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

This section describes the datasets, the steps taken to prepare and process the different datasets in use, and the methodological approach.

3.1 Datasets

The Movebank database Kays et al. (2022) allows researchers to publish animal tracking data for public use. Relying on externally contributed data presents challenges because data is used for purposes it was not originally collected for, and compared between studies. We selected red fox data for outskirt areas in Wiltshire, UK Porteus et al. (2024) and for uninhabited islands in Canada Lai et al. (2022), and bobcat and coyote data for remote areas in northeastern Washington, US Prugh et al. (2023). Additional, the global terrestrial human footprint Gassert et al. (2023) and satellite land cover data Zanaga et al. (2022) were employed.

3.2 Data preparation and processing

This section describes data preparation and processing for all the datasets employed.

3.2.1 Movebank

All Movebank datasets have the same schema. This simplifies enables code re-use, and requires data contributors do perform preprocessing on their side to provide the data in an appropriate format. Libraries for data processing and trajectory handling in R are provided Kranstauber, Safi, and Scharf (2024) Signer, Fieberg, and Avgar (2019).

The R code for data download, preprocessing, and serialization of data and charts can be found in: Red fox: UK wader nesting season home ranges, Red fox: montly home ranges, Bobcat/coyote: data preparation and statistical modelling.

3.2.2 Human footprint

The global 100 meter resolution terrestrial human footprint data (HFP-100) is raster data using Mollweide projection Lapaine (2011). The 2020 version of the data was downloaded for Washington, and projected to the WGS84 coordinate system: HFP-100 download.

3.2.3 Land cover

The relevant European Space Agency (ESA) WorldCover 2021 data at 10 m resolution was downloaded via the Microsoft Planetary Computer STAC API: ESA download.

3.3 Data exploration and analysis

This section describes the data exploration steps taken.

3.3.1 Red fox

Data from Wiltshire (see Figure 1) was collected between 2016 to 2019 during the UK wader nesting season, which was defined to be March 15th to June 15th, for 35 foxes in total. It was sampled at 10 and 60 minute rates. The research team controlled the sampling rate remotely to save battery at times the data was considered less interesting.

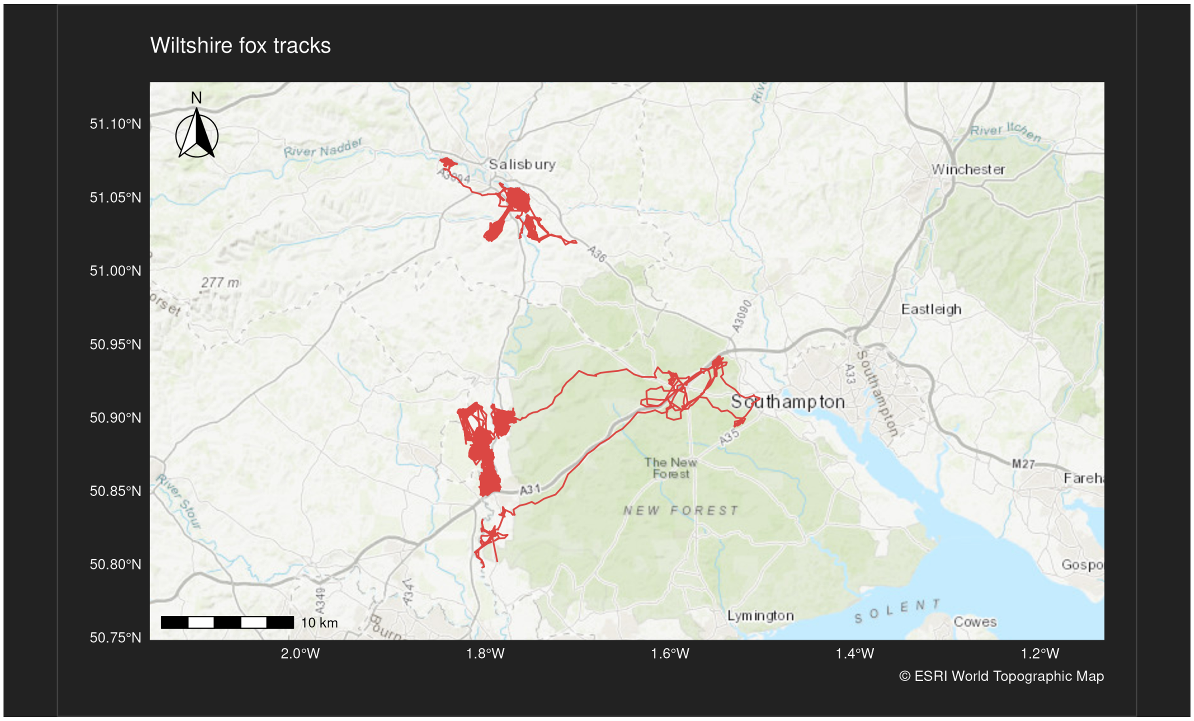
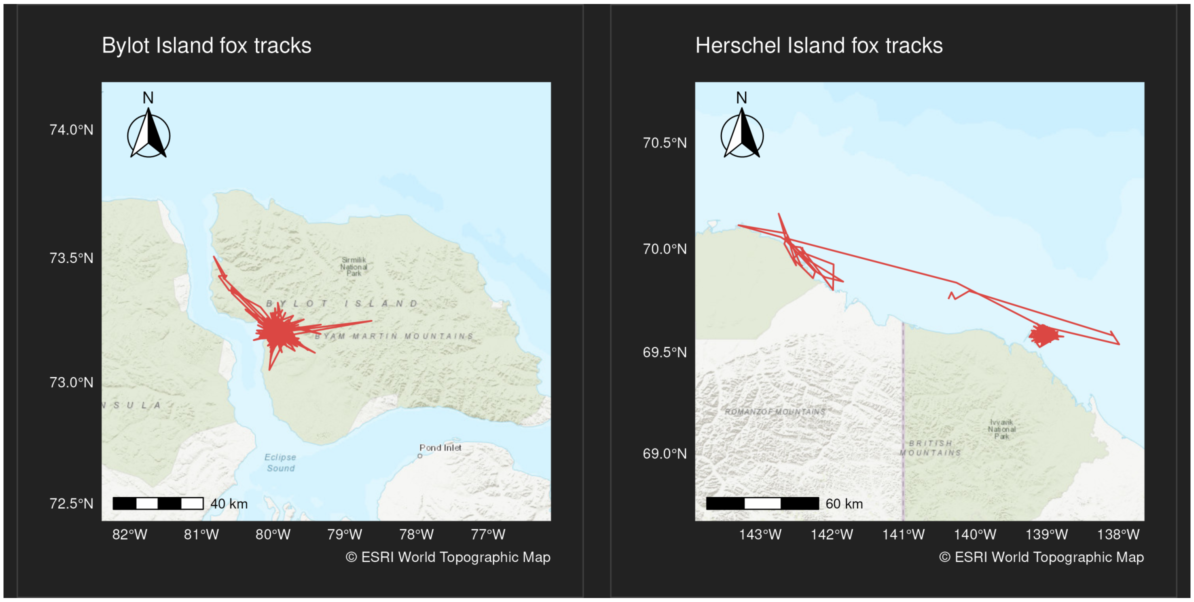


Figure 1: High level view of animal GPS tracks in Wiltshire

Data from Bylot (see Figure 2a) and Herschel (see Figure 2b) was collected all year round, at a much lower sampling rate of once per day at random afternoon times. The collection period was June 2009 to Feb 2010 for Herschel and from 2011 to 2015 for Bylot, for two foxes each per island. Figure 3a provides an overview of the amount of data points available per year. There is much more data from Wiltshire because of the higher number of foxes and the higher sampling rate. Looking at the breakdowns by month as shown in Figure 3b reveals seasonal differences in the amount of data available.

