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Where will the cat cross the road? Comparing camera and GPS-based models for identifying wildlife corridors

Read Barbee [a,b,*], L. Mark Elbroch [a], Kimberly Sager-Fradkin [c], Kristen Phillips [d], Dylan Bergman [e], Bethany Ackerman [f], Shannon Murphie [g], Andrew Stratton [a], Caitlin Kupar [a], Cassandra Sullivan [h], Glen Kalisz [i], Sarah N. Sells [j], Mark Hebblewhite [b], Hugh Robinson [a,b]

[a] Panthera, 8 West 40th Street, 18th floor, New York, NY, 10018, USA
[b] Wildlife Biology Program, W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT, 59812, USA
[c] Lower Elwha Klallam Tribe Wildlife Program, 2851 Lower Elwha Road, Port Angeles, WA, 98363, USA
[d] Quinault Indian Nation, 1214 Aalis Drive, Taholah, WA, 98587, USA
[e] Point No Point Treaty Council, 19472 Powder Hill Pl NE, Poulsbo, WA, 98370, USA
[f] Skokomish Tribal Nation, North 80 Tribal Center Rd., Shelton, WA, 98584, USA
[g] Makah Nation, PO Box 115, Neah Bay, WA, USA
[h] Port Gamble S'Klallam Tribe, 31912 Little Boston Rd NE, Kingston, WA, 98346, USA
[i] Washington State Department of Transportation, Fish and Wildlife Program, 310 Maple Park SE, Olympia, WA, 98504, USA
[j] U.S. Geological Survey, Montana Cooperative Wildlife Research Unit, Wildlife Biology Program, Ecology & Evolution Program, University of Montana, Missoula, MT, 59812, USA

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ABSTRACT

Designing effective wildlife corridors is a critical conservation challenge in fragmented landscapes. GPS-based step selection functions strongly predict dispersal corridors and connectivity, but GPS collaring can be expensive and invasive. Camera-based occupancy models are widely used for connectivity analyses but may involve trade-offs in data resolution. Despite widespread use of both approaches, few studies have directly compared them using concurrent datasets. We developed a stacked single-species, single-season occupancy model and a Circuitscape connectivity surface for mountain lions (*Puma concolor*) on Washington's Olympic Peninsula, USA, and compared them with a connectivity surface from an existing integrated step selection function. Both models predicted mountain lion GPS locations well, with binned Spearman rank correlations of 1 for Circuitscape and 0.96 for the step selection function, though step selection better identified habitat use by dispersers. Connectivity predictions were moderately correlated across the landscape ($r = 0.26$), but agreement was strongest in human-dominated areas most critical for corridor planning. We conclude that GPS-based approaches are advantageous when data collection is feasible and the focus is on dispersal or fine-scale movement. However, camera-based approaches may be preferable for multi-species monitoring, large spatial and temporal scales, noninvasive sampling, when resources are limited, or when fine-scale or dispersal-specific inference is not required.

1. Introduction

Connectivity between wildlife populations is vital for maintaining biodiversity, genetic diversity, population viability, and other essential qualities of healthy landscapes (Haddad et al., 2015; Lindenmayer and Fischer, 2013; Whittaker et al., 2017). Protecting large, continuous areas of land is a foundational conservation strategy, as larger areas tend to support greater biodiversity (MacArthur and Wilson, 1967; Prugh et al., 2008). However, growing human infrastructure and increasing landscape fragmentation are making that task increasingly challenging. Identifying and maintaining viable corridors between existing protected areas is critical in such landscapes, as maintaining connectivity allows the recolonization of unoccupied areas, reduces the probability of local extinction, and facilitates ecological processes such as gene flow that contribute to the long-term resilience and persistence of wildlife populations (Hilty et al., 2020; Prugh et al., 2008).

Fahrig et al. (2021) define connectivity as "the ability of individuals to successfully move across landscapes to maintain population viability

* Corresponding author at: Panthera, 8 West 40th Street, 18th floor, New York, NY, 10018, USA.
E-mail address: rbarbee@panthera.org (R. Barbee).

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or population performance". Occupancy models based on remote cameras and step selection analyses based on GPS locations are two common approaches to modeling connectivity. Both methods reflect habitat use, but with different mechanisms and underlying assumptions. Camera data are generally inherently coarser than GPS data. However, cameras are often more widely available, less expensive, and easier to obtain than GPS tags, and they have the advantage of monitoring multiple species simultaneously. If spatial connectivity maps from occupancy models were shown to capture the essential elements of animal movement well enough to identify functionally equivalent corridors to those identified in GPS analyses, this could support the wider application of remote cameras and similar data types to predict large-scale connectivity.

Other studies have found that GPS-based approaches tend to outperform camera-based approaches for modeling connectivity, but that the different approaches tend to produce qualitatively similar results (Cushman et al., 2014; Zeller et al., 2018). In a multi-carnivore habitat-selection study in eastern Washington, Bassing et al. (2022) found that camera-based occupancy models and GPS-derived resource selection functions (RSFs) produced differing covariate-specific estimates but aligned more closely at broader, qualitative scales. Agreement between the approaches varied across species and season, but even weakly correlated model pairs highlighted similar areas of high and low predicted use. However, though informative for resource selection studies, Bassing et al.'s results did not address integrated step selection functions (iSSFs) or connectivity directly. Further research comparing the predictive capacity of occupancy models to iSSFs is needed to understand where camera-based occupancy models may be appropriate for corridor planning and what information may be lost.

Our objective for this analysis was to determine if camera-based occupancy models identified functionally equivalent movement corridors to those identified using GPS-based step selection functions from a concurrent dataset for a wide-ranging carnivore in a heterogeneous coastal landscape. We accomplished this by developing occupancy models (MacKenzie et al., 2017) as the basis for modeling connectivity using Circuitscape 5.0 (Anantharaman et al., 2020) and electrical circuit theory to approximate animal movement as current flow between a set of nodes within a landscape resistance matrix (Fig. S1). We then compared Circuitscape outputs to those from a step selection simulation model based on locations from GPS-collared mountain lions (*Puma concolor*) collected concurrently and developed using the same spatial data layers. We evaluated model performance using GPS locations withheld from model training and quantified spatial model agreement by calculating localized and global correlations between the two predictive surfaces. Mountain lions are an excellent focal species for the comparison because they are highly mobile, sensitive to human disturbance, and rely on many of the same habitats and movement corridors as other species, including deer, elk, bobcats, and bears (Noss et al., 1996; Ripple et al., 2014; Soulé and Terborgh, 1999). Based on previous research (Cushman et al., 2014; Zeller et al., 2018; Bassing et al., 2022), we predicted that connectivity estimates from the two models would differ at fine scales but produce sufficiently similar patterns at larger scales to support the continued use of occupancy modeling for connectivity analysis.

