

How does human activity affect the movement patterns of wild animals?

An analysis of selected datasets from the Movebank animal tracking database

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1 Abstract

We investigate how human activity influences the movement patterns of wild animals. Using tracking data from red foxes and coyotes across rural and remote areas in England, Canada, and the US, we analyze home range sizes and habitat selection in relation to human footprint and land cover.

2 Introduction

Disturbance by humans has widespread impacts on the movements of animals, as confirmed by a large-scale meta study Doherty, Hays, and Driscoll (2021). In this paper, two related research questions are addressed:

1. Home range size implications: Do animals exhibit smaller home ranges in high human impact areas?
This is examined by comparing red fox (*vulpes vulpes*) home ranges in low and high human impact areas.
2. Habitat selection in human-influenced landscapes: How do animals select habitats under varying levels of human presence? This is analysed based on bobcat (*lynx rufus*) and coyote (*canis latrans*) data from a national park area.

Together, these analyses allow us to evaluate both large-scale home range adjustments and fine-scale habitat preferences in response to human activity.

3 Data and methods

3.1 Datasets

We analyzed four animal tracking datasets obtained from the Movebank database Kays et al. (2022), including red fox (*Vulpes vulpes*) tracks from Wiltshire, UK Porteus et al. (2024), Bylot Island, Canada, and Herschel Island, Canada Lai et al. (2022), as well as bobcat (*Lynx rufus*) and coyote (*Canis latrans*) tracks from northeastern Washington, USA Prugh et al. (2023). The tracking data varied in temporal resolution and geographic context, with sample sizes and data characteristics summarized in Table 1.

Table 1: Summary of animal tracking datasets used in the analysis.

Dataset	Species	Years	Individuals	Sampling interval	Total fixes
Wiltshire	Red fox	2016–2019	35	10–60 min	146072
Bylot	Red fox	2011–2015	2	1/day (afternoon)	2086
Herschel	Red fox	2009–2010	2	1/day (afternoon)	223
Washington	Coyote	2014–2015	34	4-hour programmed	72893
Washington	Bobcat	2014–2015	36	4-hour programmed	48813

In addition to movement data, we used global covariate datasets: the 2020 global terrestrial Human Footprint Index (HFP-100) at 100 m resolution (Gassert et al. 2023), and the ESA WorldCover 2021 land cover dataset at 10 m resolution (Zanaga et al. 2022).

Detailed descriptions of data preprocessing, filtering, and acquisition procedures are provided in the [supplementary material](#).

3.2 Exploratory data assessment

3.2.1 Red fox

Data from Wiltshire (Figure 1) were collected between 2016 to 2019 during the UK wader nesting season, defined as March 15th to June 15th, for a total of 35 foxes. Locations were recorded every 10 to 60 minutes, with the sampling rate remotely reduced during periods deemed less informative to conserve battery.

Data from Fig. 2A and Fig. 2B were collected year-round, at a lower sampling rate of once per day at random afternoon times.

Data from Bylot (Figure 2a) and Herschel (Figure 2b) were collected year-round, at a lower sampling rate of once per day at random afternoon times. Data collection spanned 2009–2010 for Herschel and 2011–2015 for Bylot, with two foxes monitored per island. Figure 3a

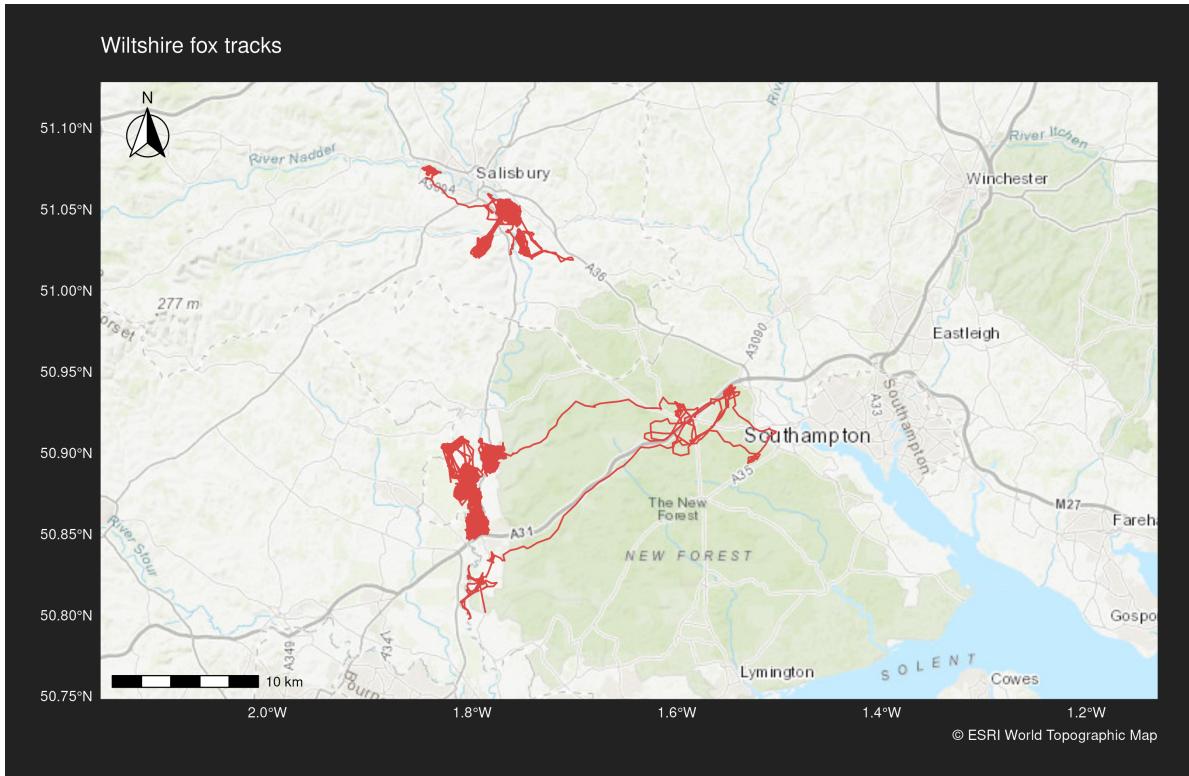
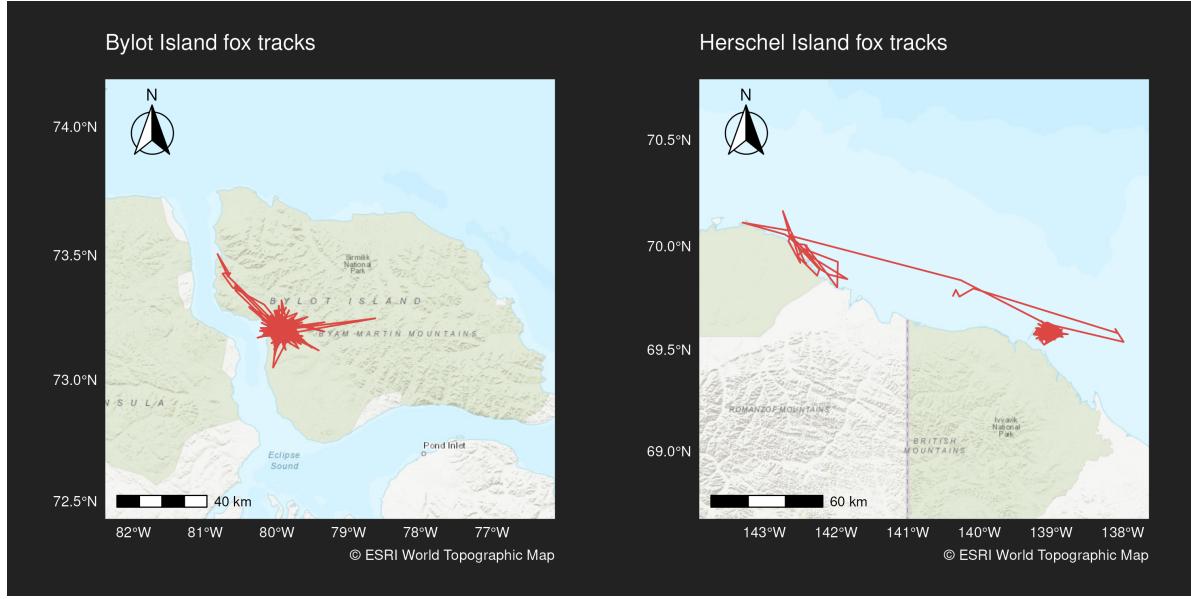


Figure 1: High level view of animal GPS tracks in Wiltshire.