3.3.2 Bobcat and coyote

Figure 4 shows that the two species reside in two separated geographical areas and have interspersed home ranges. It also features a plot of the animal locations in the context of the



(a) Bylot island (11.067 km2) (b) Herschel island (116 km2), some tracks irregular

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

extracted land cover data. Figure 5 reveals the human footprint in the area, which is generally low except for some settlements and country roads.

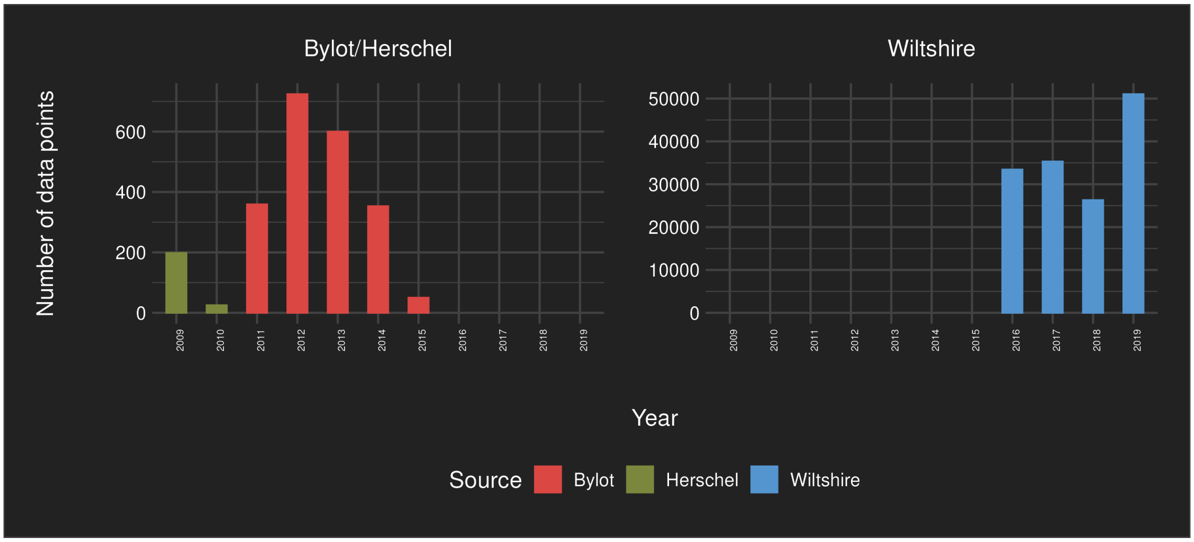
Although all GPS collars were programmed to record locations at four-hour intervals, the actual sampling was irregular and included numerous outliers (see Figure 6). Sampling intervals for bobcats were particularly sparse and inconsistent compared to those for coyotes.

3.4 Analytical methods

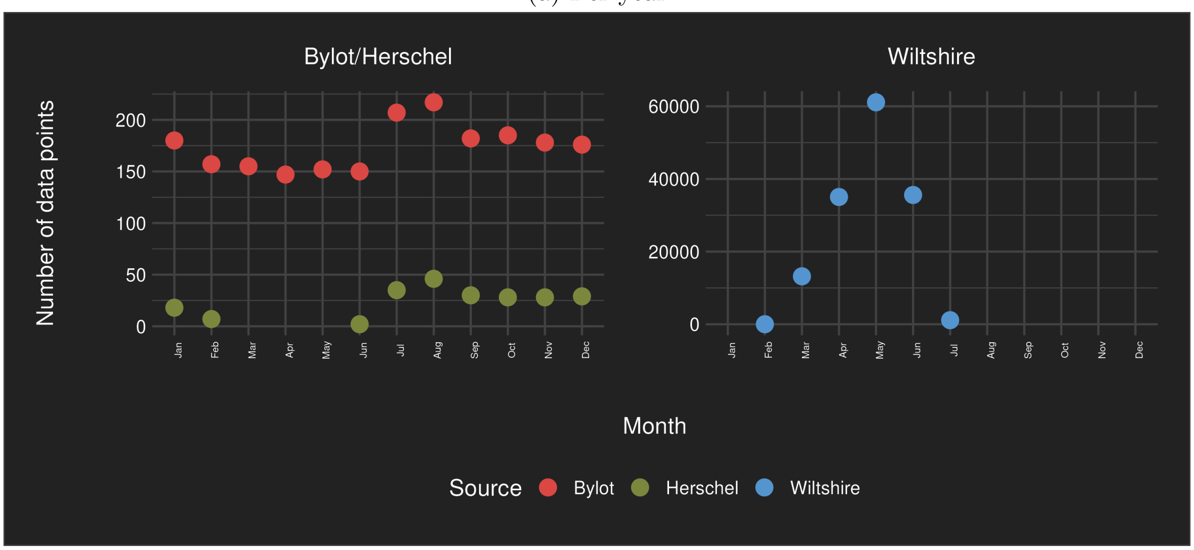
We applied two analytical approaches: (1) home range estimation for red foxes and (2) habitat selection modeling using step-selection functions for coyotes.

3.4.1 Home range size assessment

Home range sizes were calculated using minimum convex polygons, which provides easily comparable estimates of the area used by each individual animal. As discussed in Section 3.3.1, the datasets for the two locations have different temporal scale. The choice of temporal scale has considerable effects on movement parameter calculations Laube and Purves (2011), in turn affecting home range results. How to make this data comparable? Problem #1 is that the sampling intervals are different. Problem #2 is that the data coverage varies by time of the