2. Methods

2.1. Study area

Our study area encompassed the Olympic Peninsula, the Willapa Hills, and adjacent lands west of the Interstate 5 (I-5) corridor north of the Columbia River in Washington state, USA. While data collection was limited to this area, we extended our model prediction area east to the

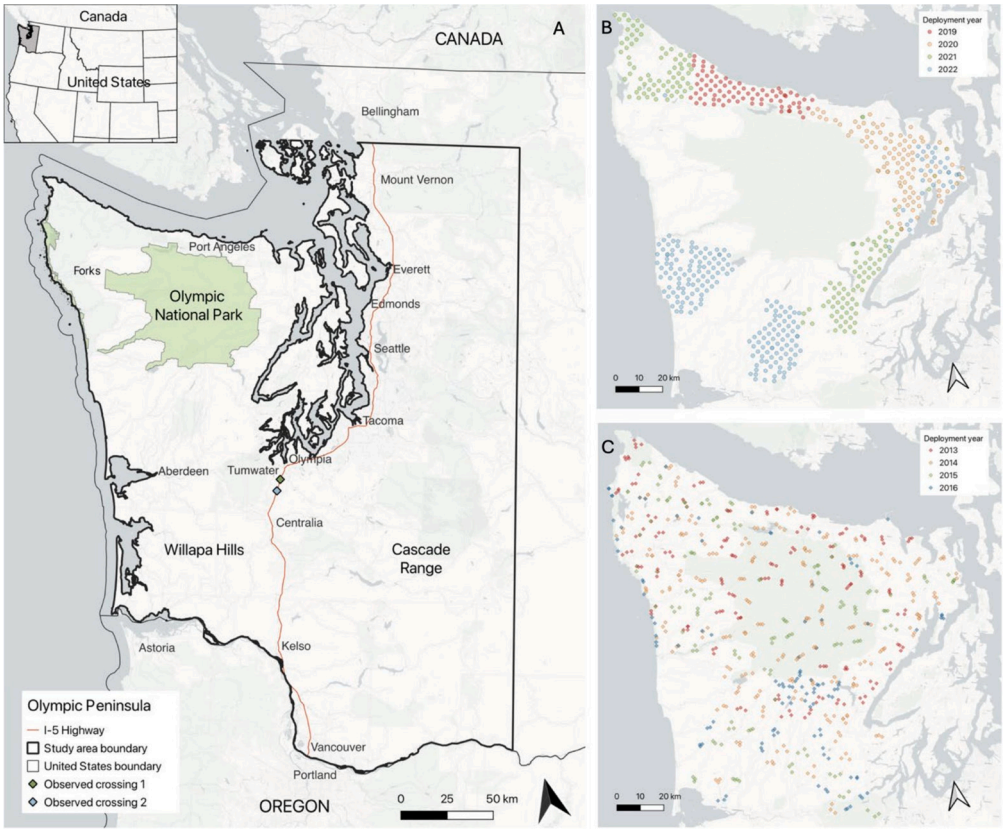


Fig. 1. A) Study area boundary for projection of occupancy and integrated step selection models for mountain lions (Puma concolor) in western Washington, USA with approximate locations of successful highway crossings by two individuals shown as colored diamonds. Camera locations by year for B) the Olympic Cougar Project, and C) the Olympic National Park Fisher Restoration Program.

Cascade mountains to capture land on both sides of the I-5 highway corridor (Fig. 1). Most of the peninsula lies within Olympic National Park (3734 km^2) and Olympic National Forest (2540 km^2). Remaining areas consist of publicly and privately managed forestry lands and Tribal lands interspersed with small to medium-sized municipalities. The landscape is composed of temperate rainforest, glaciated mountains, and rugged coastline, with elevations ranging from 0 to 2430 m. The region contains a dense network of anthropogenic linear features, including logging roads, recreation trails, and major highways. The Olympic Peninsula is an opportune system in which to study landscape fragmentation, as ongoing expansion of human infrastructure—particularly along the I-5 corridor—poses increasing threats to wildlife connectivity in the broader region (Warren et al., 2016; Zeller et al., 2023).

2.2. Camera data

We used mountain lion trail camera detections from two separate studies: a collaborative effort of the Lower Elwha Klallam, Skokomish, Makah, Jamestown S'Klallam, and Port Gamble S'Klallam Tribes, the Quinault Indian Nation, and the nonprofit Panthera called The Olympic Cougar Project (2019 - present), and the Olympic National Park Fisher Restoration Program conducted from 2013 to 2016 (Happe et al., 2017). The Olympic Cougar Project used a systematic random sampling design with 2 km × 2 km spacing. Because of the extreme density of vegetation, the camera position could be adjusted within a 50–100 m radius of the random point to obtain a viewshed large enough to detect the species of interest without explicitly selecting for linear features. Vegetation was also cleared as needed to improve visibility and reduce false triggers. Browning trail cameras were programmed for 24-hour motion detection and attached to trees 18 in (46 cm) above ground facing north to maximize potential for detection of mountain lions, bobcats, coyotes, deer, and elk and to minimize false triggers from sunlight. Field crews checked stations every one to two months depending on anticipated trigger rates. Cameras were deployed from April to December each year with the full grid operational from June 1st to October 1st. No stations were baited. The number of camera stations increased over time from 76 in 2019 to 518 in 2022 (Fig. 1). Due to processing constraints, only 454 of these sites had data available at the time of analysis (Table S1).

The Olympic National Park Fisher Restoration Program utilized a systematic sampling design over a 24 km^2 hexagonal sampling grid covering nearly the same area as the Olympic Cougar Project. Instead of sampling every cell within multiple concentrated grids, the Fisher Restoration Program selected every other cell across the entire area for sampling based on a random starting point and then used Generalized Random Tessellation Stratified (GRTS) sampling (Stevens and Olsen, 2004) to determine the sampling order. Three camera stations were placed randomly within suitable fisher habitat at least 1 km apart within each sampled cell. At each station, the camera was focused on a piece of chicken bait and "Gusto" scent lure (Minnesota Trapline Products, Inc.) attached to a nearby tree and a triangular cubby box for hair collection that was also baited with chicken. Field crews visited each station three times at 14-day intervals following setup, resulting in 6 weeks of sampling within each cell. Cameras were deployed between May and November each year (Happe et al., 2017) (Fig. 1).