(a) Bylot island (11.067 km²)

(b) Herschel island (116 km²)

Figure 2: Maps of Bylot and Herschel island, with high level view of animal GPS tracks.

shows annual data availability, highlighting the much larger dataset from Wiltshire due to more animals and higher sampling frequency. Monthly patterns Figure 3b reveal seasonal differences in data availability.

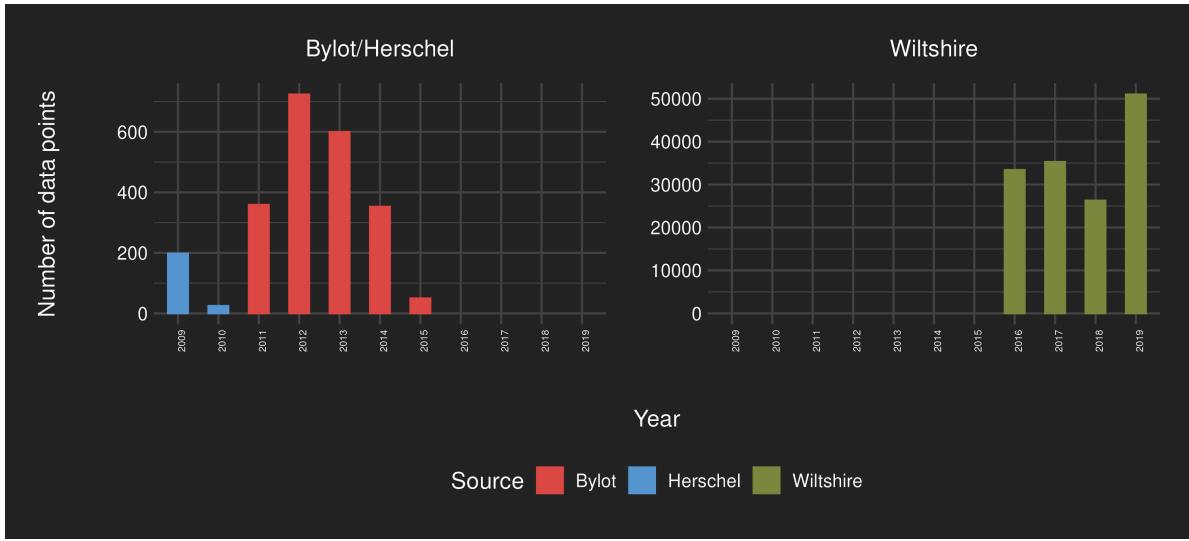
3.2.2 Bobcat and coyote

Coyote and bobcat GPS were collected in northeastern Washington between 2014 and 2015, with collars programmed to record locations every four hours. The two species occupied two distinct geographic areas with overlapping but species-specific home ranges Figure 4, shown in relation to land cover data. Human footprint was generally low across the study area, except for localized settlements and roads Figure 5.

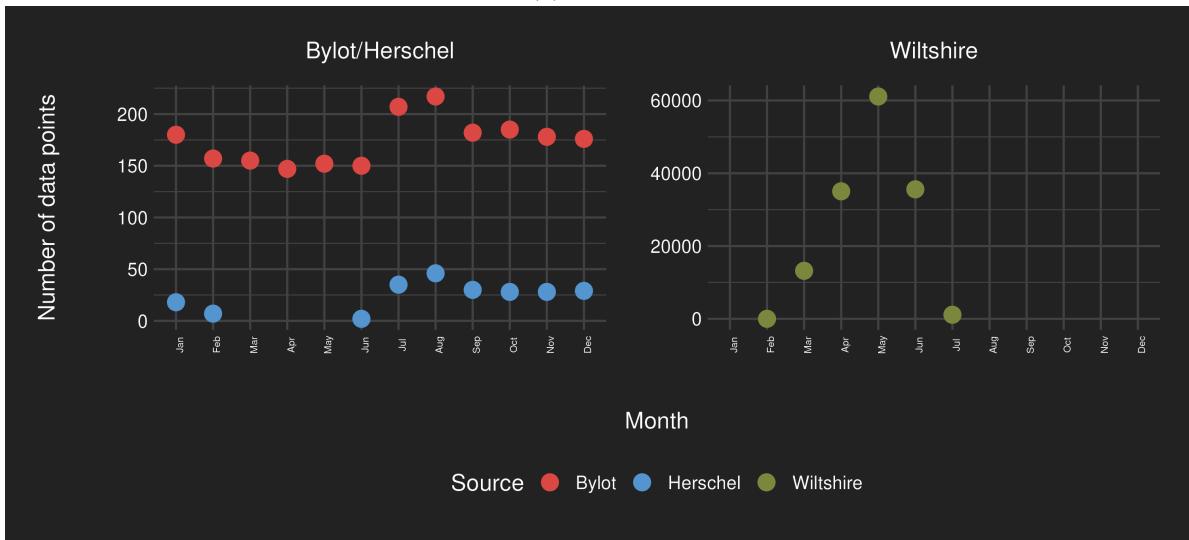
Although collars were programmed for regular sampling, actual intervals were irregular, with substantial variation, especially among bobcats. Sampling interval distributions are shown in Figure 6.

3.3 Analytical methods

We applied two analytical approaches: (1) home range estimation for red foxes and (2) habitat selection modeling using step-selection functions for coyotes.



(a) Per year



(b) Per month

Figure 3: Amount of data per year and month.