(a) Per year



(b) Per month

Figure 3: Amount of data per year and month

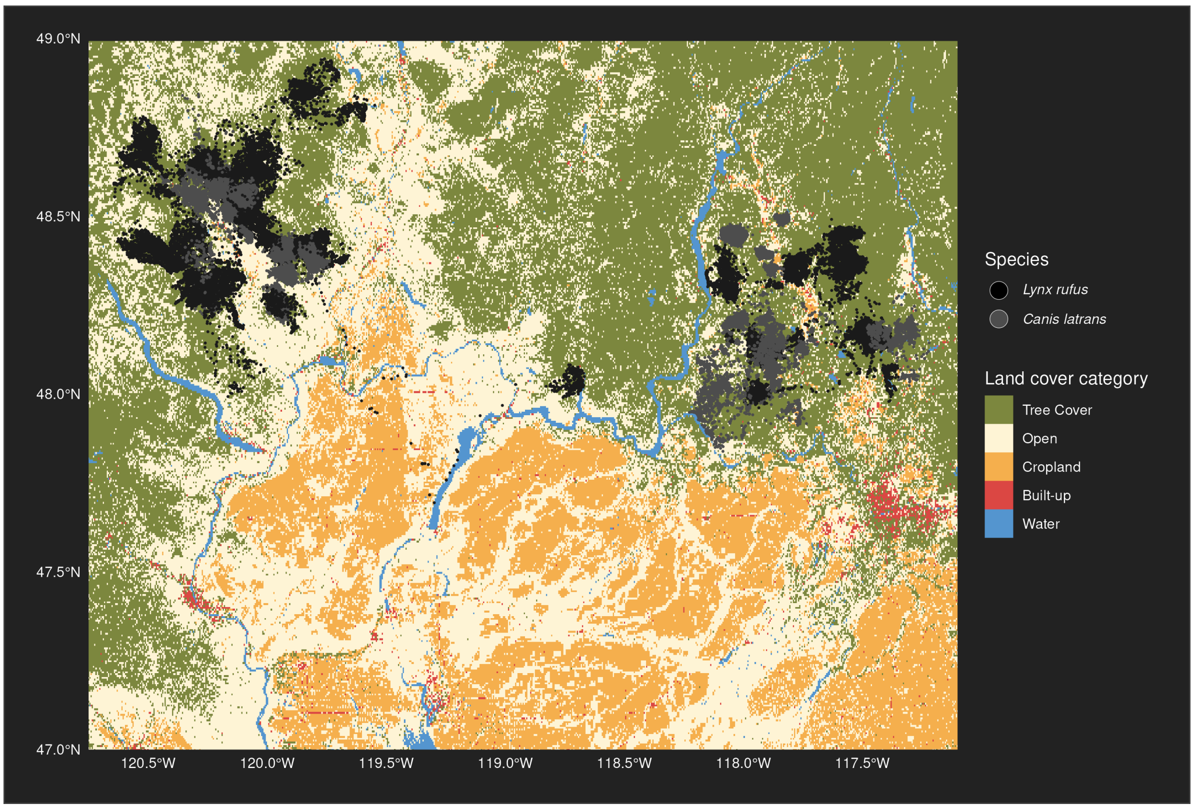


Figure 4: Bobcat and coyote locations in the context of the land cover data

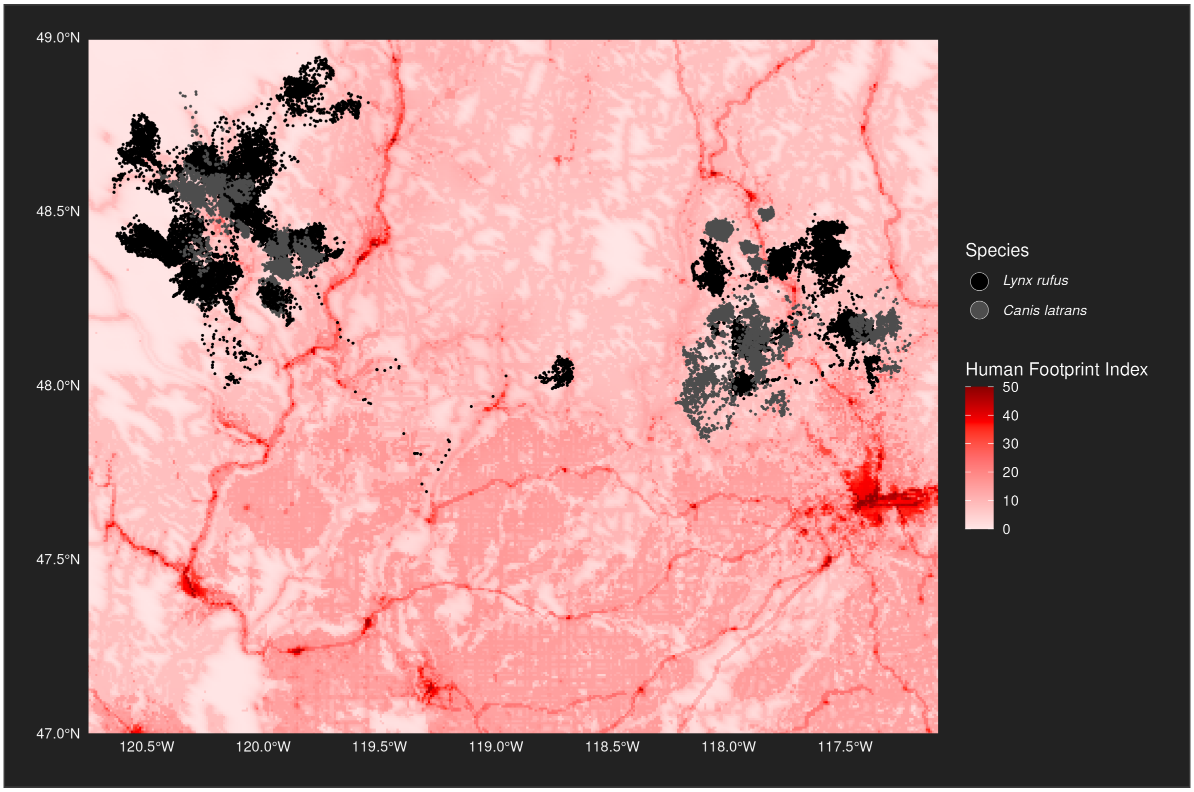
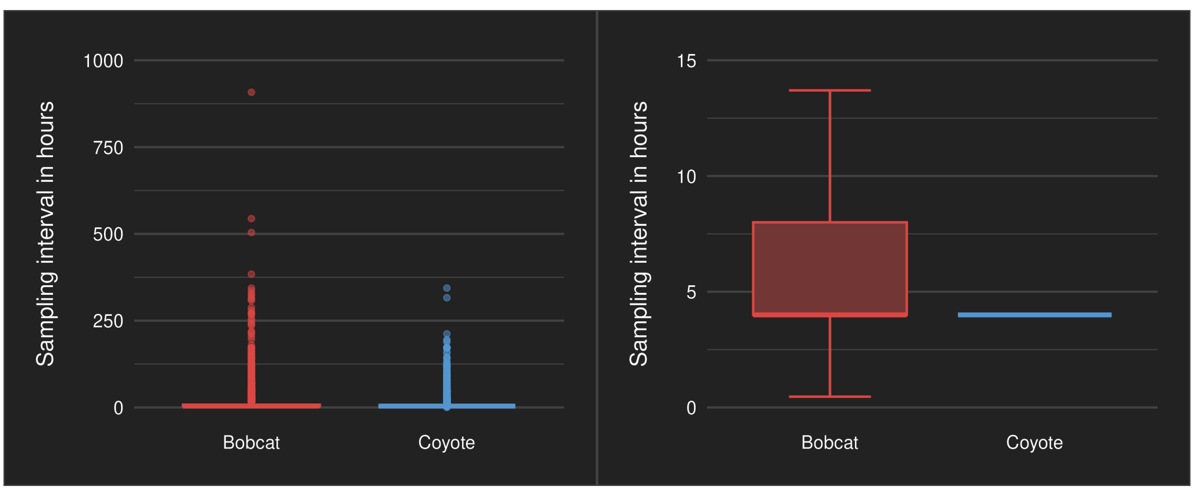


Figure 5: HFP-100 data with bobcat and coyote tracks



(a) With outliers

(b) With outliers removed

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

year. Problem #3 is that there are highly different amounts of data. Selecting the means and parameters for the comparison involves complex choices that will influence the results. For #1, a possible approach to achieve similar sampling intervals would be to sample a random afternoon data point for each 24 hour window. However, this would include the implicit assumption that foxes will follow similar daily patterns in the different environments. For #2, a possible approach would be to compare the data for the same time of the year. But since the geographical locations are different, the seasonal weather conditions will differ for the same day of the year, likely leading to different animal behavior. For #3, aggregated comparisons can solve the issue, assuming there is enough data for the smaller data source.

For data exploration the simplest possible imperfect approach was employed, which was to ignore the different sampling intervals for problem #1, to compare the data for the same time of the year for problem #2 even if animal behavior might be different, and to use exploratory data analysis to find out if a representative answer can be found given the amount of data present for problem #3. Note that this approach has obvious limits. Among them is that the Herschel data is not applicable, since it has minimal overlaps with the Wiltshire data (see Figure 3b). To explore the impact of sampling intervals for problem #1, the home ranges for the Wiltshire data were additionally calculated on downsampled data, where a random data point from every 24 hour period was selected. Finally, an analysis of monthly home ranges was conducted on all three datasets as an alternative solution to address problem #2.