Due to differences in time and sampling designs, we chose to analyze the data as a point process with the camera stations as sampling units rather than the grid cells (Steenweg et al., 2018). We also accounted for differences in sampling designs by including a study covariate in the detection portion of the occupancy models. We evaluated presence and absence within discrete 2-week intervals (Steenweg et al., 2016).

2.3. Environmental data

We assembled a broad range of environmental and anthropogenic covariates previously shown to influence mountain lion movement and resource selection. These included vegetation greenness and productivity as proxies for prey availability, forest and vegetation composition to represent cover for hunting and denning, and measures of human population and road density, among others (Bassing et al., 2022; O'Malley et al., 2024; Zeller et al., 2017b). We hypothesized that mountain lions would select areas offering abundant prey, adequate cover for ambush hunting and denning, and limited human disturbance (Coon et al., 2020; Gaston et al., 2024). Initially, we compared the performance of a number of covariates that could be used to assess these hypotheses, and then we selected the one from each grouping that exhibited the strongest relationship to mountain lion occupancy. These groupings included 1) covariates that might be proxies for prey availability: the Normalized Difference Vegetation Index (NDVI), the Enhanced Vegetation Index (EVI), Gross Primary Productivity (GPP), Net Primary Productivity (NPP), precipitation (mm/year) and distance to water, 2) covariates associated with vegetative cover for hunting and denning: percentage cover of trees, non-tree vegetation and non-vegetated area, and 3) covariates for human disturbance: road density (km/km^2), distance to roads, and human impact drivers (population, infrastructure, and land use). NDVI and EVI both measure the concentration of green leaf vegetation using near infra-red and visible radiation reflected from the earth's surface. EVI uses the blue band to apply additional corrections for atmospheric distortions and does not become saturated as easily in densely vegetated areas. GPP represents the total energy captured by photosynthesis in an area, and NPP, calculated as GPP – Respiration, represents the rate of biomass accumulation (CEOS Land Product Validation Subgroup, 2026; Measuring Vegetation (NDVI and EVI) - NASA Science, 2026). We also examined a range of topographic covariates including elevation, slope, aspect, terrain ruggedness index (TRI), and topographic position index (TPI) due to their importance for ambush cover and their influence on the energetic costs of movement. Additional details and citations for each of these covariates and their hypothesized effects are available in Table S2. For temporal covariates, we generated annually averaged rasters for each year (2013–2023) and matched them to the appropriate sampling year. We generated distance to and density metrics from OpenStreetMap roads, which we reclassified into "major", "residential", "service roads and tracks", "non-motorized", "paved", and "unpaved" classes to capture effects of different road types. Major roads included all motorways, primary, secondary, tertiary, trunk, and link roads. Residential roads included lower-trafficked roads in urban environments or near major roads. Service roads and tracks included all service and track categories. Non-motorized roads included any roads where vehicles are not permitted. Paved and unpaved categories were based purely on pavement status and not traffic or use. (Table S3) (OpenStreetMap contributors, 2025). To maximize spatial precision in predicting road-crossing locations and to facilitate comparison with existing step-selection models, we retained all covariate layers at their original spatial resolution, ranging from 30 m to approximately 5 km (Zeller et al., 2017a). We generated all layers using Google Earth Engine (Gorelick et al., 2017) or QGIS (QGIS.org, 2024).

2.4. Occupancy model construction

We fit stacked, single-species, single-season occupancy models in a Bayesian framework using the R package ubms (Kellner et al., 2021). We ran models for three chains of 1500 iterations each in the univariate feature selection phase and 10,000 iterations each for the final stages of model selection and validation. We verified convergence by examining trace plots and ensuring that all $\widehat{R} \leq 1.05$ and compared models using the Leave One Out Cross-Validation (LOOCV) methods for ubms models available in the R package loo (Vehatri et al., 2023). Higher leave one out expected log predictive density (ELPD_LOO) scores and lower Leave One Out Information Criterion (LOOIC) scores indicated better performing models with higher predictive capacity.

Following standard procedure in the development of occupancy models, we first identified the detection submodel that best fit the data (MacKenzie et al., 2017). Covariates considered for the detection model included the number of active camera days per sampling interval, continuous and binary variables for tree bait and snare bait presence, both fixed and varying through time, and a binary variable for study. Because the number of candidate terms was relatively small, we fit models with all combinations of the top performing variables from each group (effort, bait, snare, study) to the data. We compared their ELPD_LOO scores and their LOOIC scores and selected the model that optimized model fit while most parsimoniously capturing the variation in detection.

Holding the top detection model constant, we fit univariate models for each covariate with and without quadratic terms and with a random effect for camera station. For each covariate, we selected the quadratic model only if it had an ELPD_LOO score at least 4 units greater than the linear model and if the 90% credible interval of its coefficient estimate did not cross zero (Sivula et al., 2020). We divided covariates into five functional groups: terrain, vegetation productivity, vegetation composition, human impact, and road metrics. For each of these groups, we retained the covariate with the highest ELPD_LOO score. If ΔELPD_LOO $\leq$ 4 between two models, we selected the covariate with the lower LOOIC (ΔLOOIC $\geq$ 2). Failing that criterion, we selected the covariate with a 90% credible interval not crossing zero. If neither crossed zero, we selected the covariate with the largest absolute effect size. We repeated the above selection process for each remaining pair of covariates correlated with $|r| \geq 0.5$ and combined all remaining covariates into a global model. We considered effects to be statistically significant when the 95% credible interval of the coefficient estimate did not overlap zero. However, we used this only as a tool for interpretation and did not exclude variables on this basis. We refer to our occupancy model outputs as probability of use throughout, as this presents a more accurate interpretation than true occupancy when the closure assumption is violated by highly mobile species (Mackenzie and Royle, 2005; Steenweg et al., 2018).

2.5. Circuitscape

We used outputs from our top occupancy model to create a resistance surface to estimate landscape connectivity using Circuitscape 5.0 implemented in Julia (Anantharaman et al., 2020). Circuitscape uses electrical circuit theory to estimate current flow between a set of defined nodes across a heterogeneous landscape resistance matrix. We calculated the probability of use by mountain lions for each 30 m × 30 m pixel in the study area using the formula $p(x) = plogis(\sum x\beta)$ where x is a vector of habitat covariates, β is the coefficient vector estimated from the model, and the *plogis*() function transforms the output from the logit scale to a probability scale bounded [0,1] (Brennan et al., 2020) (Figs. S2-S3). Following Zeller et al. (2012) and Brennan et al. (2020), we derived the resistance surface using the inverse transformation where *resistance* $= 1 -$ *probability of use*. We generated 20 source nodes evenly spaced along the perimeter of a 20% buffer around the study area (Koen et al., 2014). We stretched resistance values to a 1 to 100 scale using the stretch function in the terra package (Hijmans, 2025), set ocean areas between the nodes and the peninsula to the maximum resistance of 100, and set permanent inland water bodies with an area $\geq$ 2 km^2 to a very high but not impassable resistance value of 90 (Fig. S4). We then created a constant resistance surface with all values equal to 1, ran Circuitscape on both surfaces with the same nodes using the all-to-one method and the cg + amg solver, and calculated a normalized connectivity surface by dividing the cumulative current map of the empirical surface by that of the constant surface (Anantharaman et al., 2020). This normalizing operation served to remove the effects of node placement and study area shape on the model outputs (Brennan et al., 2020). Lastly, we capped extreme values at the 95th percentile using the clamp function in the terra package and masked all non-land pixels from the final output (Fig. S5).