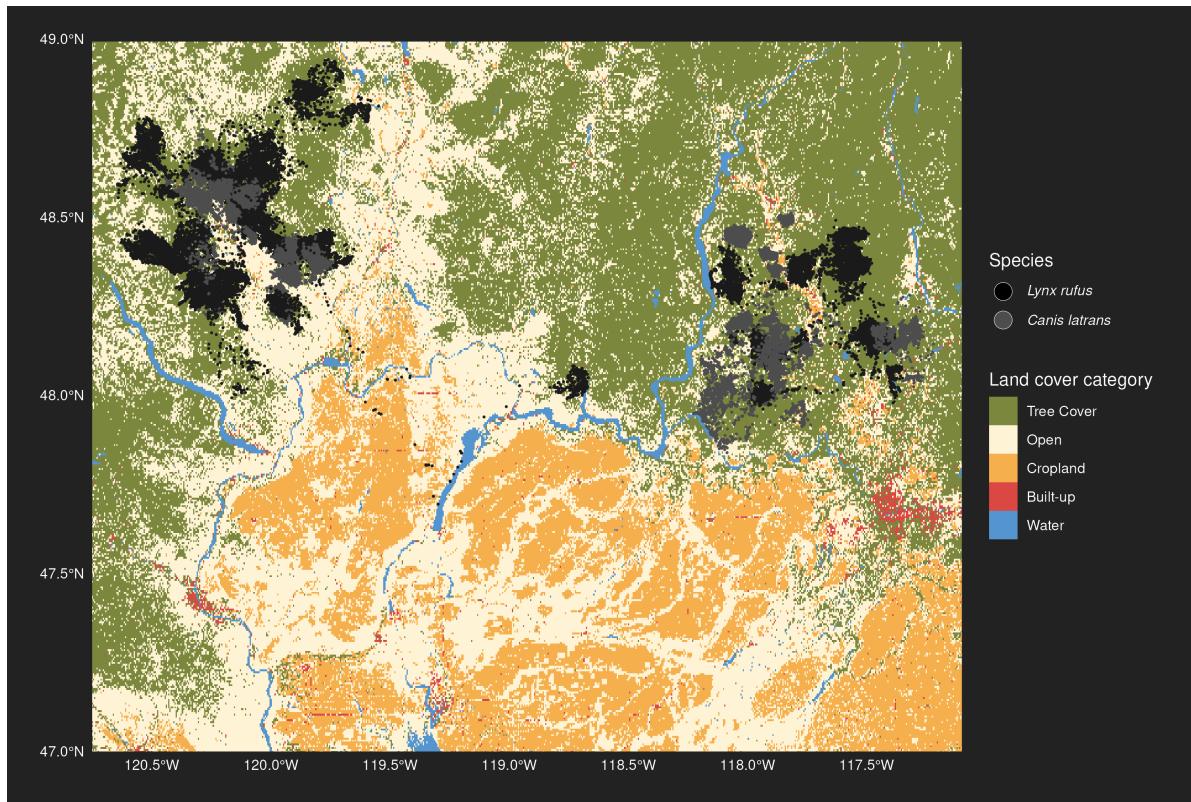


Figure 4: Bobcat and coyote locations in the context of the land cover data.

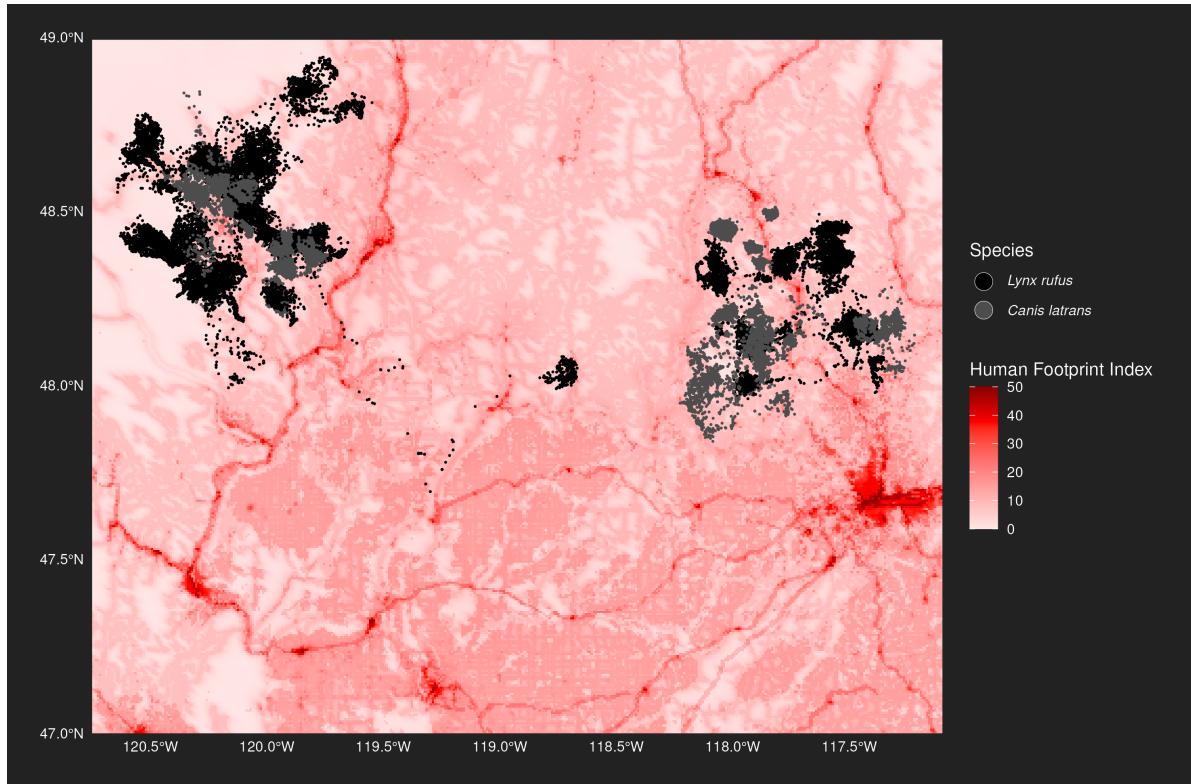
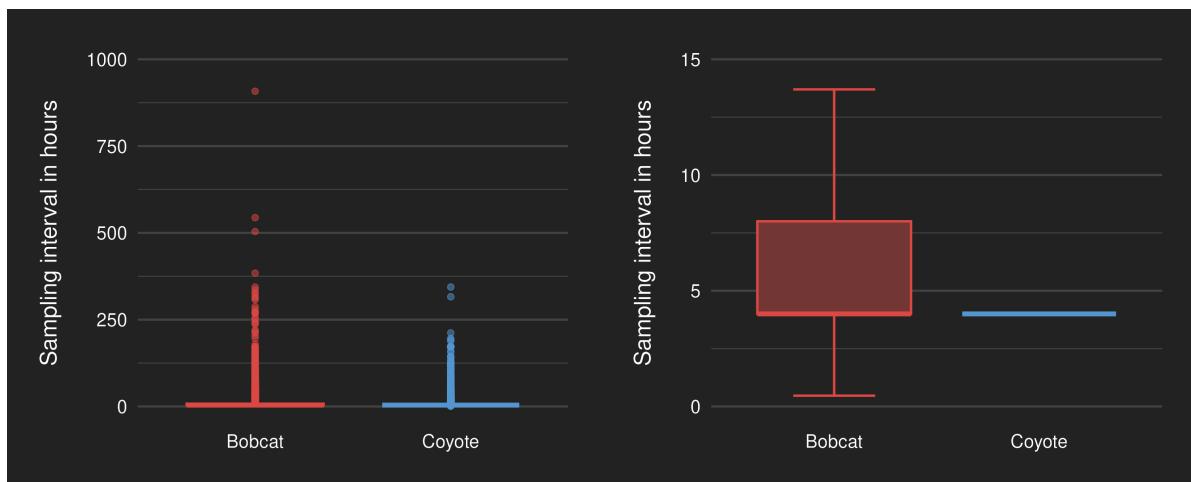


Figure 5: Bobcat and coyote locations overlaid on human footprint index (0 = wilderness; 50 = highly urbanized).



(a) With outliers

(b) With outliers removed

Figure 6: Box plots of sampling rates for bobcat and coyote data.

3.3.1 Home range size assessment

We estimated home range sizes using minimum convex polygons (MCP), providing standardized, comparable measures of space use across individuals. However, differences in temporal scale between the datasets posed challenges for comparability. The Wiltshire data were sampled at 10–60 minute intervals, while the Bylot and Herschel datasets were sampled once daily. Additionally, data coverage varied across seasons and years, and sample sizes differed substantially.

These discrepancies introduce potential biases in home range estimation Laube and Purves (2011). To mitigate these effects, we employed three strategies:

1. We limited analyses to the same seasonal period (March 15th – June 15th) across datasets to control for seasonal variation. Due to limited data from Herschel Island (Figure 3b) for that timeframe, we focused comparative analyses on the Wiltshire and Bylot datasets.
2. We generated a downsampled Wiltshire dataset by selecting a random daily location per individual, matching the lower sampling frequency of the Arctic datasets.
3. We computed monthly home ranges for all datasets to explore temporal variation.

3.3.2 Habitat selection modeling

To model fine-scale habitat preferences, we used step-selection functions (SSFs) Fortin et al. (2005). These compare environmental attributes at “used” locations to those at randomly sampled “available” locations along the animal’s movement path. This allows to quantify how animals respond to environmental covariates, such as human footprint and land cover. Selection patterns are then compared to assess how habitat preferences vary with human influence.