3.4.2 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.

3.4.2.1 Step Generation and Covariates

Coyote and bobcat GPS tracks Prugh et al. (2023) were irregularly spaced (see 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 (see Table 1). Human footprint index (HFP) values were standardized across the dataset for modeling.

Table 1: Reclassification of ESA WorldCover classes into five ecologically meaningful categories.

Class	**Description**	**Used original classes**
TreeCover	Areas dominated by trees with a cover of 10% or more	Tree Cover
Open	Open natural habitats or low-intensity agricultural areas	Grassland, Bare/sparse vegetation, Moss and lichen
Cropland	Areas used for intensive agricultural production	Cropland
BuiltUp	Urban and developed areas with infrastructure	Built-up
Water	Aquatic and 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 (see 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 (see Figure 17).

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 (see 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.

3.4.2.2 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`;

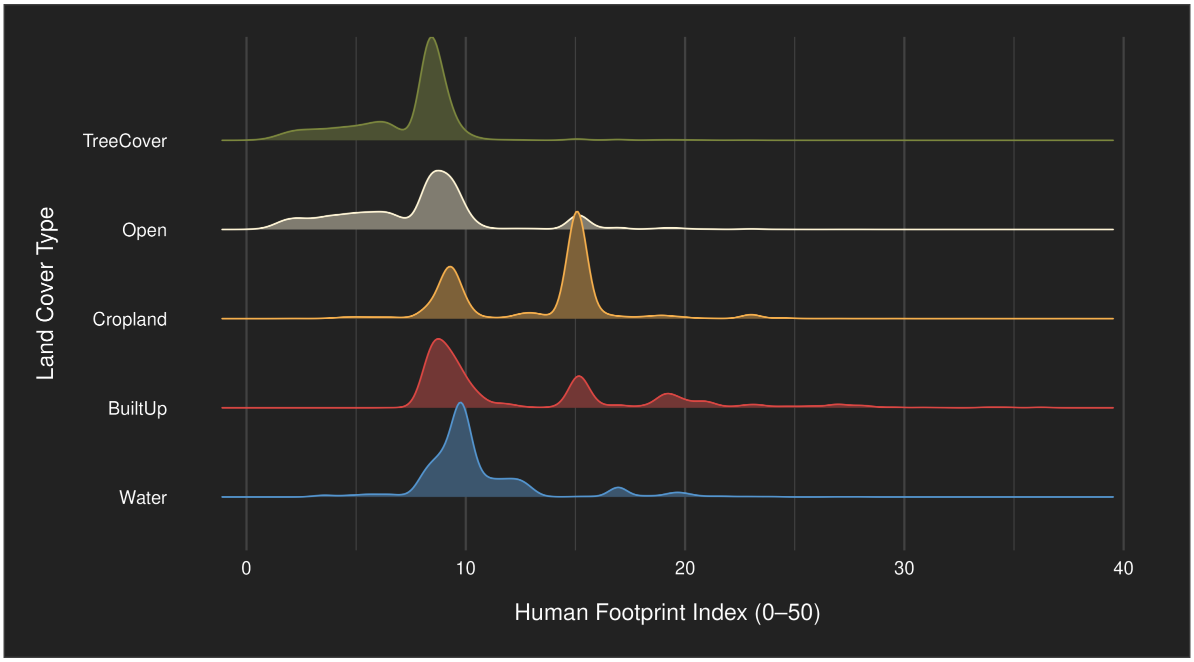


Figure 7: Human footprint distribution by land cover type

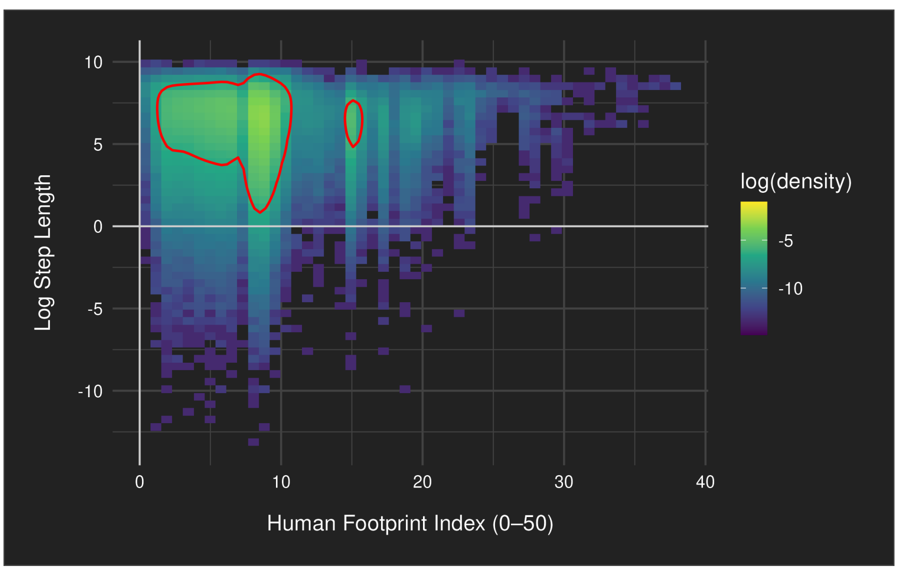


Figure 8: Relationship between movement and human footprint

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 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 `clogit` 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_sl_`) to control for movement bias. Human footprint index (HFP) values were standardized before modeling.

The model can be expressed as:

$$\log(\lambda_{ij}) = \beta_1 \cdot \mathrm{LC}_{ij} + \beta_2 \cdot \mathrm{HFP}_{ij} + \beta_3 \cdot \mathrm{HFP}_{ij}^2 + \beta_4 \cdot \log(\mathrm{StepLength}_{ij}) + b_{0,step(i,j)} + u_i$$

where:

- 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,
- $b_{0,\mathrm{step}(i,j)}$ 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 gradient of human footprint (HFP). These metrics were computed from the fitted model to provide an interpretable scale of selection intensity.

3.4.2.3 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

This section describes the results.

4.1 Fox home ranges

The resulting fox home ranges for the UK wader nesting season time frame are shown in Figure 9 and Figure 10a. The median home range size for the remote foxes in Bylot (75.3 km2) is more than 65 times larger compared to the one for rural foxes in Wiltshire (1.1 km2). The home ranges for the sub-sampled Wiltshire data are shown in Figure 10b. The median home range size is 0.56 km2 for the sampled data, which is roughly half as much as for the full data.