2.6. Step selection movement simulation

We developed a movement-based connectivity surface from a population-level Poisson integrated step selection function with random slopes for individual animals. As described by Muff et al. (2020), the inclusion of random slopes allows each animal to respond differently to landscape features and accounts for that variation in the population-level coefficient estimates. The training dataset included 328,462 GPS locations from 82 mountain lions (13 dispersing females, 27 resident females, 21 dispersing males, 21 resident males) collected between 2011 and 2023 (Table S4) with the approval of the Institutional Animal Care and Use Committee at the University of Idaho (IACUC-2020-15). Individuals were fitted with Lotek LiteTrack Iridium and Vectronic GlobalStar and VERTEX Lite GPS transmitters programmed to record locations every 1 to 4 h. Tracks were resampled to 2-hour intervals (+/− 45 min) to standardize the duration of steps, resulting in 34,247 steps for analysis. We removed steps of <100 m, which may be considered stationary, and steps >20 km which were likely to be erroneous. We then excluded individuals with <30 steps or <20 days of steps to ensure all individuals had enough data for reliable inference (Sells et al., 2022). We identified dispersers as individuals between 12 and 18 months old exhibiting a clear dispersal event, indicated as a spike in net squared displacement over time (Bunnefeld et al., 2011) and/or by visual inspection of the track line. For the iSSF analysis, we generated ten available steps for each observed step by randomly drawing from the step length (gamma) and turn angle (Von Mises) distributions for each individual and extracting covariate values at the end of each step, matching environmental data to the year in which each step occurred (Signer et al., 2019).

We fit all models in a Bayesian framework using the INLA package in R (R Core Team, 2025; Rue et al., 2009). We first fit univariate Poisson point process models with random slopes for each covariate, testing linear and quadratic forms. We used 4-fold cross-validation of Spearman rank correlations as our primary model selection metric and used the Watanabe-Akaike Information Criterion (WAIC) only to break ties, as information-theoretic metrics can favor overly complex models and may not reflect predictive capacity (Sells et al., 2022; Squires et al., 2013). We retained quadratic terms when their cross-validation score exceeded the linear model by $\geq$0.1, or when scores were comparable and ΔWAIC $\geq$2.

To formulate the global model, we grouped covariates into five functional categories (terrain, vegetation productivity, vegetation composition, human impact, and road metrics) and retained the top-performing covariate per group based on cross-validation score, using credible intervals and effect size to break ties. We favored more specific covariates over general ones only when ΔWAIC $\geq$2, and removed correlated covariate pairs ($|r| \geq 0.5$) retaining the higher-scoring variable. Covariates with cross-validation scores <0 were excluded. All remaining covariates were included in the global model with movement terms and individual-level random effects. We intentionally chose not to include explicit variables for sex and dispersal status in the iSSF model and to simulate movement with population-level coefficients in order to make our iSSF approach more directly comparable to the occupancy approach, which lacks demographic distinctions.

Following the general approach of Sells et al. (2022, 2023), we projected the top model to the landscape using the same method and environmental data as the occupancy model (Section 2.5). The step selection model and projected surface were then used to simulate 200,000 paths of 4380 steps starting at random points within the study area, representing 200,000 individual mountain lions with population-level movement parameters and selection preferences moving freely and continuously around the landscape for approximately one year of 2-hour steps without rest periods. Each simulation began at a random point within the study area on either side of the I-5 highway corridor and

progressed by selecting one of ten possible steps drawn randomly from empirical gamma and von Mises distributions fitted to the full population. Step selection was random but weighted by the probability of use value at the end of each step, with higher values more likely to be selected. We estimated connectivity values as a count of the number of simulated points that fell within each pixel. Further information regarding our step selection simulation procedure is available in the supplementary material.

2.7. Comparing models of occupancy-based circuit connectivity to iSSF-derived movement

We compared the predictive performance of the Circuitscape and iSSF models by classifying each surface into ten equal-area quantile bins, extracting the bin ranks for a set of 193,023 GPS locations collected from 55 female and 48 male mountain lions in the same area between 2011 and 2024, and calculating the Spearman rank correlation of the number of locations that fell within each bin (Sells et al., 2022, 2023) (Table S5). We then assessed the spatial agreement of predictions by calculating the pixelwise Pearson correlation between them at the landscape level in base R (Brennan et al., 2020) and at the local level using a 1 km moving window via the corLocal() function in the raster package (Hijmans, 2023).

3. Results

3.1. Occupancy and Circuitscape models

The camera dataset ranged from 2013 to 2022 and covered 1210 sites with a total of 2065 station-years and 16,139 active 2-week sampling periods across all sites and years. Mountain lions were detected at 251 sites across all years. The top occupancy model contained the Multi-scale Topographic Position Index (mTPI), aspect, EVI, percent non-vegetated area, the WCS Human Impact Index and the density of all roads (km/km^2) on probability of use (ψ) (Fig. 2a). The detection sub-model (p) included days of camera activity and a binary variable for study (Fig. 2b). Days of camera activity during the 2-week sampling period at each site was the only variable that consistently and significantly influenced detection probability ($\beta = 0.70$; 95% CrI: 0.45, 0.97) (Table S6). Probability of use increased with more western aspects ($\beta = -0.23$; 95% CrI: −0.45, −0.02) and decreased with higher human impact ($\beta = -0.34$; 95% CrI: −0.61, −0.09). Additional positive effects of higher topographic positions ($\beta = 0.23$; 95% CrI: −0.02, 0.50), and EVI values ($\beta = 0.23$; 95% CrI: −0.03, 0.50), and negative effects of higher road densities ($\beta = -0.18$; 95% CrI: −0.41, 0.04), and percentages of non-vegetated areas ($\beta = -0.17$; 95% CrI: −0.42, 0.07) on probability of use were notable but had 95% credible intervals marginally overlapping 0 (Fig. 2a, Table S7).