3.3.2.1 Step Generation and Covariates

Coyote and bobcat GPS tracks Prugh et al. (2023) were irregularly spaced (Figure 6b) and were resampled for temporal consistency — coyotes to 4-hour intervals and bobcats to 8-hour intervals, both with a 10-minute tolerance - using the `amt::track_resample` function Signer, Fieberg, and Avgar (2019). Steps were then generated using the `amt::steps_by_burst` and `amt::random_steps` functions. For each used step, ten random available steps were generated based on empirical step length (gamma distribution) and turning angle (Von Mises distribution). Log-transformed step lengths were calculated for modeling to account for potential bias in the availability distribution.

Each observed step and its corresponding random steps were grouped into strata using a unique step ID, following a matched case-control design Prugh et al. (2023). Habitat covariates (land cover and human footprint) were extracted for each step endpoint.

Land cover was reclassified into five ecologically meaningful categories to improve interpretability and model convergence (Table 2). Human footprint index (HFP) values were standardized across the dataset for modeling.

Table 2: Reclassification of ESA WorldCover classes into five ecologically meaningful categories.

New class	Description	Used original classes
TreeCover	Tree-dominated areas (>10% cover)	Tree Cover
Open	Open natural or low-intensity land use	Grassland, Bare/sparse vegetation, Moss & lichen
Cropland	Intensive agricultural areas	Cropland
BuiltUp	Developed areas with infrastructure	Built-up
Water	Aquatic & semi-aquatic environments	Permanent water bodies, Herbaceous wetland

Refer to the [ESA WorldCover user manual](#) for detailed original class definitions.

To assess the distribution of human footprint across land cover types, we visualized the HFP values at used locations using a ridgeline density plot (Figure 7). The figure illustrates that TreeCover was generally associated with lower human footprint, while BuiltUp and Cropland had higher HFP values, supporting the relevance of the interaction terms in our model. As a complementary visualization to the ridgeline plot, we include a boxplot in the Appendix showing the spread of human footprint values across land cover types (Figure 14).

To explore the relationship between movement behavior and human disturbance, we visualized the joint distribution of the Human Footprint Index (HFP) and log-transformed step length using a hexbin density plot (Figure 8). Most steps occurred under conditions of low human footprint and were characterized by short to moderate movement distances. By including log-transformed step length as a covariate, the model accounts for underlying variation in movement intensity that could otherwise confound habitat selection estimates.

3.3.2.2 Statistical model

Step selection functions (SSFs) are commonly modeled using conditional logistic regression, which compares observed and available steps within matched strata (e.g., `survival::clogit`; Manly et al. (2007)). However, for datasets involving multiple individuals, this approach can be limiting in terms of flexibility. Since conditional logistic regression is likelihood-equivalent to a Poisson regression model with stratum-specific fixed intercepts, these can be treated as random effects with a large fixed variance Muff, Signer, and Fieberg (2020). By treating these

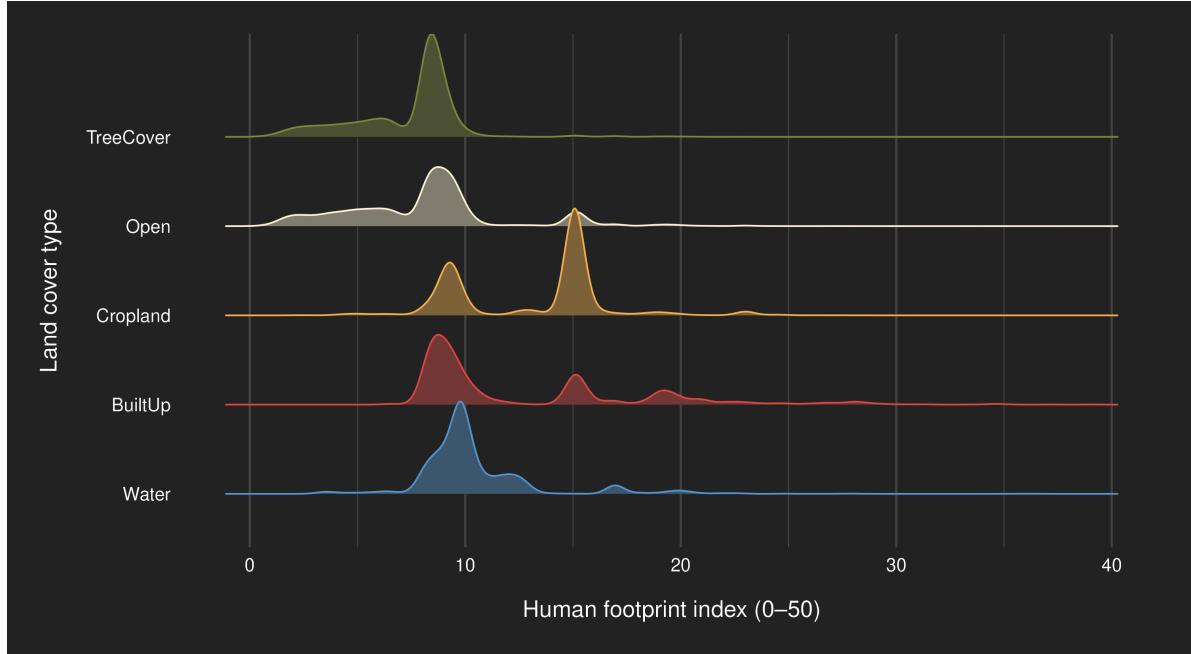


Figure 7: Ridgeline density plot of human footprint index across land cover types at used locations.

intercepts as random effects with a large fixed variance, the model can be reformulated as a generalized linear mixed-effects model (GLMM), allowing for the inclusion of random slopes to account for individual variation in habitat selection.

Following this framework, we modeled habitat selection in relation to human impact using a Poisson GLMM with a log link, implemented via `glmmTMB::glmmTMB`. Stratum-specific intercepts (one per `step_id_`) were modeled as random effects with a fixed, large variance to approximate the conditional logistic structure, enabling the inclusion of individual-level random slopes and better capturing heterogeneity in selection behavior.

The fixed effects included a two-way interaction between land cover class and both the linear and quadratic terms of standardized human footprint, as well as the natural logarithm of step length (`log_s1_`) to control for movement bias. Human footprint index (HFP) values were standardized before modeling.

The model can be expressed as:

$$\log(\lambda_{ij}) = \beta_1 \cdot LC_{ij} + \beta_2 \cdot HFP_{ij} + \beta_3 \cdot HFP_{ij}^2 + \beta_4 \cdot \ln(SL_{ij}) + b_{0,step(i,j)} + u_i$$

where:

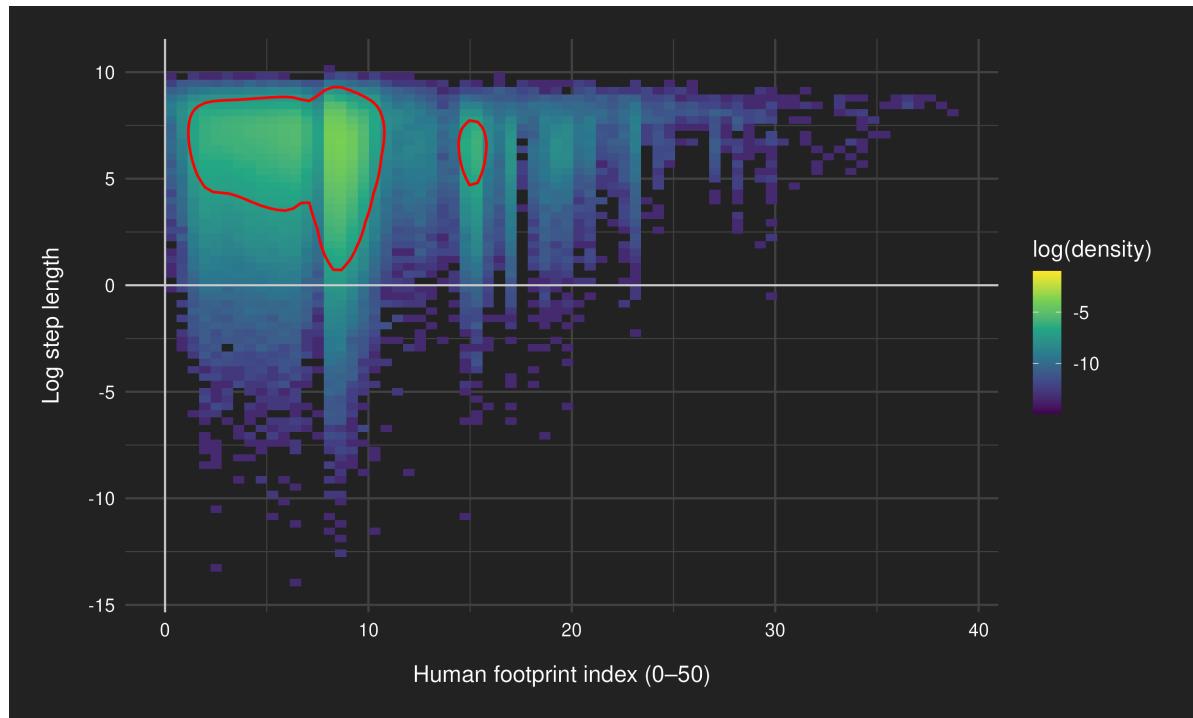


Figure 8: Joint distribution of human footprint index and log-transformed step length for coyotes, with the red contour marking the 95% density region.

- λ_{ij} is the expected relative selection strength for step j of individual i ,
- LC_{ij} is the land cover class,
- HFP_{ij} is the standardized human footprint value,
- SL_{ij} is the step length,
- $b_{0,\text{step}(i,j)}$ is a random intercept for each stratum (`step_id_`),
- u_i represents individual-level random slopes.

Interaction terms between land cover and human footprint (both linear and quadratic) were also included but are omitted here for clarity.

Following model fitting, we used average marginal effects and relative selection strength (RSS) to visualize how habitat selection varied across the human footprint gradient. These metrics were computed from the fitted model to provide an interpretable measure of selection intensity.

3.3.2.3 Bobcat data exclusion

We initially attempted SSF modeling for bobcats, but excluded them from the final analysis due to insufficient sample sizes across land cover types and irregular sampling intervals. These issues led to poor model convergence and biologically implausible estimates. Only two land cover classes remained after filtering, limiting ecological interpretability. As a result, SSF analysis was conducted only for coyotes.

4 Results

4.1 Fox home ranges

Fox home ranges during the time period corresponding to the UK wader nesting season are visualized as proportional circles in Figure 9, providing a comparative overview of median range sizes across Bylot and Wiltshire. Individual home range areas are further summarized in Figure 10, where each point represents one animal's estimated range size. The median home range in Bylot (75.3 km²) was over 65 times larger than in Wiltshire (1.1 km²). When subsampling the Wiltshire data to a 24-hour interval, the median home range decreased to 0.56 km².

Similar differences in order of magnitude between remote and rural fox home ranges can also be observed for the monthly home range results Figure 11. Outliers are removed, in particular the irregular data for Herschel (as seen in Figure 2b).



Figure 9: Geographic comparison of median red fox home range sizes in Bylot and Wiltshire.

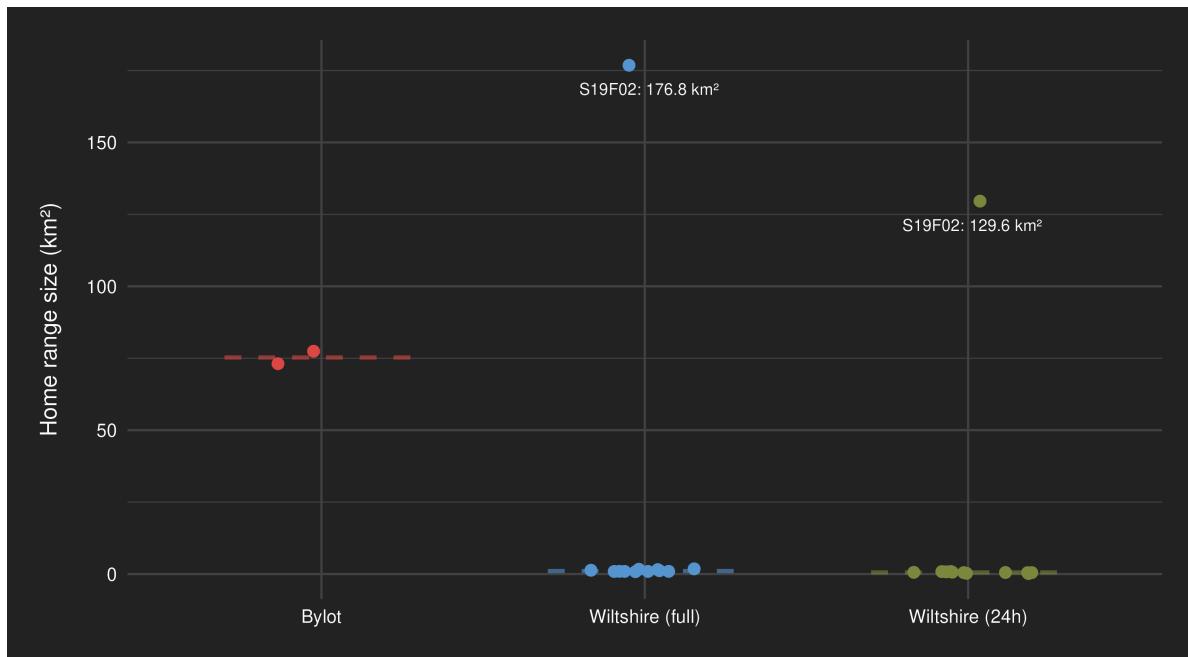


Figure 10: Home range sizes of foxes in Bylot and Wiltshire (full and 24h subsample). Each point represents an individual's home range size (km²); dashed lines indicate the median per location; outliers labeled.