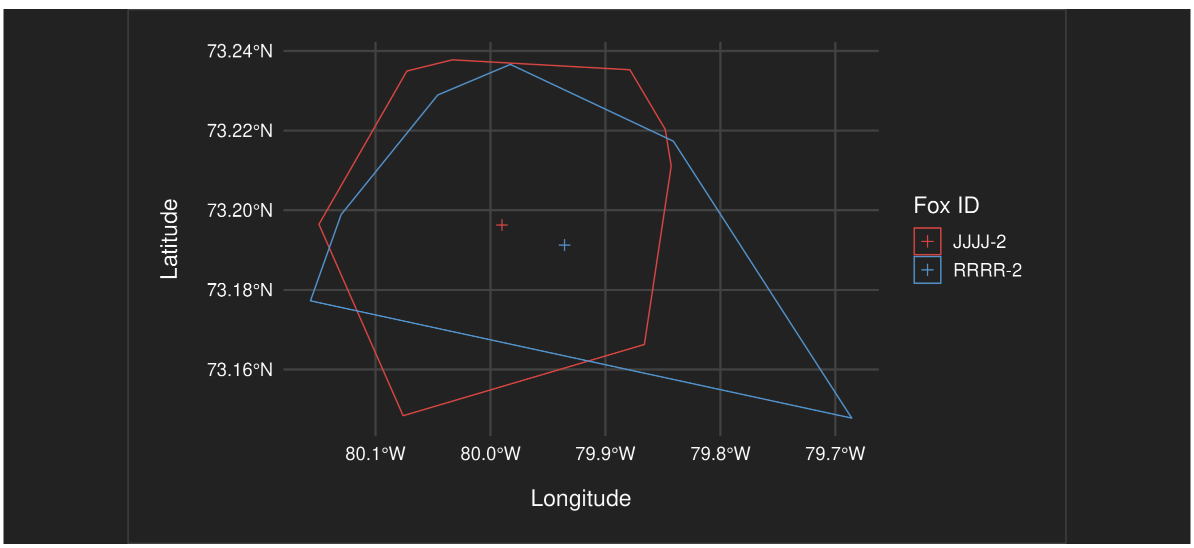
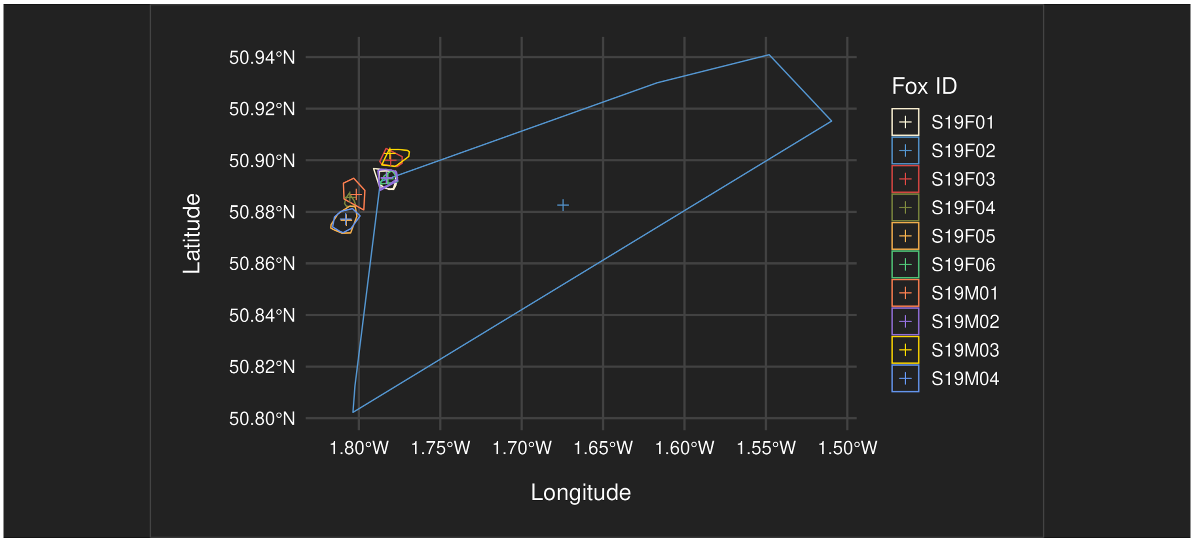
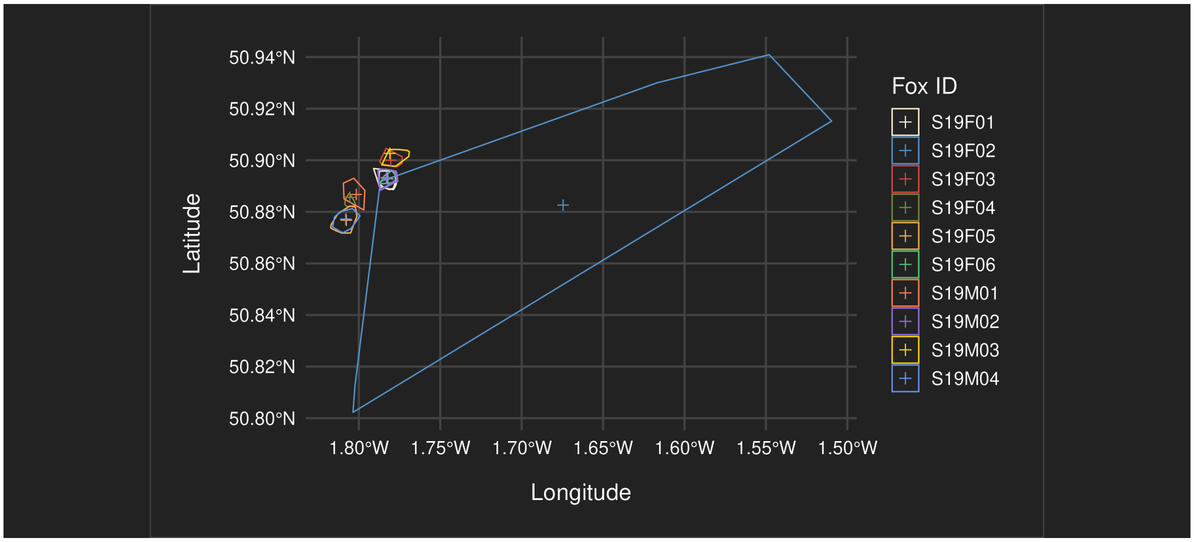


Figure 9: Home ranges for Bylot foxes (March 15th to June 15th, 2012)

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



(a) 10/60 minute sampling interval



(b) 24 hour sampling interval

Figure 10: Home ranges for Wiltshire foxes (March 15th to June 15th, 2019)

accompanying monthly home range plots can be found in the Appendix in Figure 14, Figure 15, and Figure 16.