The Circuitscape cumulative current density surface closely mirrored the occupancy prediction surface with high current flow through areas with high EVI values and low flow through areas of high human disturbance. Notable areas of high flow included the northwest and southwest regions of the peninsula. Prominent areas of low flow included population centers in the northeastern corner of the peninsula, the I-5 highway corridor, the city of Olympia at the southern end of Puget Sound, and the Seattle metropolitan area (Fig. 3).

3.2. iSSF model

The top iSSF model contained elevation, NPP, percentage tree cover, a quadratic for percentage tree cover, percentage non-vegetated area, density of all roads (km/km^2), and human population density (people / km^2) (Fig. 2c) as well as the movement parameters for step length, ln (step length), and cos(turn angle) standard for iSSF models (Avgar et al., 2016) (Table S8). Mountain lions selected for NPP ($\beta = 0.04$; 95% CrI: 0.0006, 0.08) and avoided road density ($\beta = -0.03$; 95% CrI: −0.06, −0.005) and human population density ($\beta = -0.06$; 95% CrI: −0.11, −0.02). The quadratic term for percentage tree cover was also significant and negative ($\beta = -0.03$; 95% CrI: −0.05, −0.02), suggesting selection for intermediately forested areas. The effect of percentage non-vegetated area was negative but non-significant ($\beta = -0.01$; 95% CrI: −0.05, 0.03). The effect of elevation was negative on average but varied widely ($\beta = -0.2$; 95% CrI: −0.46, 0.06) (Table S8).

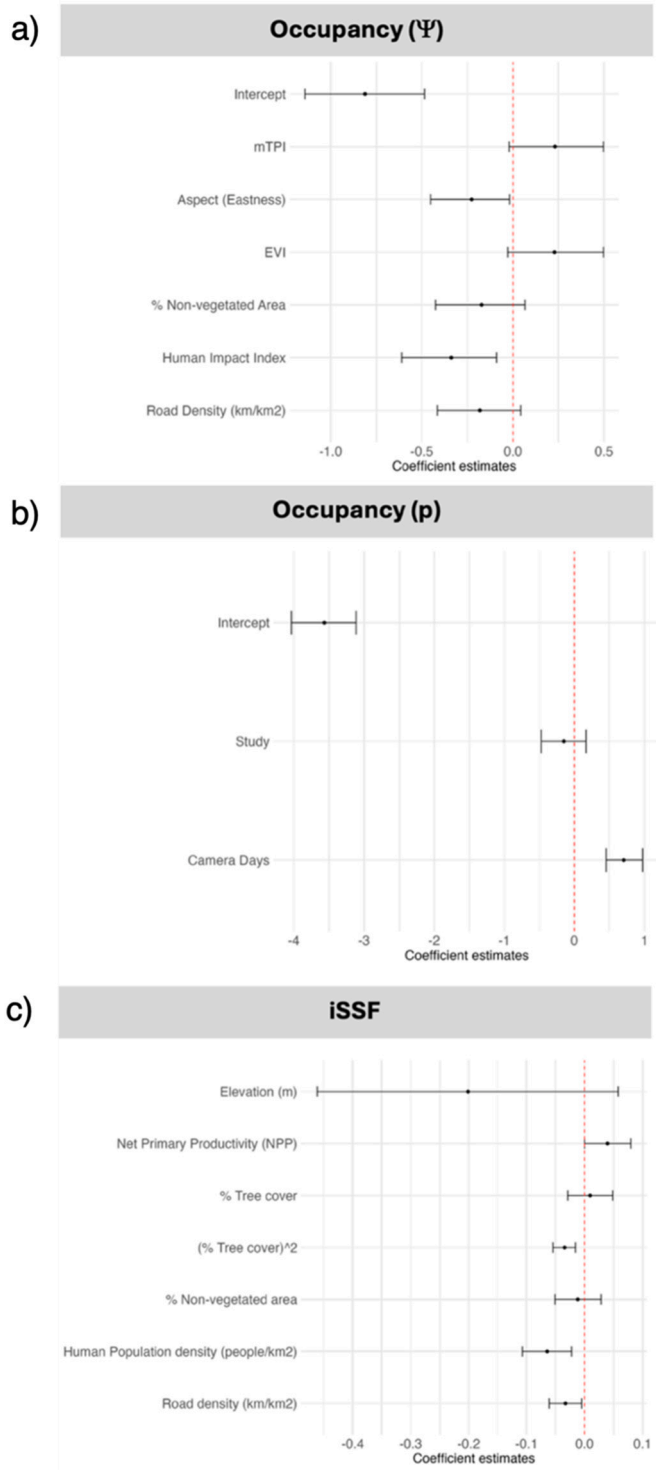


Fig. 2. Standardized, untransformed beta coefficient estimates with 95% credible intervals from the top occupancy and integrated step selection models fitted to mountain lion (Puma concolor) detections from remote cameras and GPS locations in western Washington state, USA between 2013 and 2023.