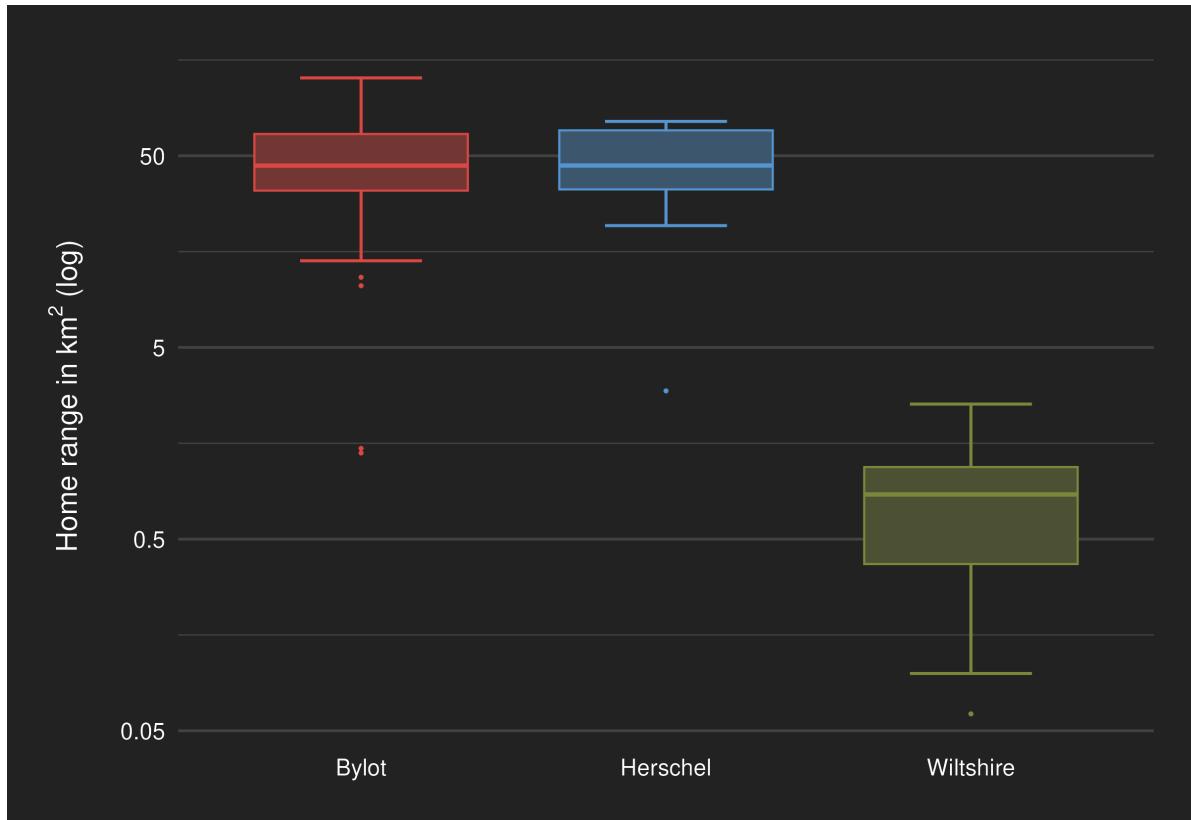


Figure 11: Box plot comparing monthly home ranges (outliers removed).

Table 3: Estimated marginal trends of human footprint on coyote habitat selection by land cover type. Includes linear (a) and quadratic (b) trends, with standard errors, 95% confidence intervals, z -ratios, and p -values.

(a) Estimated marginal linear trends					
Land cover	Linear trend (β_1)	SE	95% CI	z	p
TreeCover	+0.263	0.068	0.130 – 0.397	3.87	0.0001
Open	+0.139	0.068	0.005 – 0.273	2.04	0.0420
Cropland	-0.063	0.113	-0.283 – 0.158	-0.56	0.5770
BuiltUp	-0.062	0.309	-0.667 – 0.544	-0.20	0.8420
Water	-0.550	0.263	-1.065 – -0.035	-2.09	0.0360
(b) Estimated marginal quadratic trends					
Land cover	Quadratic trend (β_2)	SE	95% CI	z	p
TreeCover	-0.183	0.039	-0.260 – -0.106	-4.68	<.0001
Open	-0.181	0.039	-0.257 – -0.104	-4.62	<.0001
Cropland	-0.153	0.046	-0.243 – -0.064	-3.35	0.0008
BuiltUp	-0.161	0.077	-0.312 – -0.011	-2.11	0.0351
Water	-0.013	0.081	-0.172 – 0.146	-0.16	0.8700

4.2 Coyote habitat selection

The final step selection function (SSF) model included 666,248 steps from 29 coyotes. The model converged successfully and revealed significant effects of human footprint and land cover interactions on habitat selection.

Coyotes exhibited significant variation in habitat selection across land cover types and along the human footprint gradient (Table 3). Linear selection trends were significantly positive in TreeCover ($\beta_1 = +0.263$, $p = 0.0001$) and Open ($\beta_1 = +0.139$, $p = 0.042$), indicating increased selection with increasing HFP at low to moderate levels. However, significant negative quadratic trends in these habitats (TreeCover: $\beta_2 = -0.183$, $p < 0.0001$; Open: $\beta_2 = -0.181$, $p < 0.0001$) suggested that selection peaked at intermediate HFP and declined at higher human footprint levels.

Selection for Cropland and BuiltUp was weak and non-significant ($p > 0.05$). Water showed a significant negative linear trend ($\beta_1 = -0.550$, $p = 0.036$), indicating declining selection with increasing HFP.

The average marginal effect plot (Figure 12) shows highest relative selection for TreeCover and Open habitats at low to moderate human footprint, with declining selection under increased human footprint. BuiltUp, Cropland, and Water habitats were consistently selected less, regardless of human footprint level.

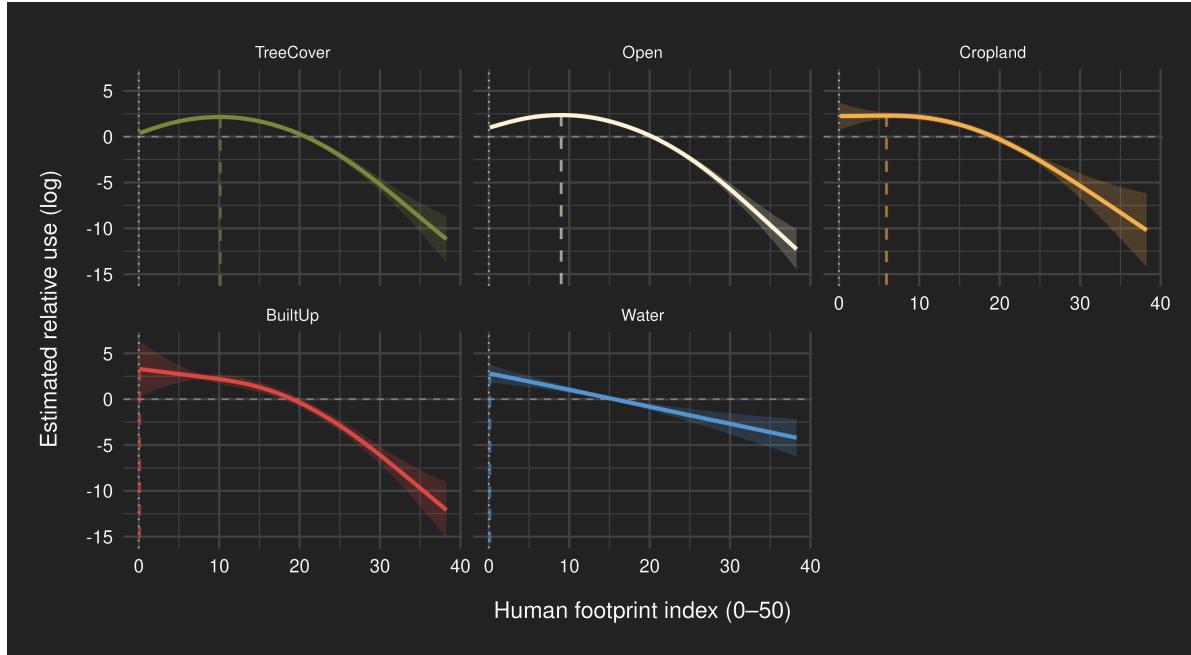


Figure 12: Average marginal effect ($\pm 95\%$ confidence interval) of human footprint on coyote habitat selection across land cover types. Plots quantify the relative change in log selection probability across the range of human footprint, while averaging over other covariates. Positive values indicate above-average selection, negative values indicate below-average selection. Vertical dashed lines indicate estimated human footprint values at peak selection.

Relative selection strength (RSS) curves (Figure 13) confirmed that coyotes preferred TreeCover and Open habitats under low human footprint conditions, with selection declining or leveling off at higher human disturbance.