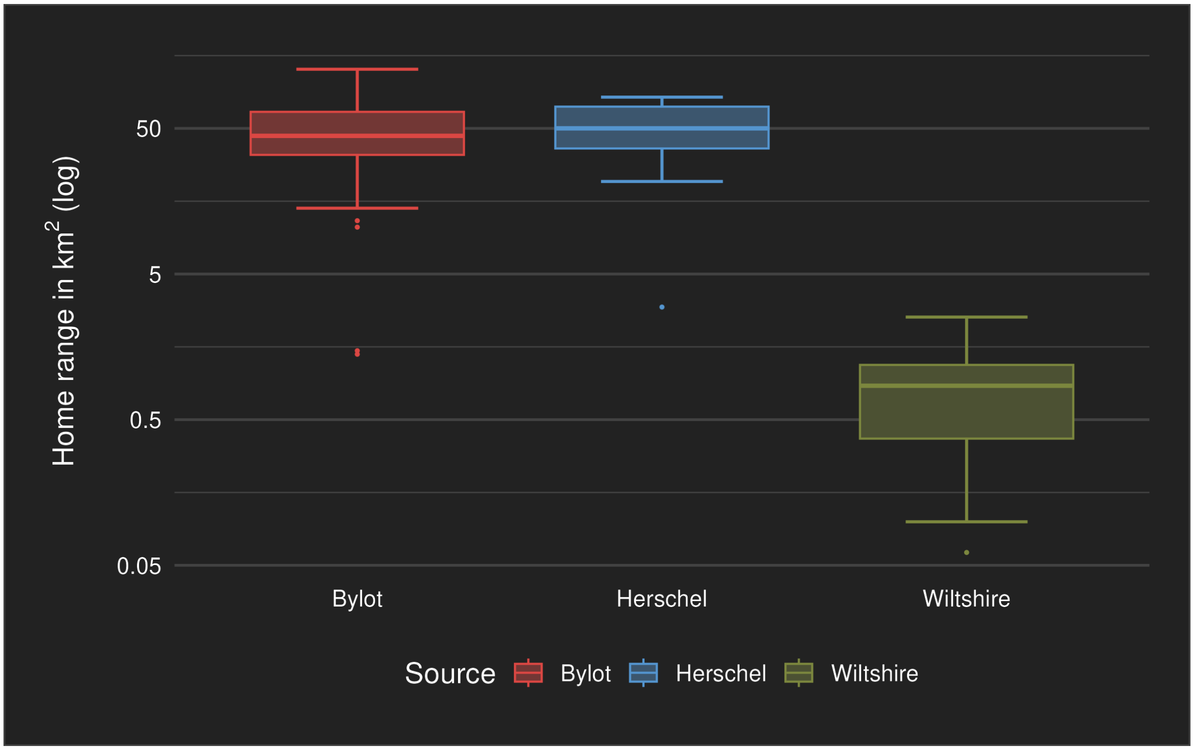


Figure 11: Box plot comparing monthly home ranges (outliers removed)

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 2a and Table 2b). Linear selection trends were significantly positive in TreeCover (β_1 = +0.263, p = 0.0001) and Open (β_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: β_2 = -0.183, $p < 0.0001$; Open: β_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 (β_1 = -0.550, p = 0.036), indicating declining selection with increasing HFP.

Table 2: 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	0.042
Cropland	-0.063	0.113	-0.283 – 0.158	-0.56	0.577
BuiltUp	-0.062	0.309	-0.667 – 0.544	-0.20	0.842
Water	-0.550	0.263	-1.065 – -0.035	-2.09	0.036

(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	0.870

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

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	0.042
Cropland	-0.063	0.113	-0.283 – 0.158	-0.56	0.577
BuiltUp	-0.062	0.309	-0.667 – 0.544	-0.20	0.842
Water	-0.550	0.263	-1.065 – -0.035	-2.09	0.036

Table 4: Estimated marginal **quadratic** trends of human footprint on coyote habitat selection by land cover type. Includes standard errors, 95% confidence intervals, z-ratios, and p-values.

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

Land Cover	**Quadratic Trend (β_2)**	**SE**	**95% CI**	z	p
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	0.870

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

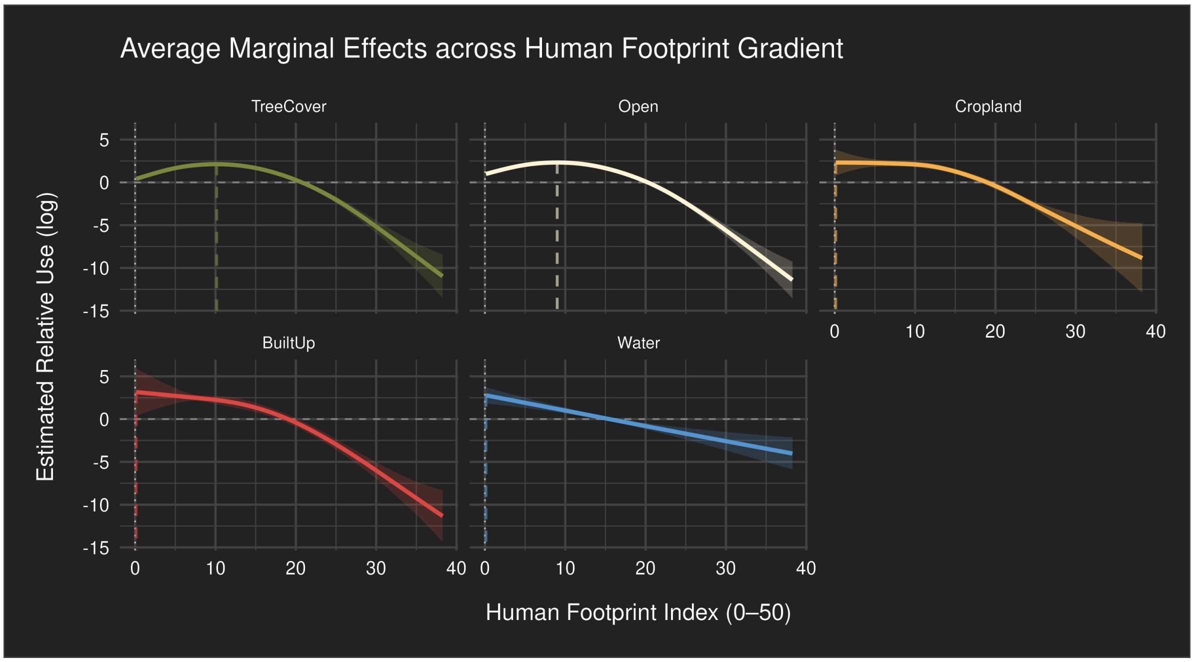


Figure 12: Average marginal effects across human footprint gradient

Relative selection strength (RSS) curves (Figure 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.

4.3 Model validation

Model validation means demonstrating that a model is acceptable for its intended use Rykiel Jr (1996). The purpose, criteria, and context of the model must be specified.

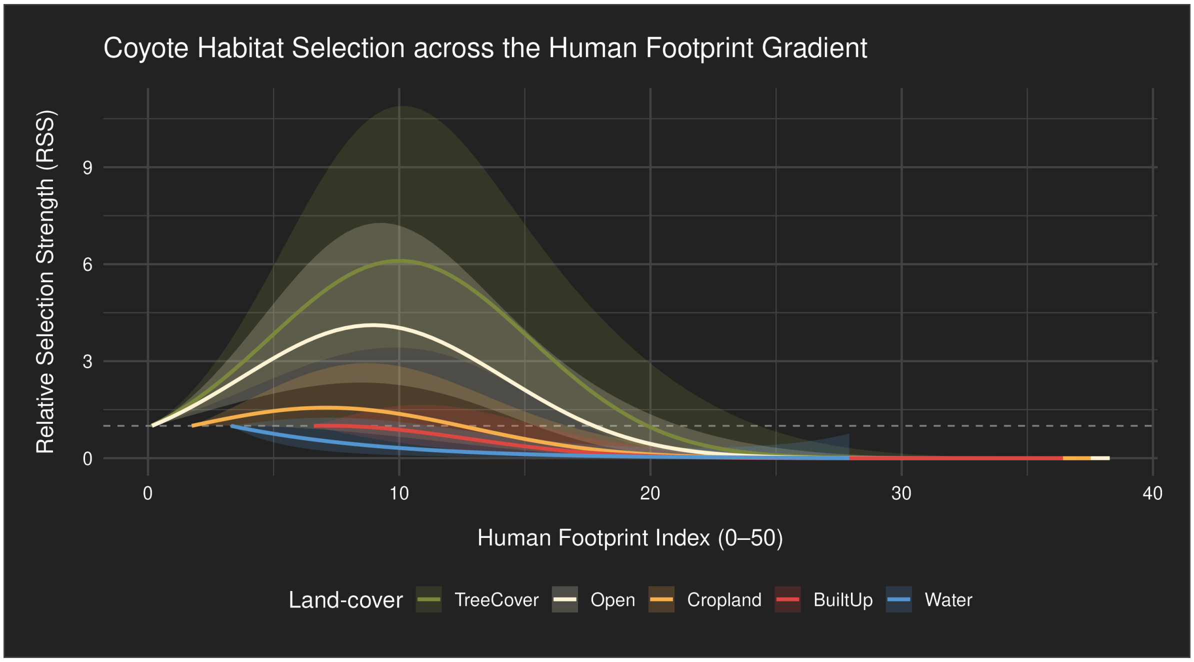


Figure 13: Coyote habitat selection across the human footprint gradient

4.3.1 Fox home ranges

For home range sizes, two models comprised of data, home range calculation based on minimum convex polygons, and median selection were compared. The validation criteria required the difference between the results to be at least 10 times larger than the effects on the results introduced by data properties. For that order of magnitude, the choice of home range estimator has a secondary impact Nilsen, Pedersen, and Linnell (2008). Since geographic location contexts were diverse, to exclude distortions in the coordinate system as a potential influence, the results for Bylot island were spot checked for three applicable coordinate systems: WGS84 (EPSG:4326), NAD 83 (EPSG:3347), and UTM zone 17N (EPSG:2958). These were identified using the CRS Explorer. The differences in the median home range size results were minor: 75.3 km2 for WGS84, 73.3 km2 for NAD 83, and 75.8 km2 for UTM zone 17N.