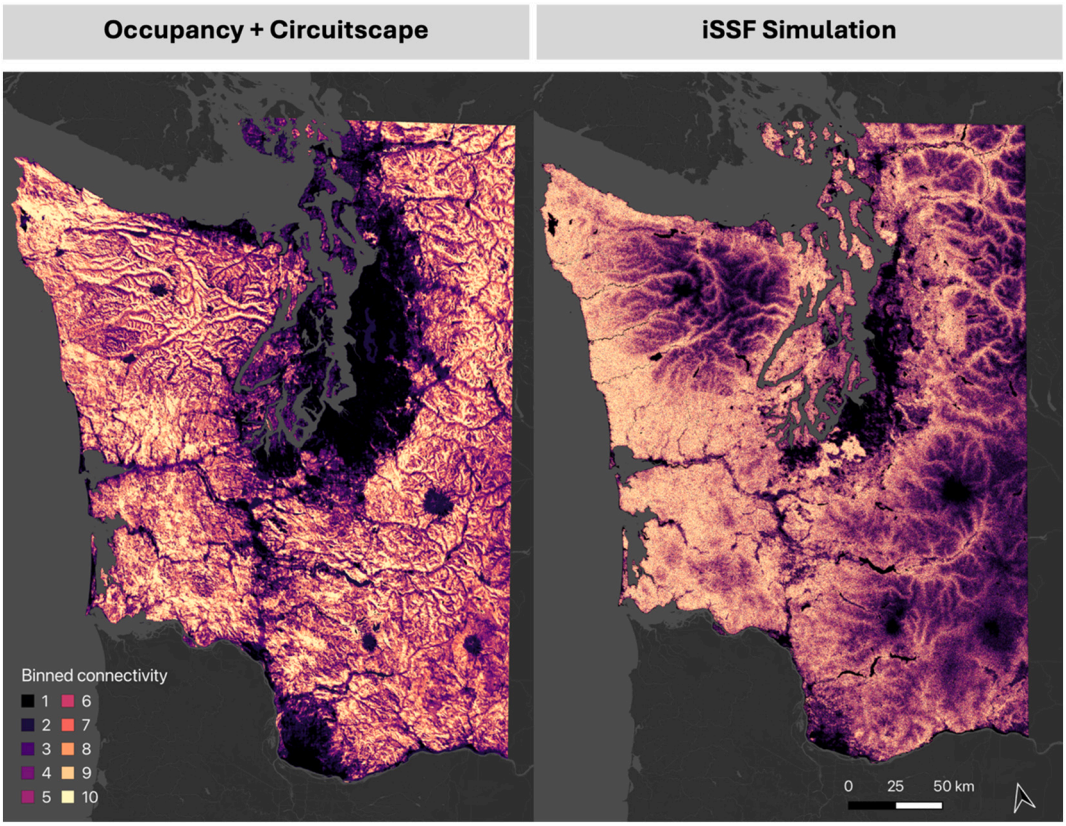


Fig. 3. Connectivity surfaces from Circuitscape and integrated step selection models for mountain lions (Puma concolor) in western Washington state, USA divided into ten equal area quantile bins. 1 indicates low connectivity, and 10 indicates high connectivity.

3.3. Comparing models of occupancy-based circuit connectivity to iSSF-derived movement

The occupancy and iSSF models differed in their top-ranked covariate sets but aligned in their identification of broad drivers of mountain lion habitat selection. Both approaches indicated negative responses to human disturbance—including human population density, road density, and the Human Impact Index—and positive associations with proxies for prey availability and ambush cover such as EVI and NPP (Fig. 2, Tables S6-S8).

Both the Circuitscape and iSSF models validated well against the 193,023 known locations from GPS-collared mountain lions at the population level, with Spearman rank correlations of 1 and 0.96 respectively. The current density surface contained 21.91% of all locations within the highest current density bin and 72.82% of locations within the top 5 current density bins, while the iSSF model contained 23.57% of locations in the top connectivity bin and 81.38% within the top 5 connectivity bins (Fig. 4).

However, the models diverged in their ability to predict mountain lion space use across demographic categories (female residents, female dispersers, male residents, and male dispersers). The iSSF simulation performed nearly identically across all categories with rho scores = 0.96 for all groups. In contrast, the Circuitscape model performed well for residents ($r = 1$ for females; r = 1 for males) but relatively poorly for dispersers ($r = 0.37$ for females; $r = 0.66$ for males) (Fig. 4). Predicted connectivity surfaces from the two approaches differed in their predictions of mountain lion space use across the landscape, with a Pearson correlation of 0.26 across all 30 m pixels. Local agreement between model predictions based on a 1 km moving window correlation was strongest in human-dominated areas such as the I-5 highway corridor and highly populated areas in the northeast of the peninsula. These human-dominated areas, which we defined as pixels with human population index scores ≥ 6, or within the top 10% of human population values across the landscape, exhibited a significantly higher median correlation than non-human-dominated areas (+0.40; 95% CI: 0.394–0.402; permutation test $p < 2.00e\text{-}04$) (Table S9-S10). Model agreement appeared weakest in the more rugged and high elevation areas of the Olympic and Cascade mountains. Local correlations between models across much of the remainder of the landscape were intermediate (Fig. 5).

4. Discussion

Our comparison of camera-based occupancy modeling to GPS-based step selection highlights the strengths and limitations of each approach to studying carnivore connectivity. The iSSF model generally outperformed the occupancy-based Circuitscape model—especially for dispersing individuals—and provided finer-resolution, behaviorally realistic predictions of connectivity. This is consistent with past work showing that GPS-derived movement models tend to capture functional connectivity more accurately than camera-based approaches, largely due to their ability to capture finer-scale movement decisions (Cushman et al., 2014; Unnithan Kumar and Cushman, 2022; Zeller et al., 2018). At the same time, both models identified similar drivers of mountain lion habitat use at broad scales, including avoidance of human disturbance and positive associations with vegetative cover and proxies for prey availability. This pattern aligns with Bassing et al. (2022), who found that camera-based occupancy and GPS-based habitat selection models often differ in covariate-specific estimates but converge at broader spatial scales.

Coefficient estimates from both models generally corresponded well with those from models previously developed for mountain lions (Bassing et al., 2022; Nisi et al., 2022; Peterson et al., 2021) (Tables S6-S8).