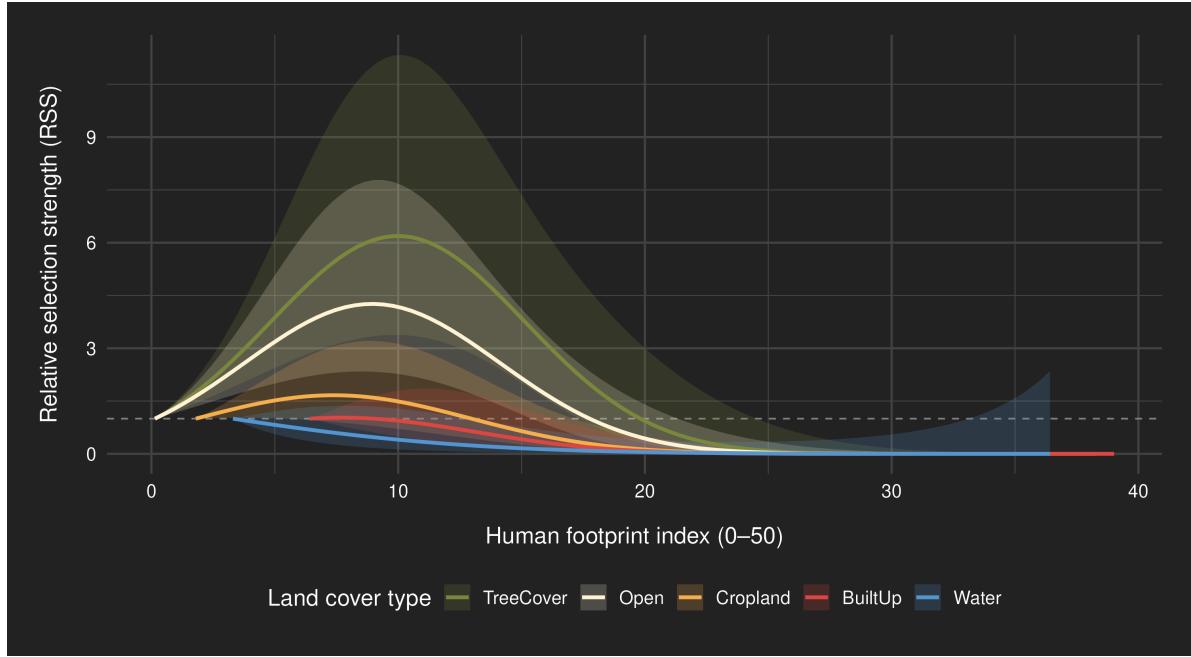


Figure 13: Relative selection strength ($\pm 95\%$ confidence interval) for coyotes across the human footprint gradient by land cover type. RSS was quantified relative to the minimum observed human footprint (corresponding to least human disturbance). Values >1 indicate selection, values <1 indicate avoidance.

4.3 Model validation

4.3.1 Fox home ranges

To validate the home range estimation, we evaluated the influence of coordinate system choice and data properties on the results. Specifically, we compared median home range sizes calculated using minimum convex polygons (MCP) across three coordinate systems: WGS84 (EPSG:4326), NAD83 (EPSG:3347), and UTM Zone 17N (EPSG:2958), identified using the CRS Explorer. The differences in median home range area were small (75.3 km² for WGS84, 73.3 km² for NAD83, and 75.8 km² for UTM Zone 17N), suggesting minimal distortion effects. Our validation criterion required that any coordinate system effect be an order of magnitude smaller than observed ecological differences (10x smaller) Nilsen, Pedersen, and Linnell (2008). Given this threshold was met, we considered the choice of coordinate system to have negligible impact on home range estimates.

4.3.2 Coyote habitat selection

For the habitat selection, model validity was assessed by inspecting fixed and random effect estimates, checking for overdispersion, evaluating collinearity among predictors, and plotting predicted values against observed use categories (Figure 15). No overdispersion was detected (dispersion ratio = 0.91; $p = 1$). Multicollinearity was low among main effects ($VIF < 5$); high variance inflation for interaction terms was expected due to model structure. Predicted relative use values were higher for used steps compared to available steps, indicating biologically plausible model behavior. Standard residual-based diagnostics were not feasible due to the conditional logistic nature of the step selection framework.

5 Discussion

5.1 Home range size assessment

The fox home range size results show enormous differences between rural and remote areas, with substantially smaller home ranges observed in Wiltshire compared to Bylot. This suggests that human presence fundamentally alters fox movement behavior, likely due to a combination of reduced space availability and access to anthropogenic food resources. Interestingly, home range sizes for Bylot and Herschel foxes are similar, even if the island sizes differ by a factor of 100, implying that environmental factors other than available land area constrain movements in these remote settings.

One fox in Wiltshire exhibited an exceptionally large home range compared to its conspecifics, as highlighted in Figure 10. This individual may represent a disperser or exhibit exploratory behavior. Similar patterns of occasional extensive movements in urban foxes have been reported elsewhere Kobryna et al. (2023), reinforcing that such variation reflects biological rather than technical factors.

Although methodological factors such as sampling interval and home range estimator can influence results, their impact appears minor relative to the overarching differences in movement behavior across landscapes. This supports the validity of comparing home range sizes across these heterogeneous datasets despite inherent differences in data collection.

5.2 Habitat selection

Coyote habitat selection was driven by both land cover and the degree of human modification. Animals strongly favored forest and open habitats under low-to-moderate human footprint but reduced use of these habitats once disturbance exceeded an apparent threshold, indicating a trade-off between resource gain and risk. Cropland, built-up areas, and water were rarely selected, revealing broad avoidance of highly modified landscapes.

Land-cover-specific relative selection strength (RSS) curves showed that human disturbance altered preferences differently among habitats—selection for forest declined more steeply with increasing footprint than did selection for open areas—echoing earlier work that forests function as crucial refuges in human-dominated settings (e.g., Riley et al. (2003)). Model diagnostics confirmed that the SSF was well specified, with no over-dispersion or problematic collinearity. A comparable analysis for bobcats was infeasible because of sparse, uneven data, underscoring the limitations of opportunistic tracking datasets.

6 Conclusion

We have performed spatial data analysis and statistical modeling on externally contributed publicly available data to demonstrate that human activity influences animal behavior significantly. We could show that (1) fox home range sizes are larger in remote areas, and that (2) coyotes prefer forests over built-up areas for habitat selection depending on human footprint.

7 Appendix

7.1 Additional charts

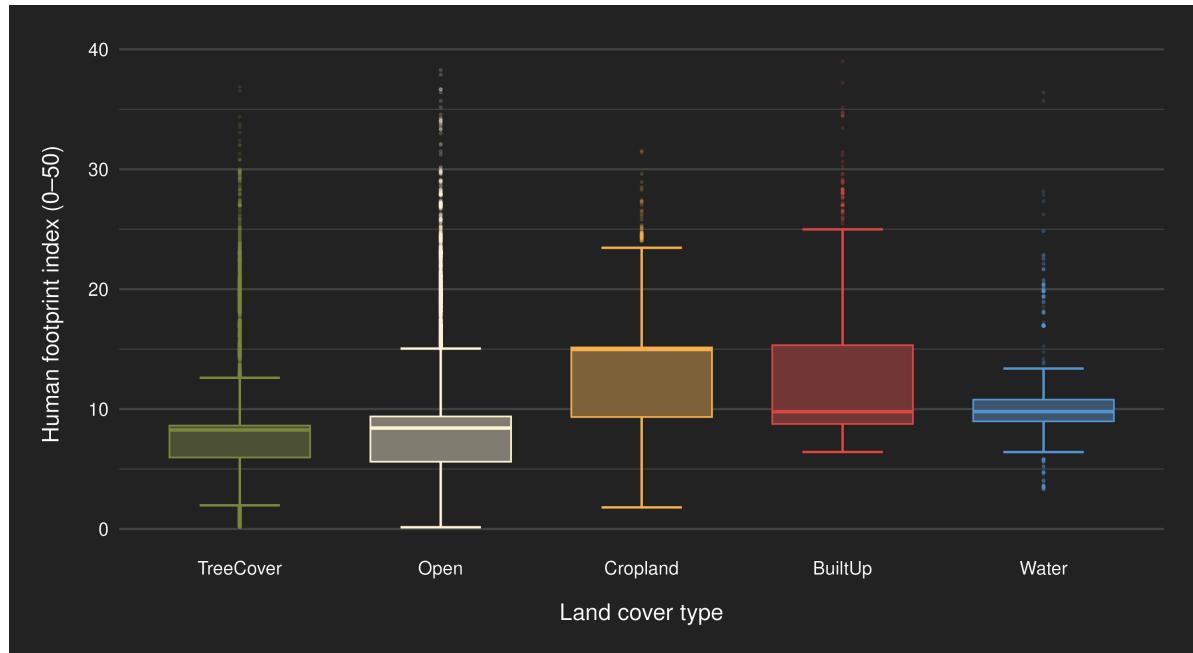


Figure 14: Human footprint index across land cover types at used locations.

