 9, no. 2: 880–890.

Soria, C. D., M. Pacifici, M. Di Marco, S. M. Stephen, and C. Rondinini. 2021. "COMBINE: A Coalesced Mammal Database of Intrinsic and Extrinsic Traits." *Ecology* 102, no. 6: e03344. https://doi.org/10.1002/ecy.3344.

Stiegler, J., C. A. Gallagher, R. Hering, et al. 2024. "Mammals Show Faster Recovery From Capture and Tagging in Human-Disturbed Landscapes." *Nature Communications* 15, no. 1: 8079.

Taylor, C. R., S. L. Caldwell, and V. Rowntree. 1972. "Running Up and Down Hills: Some Consequences of Size." *Science* 178, no. 4065: 1096–1097.

Tucker, M. A., K. Bohning-Gaese, W. F. Fagan, et al. 2018. "Moving in the Anthropocene: Global Reductions in Terrestrial Mammalian Movements." *Science* 359, no. 6374: 466–469. https://doi.org/10.1126/science.aam9712.

Tucker, M. A., M. Busana, M. A. Huijbregts, and A. T. Ford. 2021. "Human-Induced Reduction in Mammalian Movements Impacts Seed Dispersal in the Tropics." *Ecography* 44, no. 6: 897–906.

Tucker, M. A., T. J. Ord, and T. L. Rogers. 2014. "Evolutionary Predictors of Mammalian Home Range Size: Body Mass, Diet and the Environment." *Global Ecology and Biogeography* 23, no. 10: 1105–1114. https://doi.org/10.1111/geb.12194.

Tucker, M. A., A. M. Schipper, T. S. F. Adams, et al. 2023. "Behavioral Responses of Terrestrial Mammals to COVID-19 Lockdowns." *Science* 380, no. 6649: 1059–1064. https://doi.org/10.1126/science.abo6499.

Upham, N. S., J. A. Esselstyn, and W. Jetz. 2019. "Inferring the Mammal Tree: Species-Level Sets of Phylogenies for Questions in Ecology, Evolution, and Conservation." *PLoS Biology* 17, no. 12: e3000494.

Van Moorter, B., C. M. Rolandsen, M. Basille, and J.-M. Gaillard. 2016. "Movement Is the Glue Connecting Home Ranges and Habitat Selection." *Journal of Animal Ecology* 85, no. 1: 21–31. https://doi.org/10.1111/1365-2656.12394.

Wilson, M. W., A. D. Ridlon, K. M. Gaynor, S. D. Gaines, A. C. Stier, and B. S. Halpern. 2020. "Ecological Impacts of Human-Induced Animal Behaviour Change." *Ecology Letters* 23, no. 10: 1522–1536. https://doi.org/10.1111/ele.13571.

WorldPop (www.worldpop.org – School of Geography and Environmental Science, University of Southampton; Department of Geography and Geosciences, University of Louisville; Departement de Geographie, Universite de Namur) and Center for International Earth Science Information Network (CIESIN), Columbia University. 2018. "Global High Resolution Population Denominators Project – Funded by The Bill and Melinda Gates Foundation (OPP1134076)." https://doi.org/10.5258/SOTON/WP00644.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** geb70212-sup-0001-DataS1.docx.

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