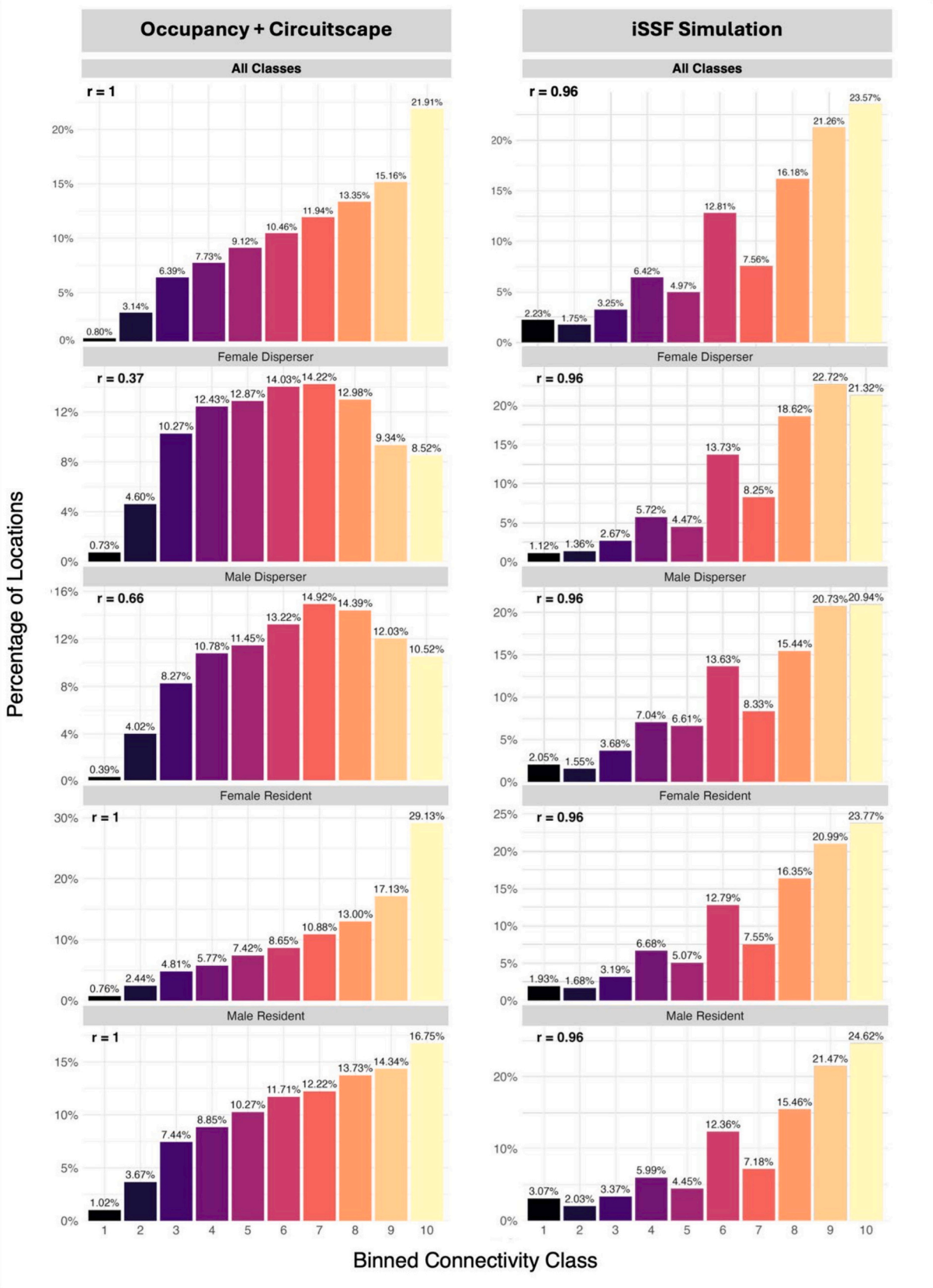


Fig. 4. Percentage of 193,023 mountain lion (Puma concolor) GPS locations from western Washington state, USA in each equal area quantile bin for Circuitscape and integrated step selection models across the population and by demographic category with Spearman rank correlations. 1 indicates low connectivity, and 10 indicates high connectivity. Higher r values indicate better predictive performance.

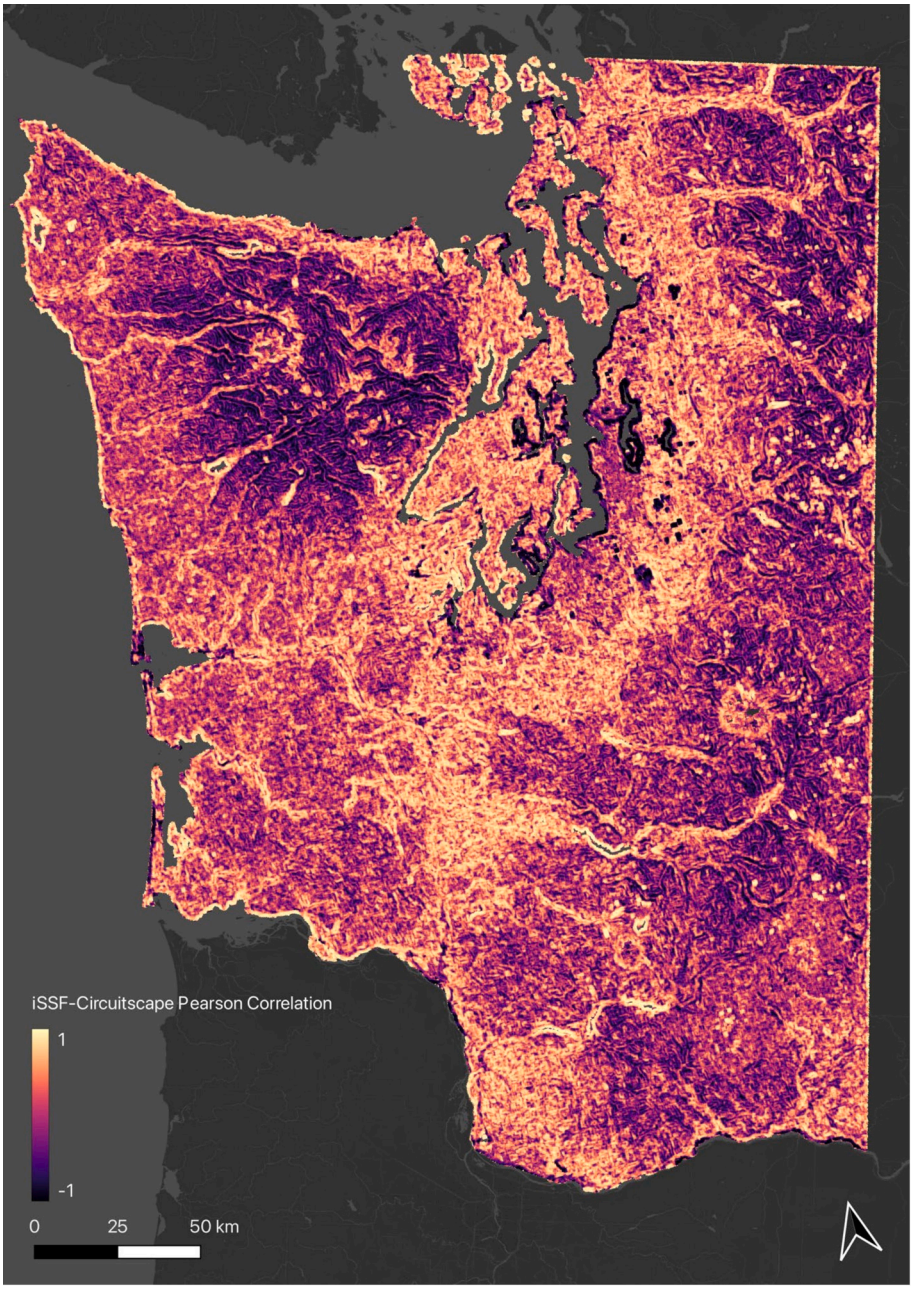


Fig. 5. 1 km moving-window Pearson correlation between the connectivity surfaces from Circuitscape and integrated step selection models for mountain lions (Puma concolor) in western Washington state, USA.