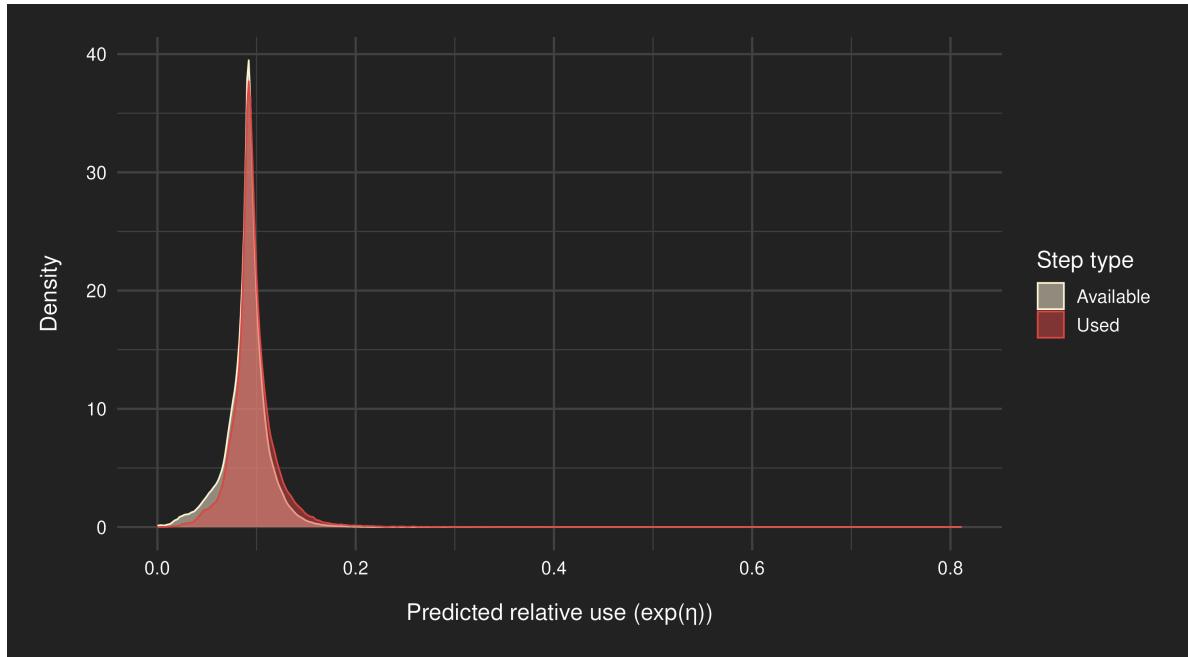


Figure 15: Density plot showing predicted relative use from the SSF model for used and available steps.

7.2 Supplementary material

All R code and preprocessing steps are publicly available:

- Red fox: UK wader nesting season home ranges
- Red fox: monthly home ranges
- Bobcat/coyote: data preparation and statistical modelling
- Human Footprint Index data preparation
- ESA WorldCover data preparation

7.3 Use of generative AI

Elke used NotebookLM for querying the papers cited, and ChatGPT for ggplot related queries. Jannis utilized GitHub Copilot for debugging and for assisting in plot creation.

References

- Doherty, Tim S, Graeme C Hays, and Don A Driscoll. 2021. “Human Disturbance Causes Widespread Disruption of Animal Movement.” *Nature Ecology & Evolution* 5 (4): 513–19.

- Fortin, Daniel, Hawthorne L Beyer, Mark S Boyce, Douglas W Smith, Thierry Duchesne, and Julie S Mao. 2005. "Wolves Influence Elk Movements: Behavior Shapes a Trophic Cascade in Yellowstone National Park." *Ecology* 86 (5): 1320–30.
- Gassert, Francis, Oscar Venter, James EM Watson, Steven P Brumby, Joseph C Mazzariello, Scott C Atkinson, and Samantha Hyde. 2023. "An Operational Approach to Near Real Time Global High Resolution Mapping of the Terrestrial Human Footprint." *Frontiers in Remote Sensing* 4: 1130896.
- Kays, Roland, Sarah C Davidson, Matthias Berger, Gil Bohrer, Wolfgang Fiedler, Andrea Flack, Julian Hirt, et al. 2022. "The Movebank System for Studying Global Animal Movement and Demography." *Methods in Ecology and Evolution* 13 (2): 419–31.
- Kobrynn, Halina T, Edward J Swinhoe, Philip W Bateman, Peter J Adams, Jill M Shephard, and Patricia A Fleming. 2023. "Foxes at Your Front Door? Habitat Selection and Home Range Estimation of Suburban Red Foxes (*Vulpes Vulpes*)."*Urban Ecosystems* 26 (1): 1–17.
- Lai, Sandra, Chloé Warret Rodrigues, Daniel Gallant, James D Roth, and Dominique Berteaux. 2022. "Red Foxes at Their Northern Edge: Competition with the Arctic Fox and Winter Movements." *Journal of Mammalogy* 103 (3): 586–97.
- Laube, Patrick, and Ross S Purves. 2011. "How Fast Is a Cow? Cross-Scale Analysis of Movement Data." *Transactions in GIS* 15 (3): 401–18.
- Manly, BFL, Lyman McDonald, Dana L Thomas, Trent L McDonald, and Wallace P Erickson. 2007. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Springer Science & Business Media.
- Muff, Stefanie, Johannes Signer, and John Fieberg. 2020. "Accounting for Individual-Specific Variation in Habitat-Selection Studies: Efficient Estimation of Mixed-Effects Models Using Bayesian or Frequentist Computation." *Journal of Animal Ecology* 89 (1): 80–92.
- Nilsen, Erlend B, Simen Pedersen, and John DC Linnell. 2008. "Can Minimum Convex Polygon Home Ranges Be Used to Draw Biologically Meaningful Conclusions?" *Ecological Research* 23: 635–39.
- Porteus, Tom A, Mike J Short, Andrew N Hoodless, and Jonathan C Reynolds. 2024. "Movement Ecology and Minimum Density Estimates of Red Foxes in Wet Grassland Habitats Used by Breeding Wading Birds." *European Journal of Wildlife Research* 70 (1): 8.
- Prugh, Laura R, Calum X Cunningham, Rebecca M Windell, Brian N Kertson, Taylor R Ganz, Savanah L Walker, and Aaron J Wirsing. 2023. "Fear of Large Carnivores Amplifies Human-Caused Mortality for Mesopredators." *Science* 380 (6646): 754–58.
- Riley, Seth P. D., John P. Pollinger, Raymond M. Sauvajot, Ellen C. York, Catherine Bromley, Tracy K. Fuller, and Robert K. Wayne. 2003. "Effects of Urbanization and Habitat Fragmentation on Bobcats and Coyotes in Southern California." *Conservation Biology* 17 (2): 566–76.
- Signer, Johannes, John Fieberg, and Tal Avgar. 2019. "Animal Movement Tools (Amt): R Package for Managing Tracking Data and Conducting Habitat Selection Analyses." *Ecology and Evolution* 9 (2): 880–90.
- Zanaga, Daniele, Ruben Van De Kerchove, Dirk Daems, Wanda De Keersmaecker, Carsten Brockmann, Grit Kirches, Jan Wevers, et al. 2022. "ESA WorldCover 10 m 2021 V200."