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 (see Figure 18). 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. We conclude that human presence changes fox movement behavior patterns fundamentally. The opportunity to move undisturbed, and the availability of anthropogenic food sources are likely the most relevant factors. Interestingly, home range sizes for Bylot and Herschel foxes are similar, even if the island sizes differ by a factor of 100. Note that there is one fox with an extraordinarily large home range in Figure 10a. The additional charts in Section 7.1 show several instances of large fox movements within a single month. Similar patterns with a small number of foxes covering much larger areas than others were found in Kobryn et al. (2023), concluding that the data is genuine and demonstrates potential for extensive movement patterns in urban foxes.

While technical aspects such as sampling intervals and home range estimator have significant influence on the calculation results, they play a secondary role in comparison to the difference in fox behavior, which enables the chosen approach of comparing data from heterogeneous sources.

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

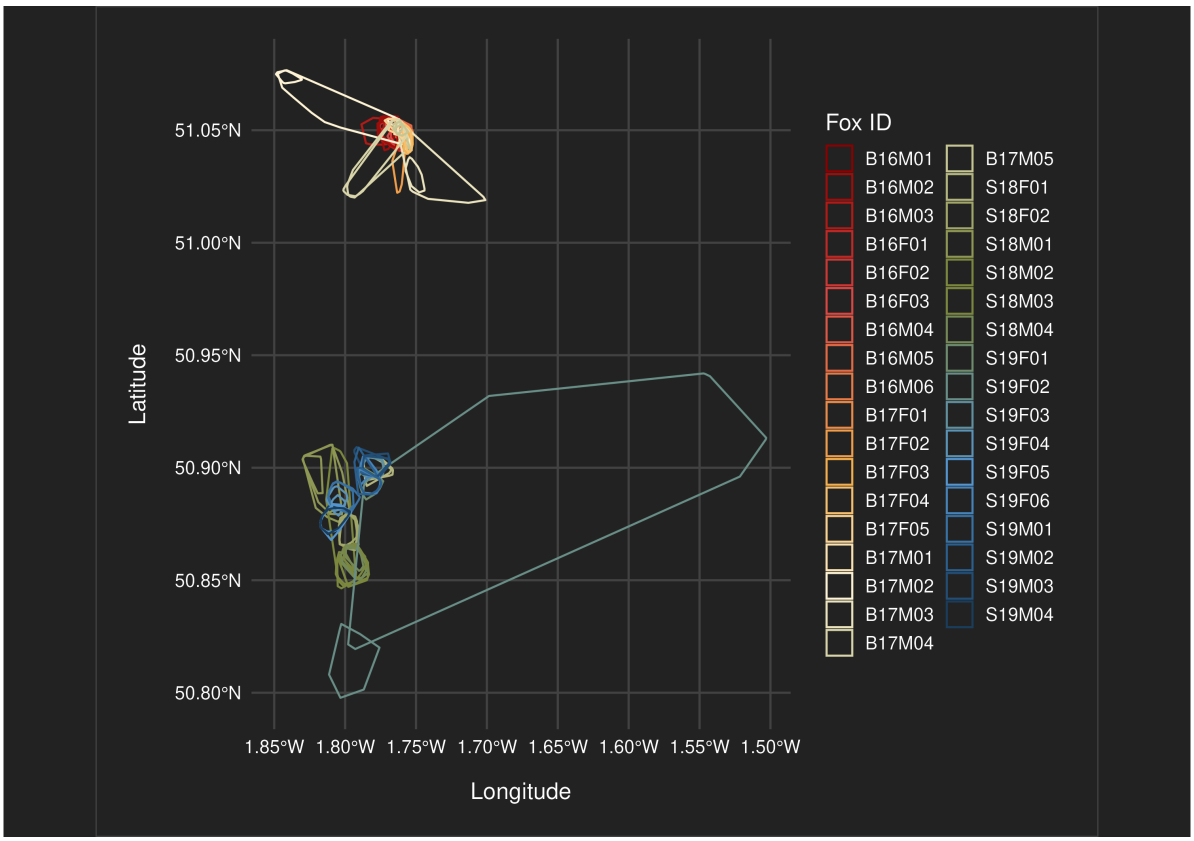


Figure 14: Monthly home ranges for Wiltshire foxes

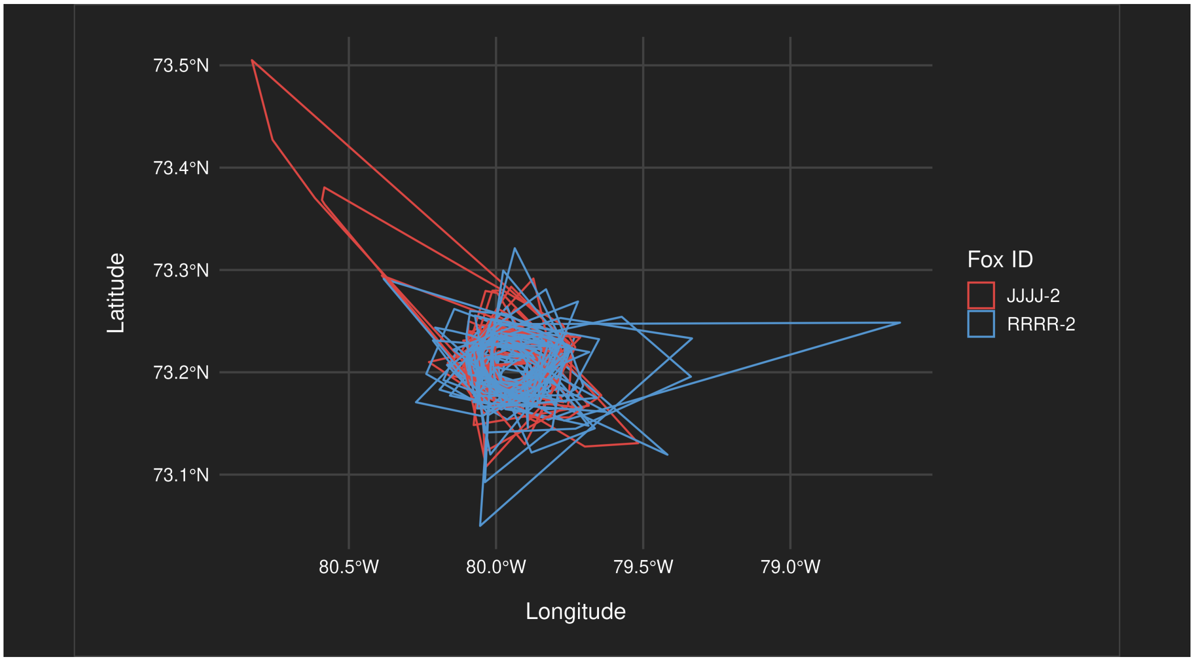


Figure 15: Monthly home ranges for Bylot foxes

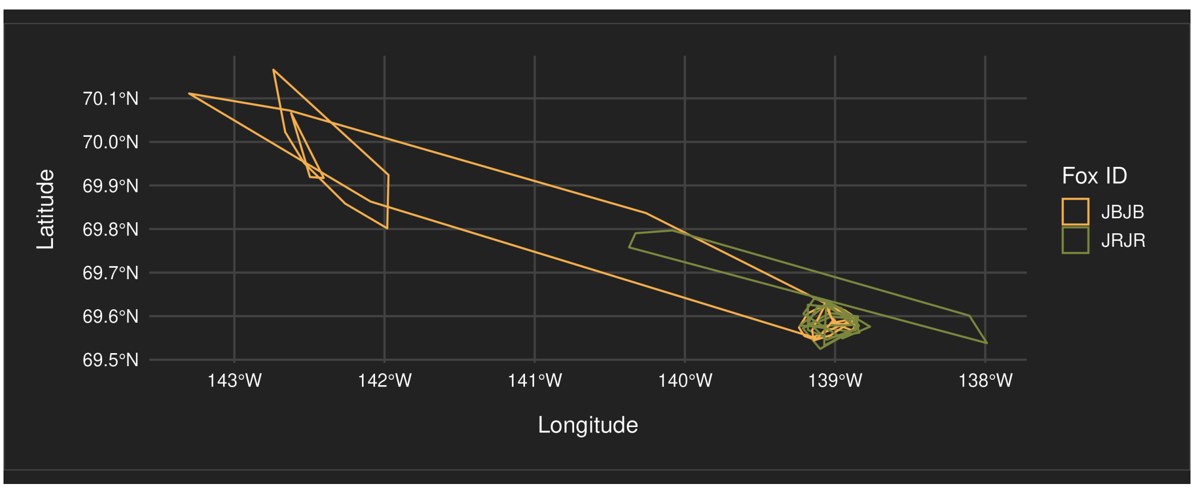


Figure 16: Monthly home ranges for Herschel foxes

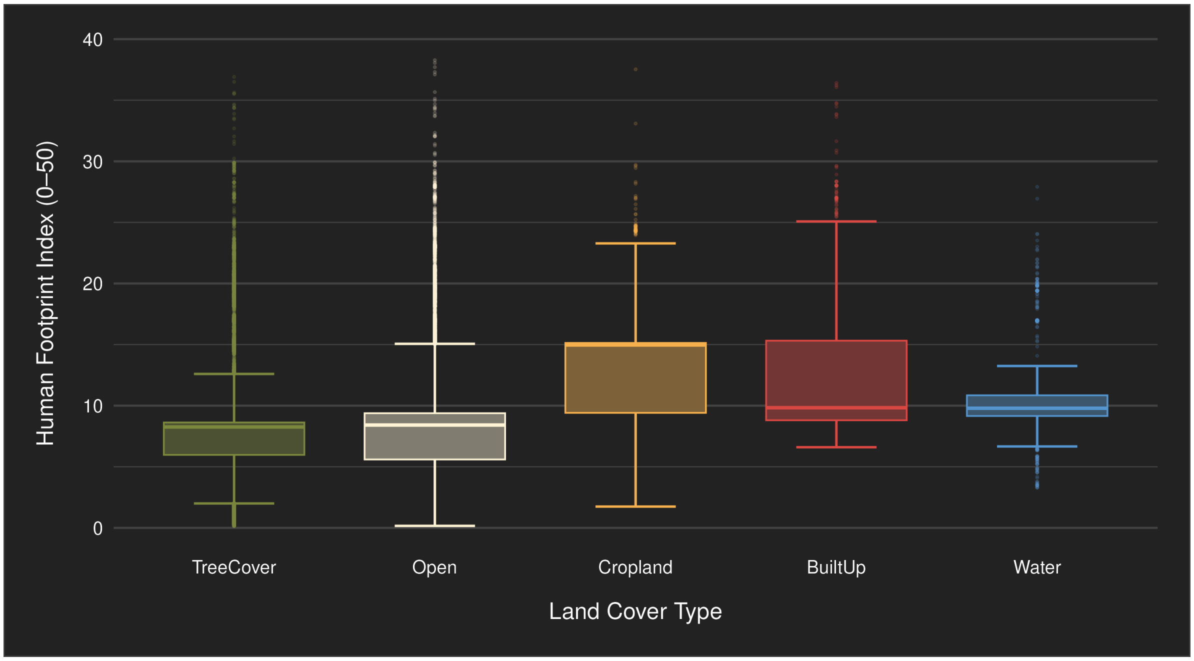


Figure 17: Variation in human footprint across and cover types

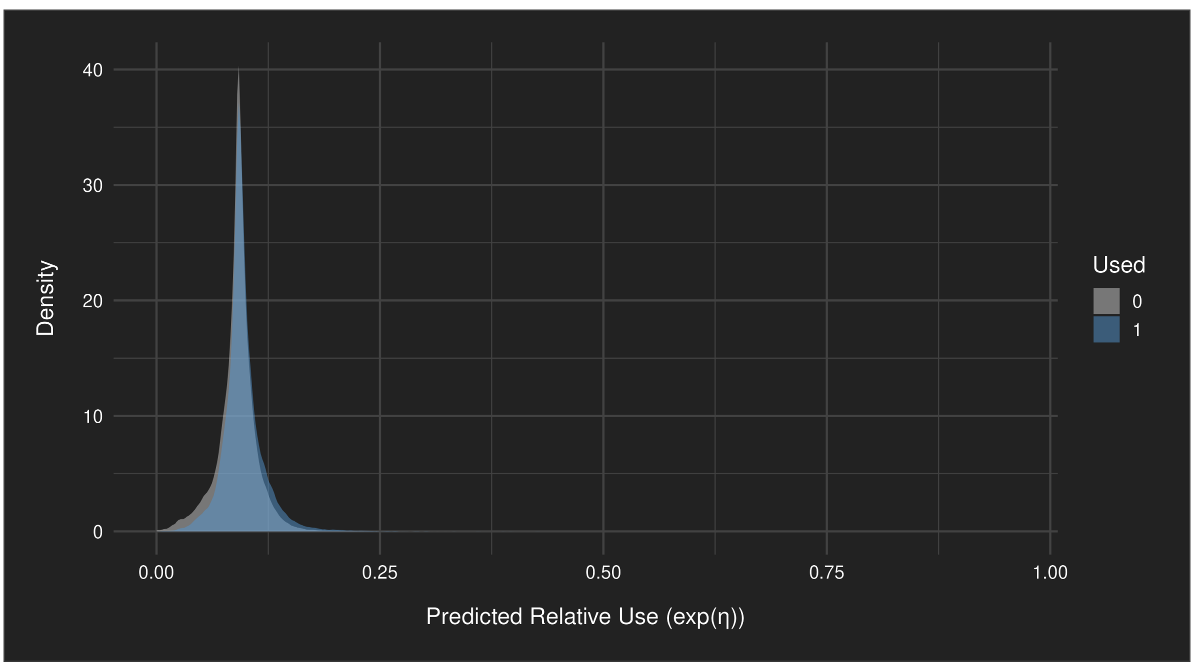


Figure 18: Predicted relative use by observed use category

7.2 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.

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