Though both models were constructed using identical candidate data layers and comparable model selection procedures, they emphasized different landscape metrics. Variable selection for the occupancy model appeared to favor coarser, more generalized measures of human disturbance such as the full Human Impact Index, whereas the step selection model selected the more specific metric of human population density. Elevation emerged as a strong predictor of mountain lion use in the step selection analysis but not in the occupancy analysis, perhaps because the GPS location data covered a wider range of elevations than the camera data (−3 to 2026 m for GPS, 6 to 1590 m for cameras). mTPI took the place of elevation in the occupancy model, but likely overestimated mountain lion use of high elevation ridgelines in the Olympic and Cascade mountains (Fig. 3). Differences in model predictions were most pronounced in areas of high elevation as a result (Fig. 5). The occupancy model also suggested a stronger avoidance of non-vegetated areas, whereas the step selection analysis highlighted an attraction to areas of intermediate to high canopy cover. Predictions from both models were projected outside of the range of observed data. Therefore, predictions from both models at extreme values, especially elevation, and those outside the peninsula should be interpreted with caution.

Although the overall correlation between predicted connectivity surfaces was modest, agreement was strongest in human-dominated areas most important for corridor planning. These areas exhibited a median between-model correlation 0.40 higher than the median for non-human-dominated areas (95% CI: 0.394–0.402; permutation test $p <$ 2.00e-04) (Fig. S6). Both models identified similar connectivity channels across the I-5 highway corridor which were broadly consistent with two crossings by GPS-tagged dispersing mountain lions observed during our study, two previously-identified expert-based least-cost paths (Washington Wildlife Habitat Connectivity Working Group, 2022), and two eco priority zones outlined in the most recent Washington statewide connectivity action plan (Washington Wildlife Habitat Connectivity

Working Group, 2025) (Fig. S7). These convergent patterns suggest that, despite differences in resolution and parameterization, camera-based models still capture the essential connectivity features of constrained landscapes where movement options are limited. However, the weaker performance of the occupancy model for dispersers indicates that camera-based approaches do have disadvantages, especially where conservation planning is attempting to facilitate the movement of dispersing animals between core populations. Dispersing animals tend to exhibit a higher tolerance for sub-optimal habitat (Keeley et al., 2017). This difference in predicted habitat use between residents and dispersers is evident in the validation scores of the iSSF predictive surface used as the landscape matrix for the simulation. Residents exhibited the expected increase in use with the model's predicted probability of use. Dispersers of both sexes, however, appeared slightly more likely to use the second-highest probability of use category than the highest, suggesting a somewhat higher tolerance for suboptimal habitat. Additional stochasticity in the movement simulation smoothed over this difference somewhat but did not eliminate it (Fig. S8).

We chose not to include sex and dispersal status explicitly in the iSSF model and to simulate movement with population-level coefficients in order to make our iSSF approach more directly comparable to the occupancy approach. However, the random slopes iSSF formulation still accounts for demographic variation implicitly at the individual level, and is therefore still more informed than occupancy models which do not distinguish between individuals at all.

All islands highlighted in the connectivity surfaces are potentially accessible to mountain lions based on the maximum swimming distance of 2.5 km observed by a dispersing male during the study. Saltwater bodies between the peninsula and the mainland were treated as no data regions in the iSSF simulations but were still occasionally traversable if smaller than the maximum possible step length. In contrast, these areas were set to maximum resistance (100) in Circuitscape due to the tendency of Circuitscape to overestimate current flow around the edges of no data regions (Belote et al., 2022). Therefore, while plausible, the frequency of visits to these islands may be somewhat overrepresented by both models.

The contrasts between the two modeling frameworks reflect important conceptual differences in how movement is represented. SSF-based simulations generate correlated random walks in which individuals make stepwise decisions based on local environmental cues and empirically derived behavioral tendencies (Avgar et al., 2016; Duchesne et al., 2015). In contrast, Circuitscape models a diffusion-like random walk whose current-flow solutions do not require animals to possess perfect knowledge of the landscape but are still influenced by the global configuration of the resistance surface (McRae et al., 2008). Consequently, SSFs capture fine-scale movement behavior and perceptual limits, whereas Circuitscape characterizes landscape-level dispersal potential. This distinction also aligns with recent findings by Sells et al. (2023) which showed that undirected simulations of grizzly bear movement outperformed directed pathways with predefined endpoints and more optimized movements, reinforcing the idea that movement is better represented by local, stepwise processes than by globally optimized or fully directional models.

Overall, our results suggest that GPS-based connectivity models remain the preferred option when the goal is to understand dispersal, individual-level movement processes, or fine-scale route selection. In contrast, occupancy-derived connectivity may be well-suited for multi-species monitoring, long-term studies, and corridor planning in highly developed landscapes where movement is strongly constrained and where noninvasive, cost-effective sampling is a priority. Importantly, our results support that dispersing individuals with higher tolerance for sub-optimal habitat may select habitat differently from resident adults, and that models based only on resident data or that do not account for individual variation may fail to capture these differences. Further investigation into intra-specific variation in habitat selection and its continued incorporation into connectivity models is needed to evaluate the extent of this effect in different systems. Scientists and managers may also carefully consider whether their corridor planning is intended to support residents in safe habitat or the temporary movement of dispersers, or both, as our work highlights potential tradeoffs in accounting for intra-specific variation when designing connectivity modeling workflows.

CRediT authorship contribution statement

Read Barbee: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **L. Mark Elbroch:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Kimberly Sager-Fradkin:** Writing – review & editing, Resources, Project administration, Investigation, Funding acquisition. **Kristen Phillips:** Writing – review & editing, Resources, Project administration, Investigation, Funding acquisition. **Dylan Bergman:** Writing – review & editing, Resources, Project administration, Investigation, Funding acquisition. **Bethany Ackerman:** Writing – review & editing, Resources, Project administration, Investigation, Funding acquisition. **Shannon Murphie:** Writing – review & editing, Resources, Project administration, Investigation, Funding acquisition. **Andrew Stratton:** Project administration, Investigation. **Caitlin Kupar:** Project administration, Investigation. **Cassandra Sullivan:** Project administration, Investigation. **Glen Kalisz:** Funding acquisition, Data curation. **Sarah N. Sells:** Writing – review & editing, Supervision, Resources, Methodology. **Mark Hebblewhite:** Writing – review & editing, Supervision, Resources, Methodology. **Hugh Robinson:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used Claude.ai and ChatGPT to assist with brevity and flow of the manuscript. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the published article.

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Declaration of competing interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.112029.

Data availability

Data contain sensitive species locations, and ownership is divided among many partner organizations, not all of which have given permission for archival. Please contact the authors for data access. Code is available on GitHub at the following URL: https://github.com/read-barbee/olympic_cougar_connectivity_occupancy.

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