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ARTICLE

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Western spotted skunk spatial ecology in the temperate rainforests of the Pacific Northwest

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Abstract

A major threat to small mammalian carnivore populations is human-induced land use change, but conservation and management are inhibited by limited knowledge about their ecology and natural history. To fill a key knowledge gap of the western spotted skunk (*Spilogale gracilis*), we investigated their spatial ecology at the landscape and home range scale in the temperate rainforests of the Oregon Cascades during 2017–2019. For the landscape scale analysis, we used detections of western spotted skunks at 112 baited camera traps and fitted a dynamic occupancy model to investigate spatial distribution and drivers of inter-seasonal and inter-annual changes in occupancy. Concurrently, we radio-collared 25 spotted skunks (9 female, 16 male) and collected 1583 relocations. Using continuous-time movement models, we estimated large home range sizes for both male and female spotted skunks, relative to their body mass, and highly overlapping home ranges that indicated a lack of territoriality. Using these home ranges, we fitted a resource selection function using environmental covariates that we assigned to various hypotheses such as resources, predator avoidance, thermal tolerance, and disturbance. Overall, western spotted skunks were widely distributed across our study area (seasonal occupancy up to $63.7 \pm 5.3\%$) and highly detectable (weekly detection probability $= 41.2\%$). At both spatial scales, spotted skunks selected wetter areas and local valleys, which we attributed to areas with more food resources. At the home range scale, spotted skunks selected locations with lower predation risk and areas surrounded by more previously logged forests. In this montane environment, inter-seasonal contractions in the spatial distributions of spotted skunks were strongly driven by their response to cold temperature and accumulated snow. This was especially evident when seasonal occupancy declined significantly following a severe heavy snow event in February 2019. Given that there is little information available on the natural history of the western spotted skunk, these results provide essential information about their ecology to focus future monitoring efforts and may help identify potential threats (e.g., forest management, severe snow events, or wildfires) to this species.

KEYWORDS
camera trap, dynamic occupancy, movement, resource selection function, small carnivore, space use, *Spilogale gracilis*

INTRODUCTION

Small carnivores (<21.5 kg) are among the most sensitive mammals to changes in environmental conditions (Jachowski et al., 2023; Marneweck et al., 2022). Recent evidence suggests that small carnivore populations are declining globally (Belant et al., 2009; Marneweck et al., 2021), threatening their ecological function as predators, insectivores, frugivores, and seed dispersers (Do Linh San et al., 2022; Marneweck et al., 2022). One of the major threats to small carnivores is human-induced land use change such as the conversion of forest into large-scale agricultural plantations, which can cause habitat fragmentation and degradation (Marneweck et al., 2021) and rapid localized extinction even for common species (Gompper & Hackett, 2005; Lindenmayer et al., 2011). Some mechanisms for localized extinction of small carnivores in these degraded landscapes could include an increase in the abundance of other larger predators or a decrease in the amount of cover, which would hinder their ability to avoid predation. Therefore, understanding the habitat requirements of species and restoring their habitat can strongly influence the success of conservation efforts (Wilcove et al., 1998), but determining habitat requirements of a species can be challenging once habitat has been converted or once the species is rare or extirpated from a region. This has led to a growing recognition of the need to study common species while they are still common (Lindenmayer et al., 2011).

In western North America, the decline of small forest carnivores such as fishers (*Pekania pennanti*) (Aubry et al., 2013; Aubry & Lewis, 2003; Zielinski et al., 2004) and martens (*Martes caurina humboldtensis*) (Moriarty et al., 2011; Slauson et al., 2007; Tweedy et al., 2019) is associated with even-aged forest management practices that convert complex multilevel forests into simple single-canopy plantations (Hayes et al., 1997) that reduce the availability of large-diameter trees, snags, logs, dense cover, and plant diversity. Another small forest carnivore, the western spotted skunk (*Spilogale gracilis*), is still relatively common within a large geographical range that spans from southwestern Canada to Mexico and as far east as Wyoming and Colorado (McDonough et al., 2022). Its congener, the eastern spotted skunk (now split into the plains spotted skunk [*Spilogale interrupta*] and the eastern spotted skunk [*Spilogale putorius*]), which was also common throughout its range in the Midwest and Southeast United States, declined by >90% within a decade (1940–1950) and >99% within four decades (1940–1980) in comparison with precrash population estimates (Gompper & Hackett, 2005). Although the causes of decline are poorly understood, population declines have been linked to habitat loss (Gompper & Hackett, 2005). The eastern spotted skunk is now listed as Vulnerable by the IUCN (Gompper & Jachowski, 2016), and although the US Fish and Wildlife Service ultimately decided that listing the species was not warranted, the plains spotted skunk was being considered for listing under the Endangered Species Act (US Fish and Wildlife Service, 2012, 2023). Eastern spotted skunk recovery efforts have been hindered by limited information due to low capture rates (<2.8% for live captures, <1.9% for camera traps, and <6.5% track plates; Hackett et al., 2007) and have relied on a handful of studies conducted after the population had already declined (Lesmeister et al., 2008, 2009, 2013).

The limited available research on western spotted skunks, including island spotted skunk subspecies (*Spilogale gracilis amphiala*), is restricted to non-forested ecosystems (Crooks, 1994a, 1994b; Crooks & Van Vuren, 1995), mesquite shrubland of Texas (spotted skunk in this area is now classified as the desert spotted skunk [*Spilogale leucoparia*]; Doty & Dowler, 2006, Neiswenter et al., 2006, Neiswenter & Dowler, 2007), and the chaparral biome of the Sierra Nevada mountains of California (Carroll, 2000). In these ecosystems, spotted skunks selected for dense cactus patches (den-site selection; Doty & Dowler, 2006), large mesquite (*Prosopis glandulosa*) trees (within home range selection; Neiswenter & Dowler, 2007), canopy cover, logs, snags, shrubs (den-site selection; Carroll, 2000), and ravines (within home range selection; Crooks & Van Vuren, 1995). Western spotted skunk ecology in forests in mountainous environments remains understudied, particularly in areas with large spatial and interannual variation in snow, but some evidence suggests that the species may be associated with old-growth forests in the temperate rainforests of the Pacific Northwest (Carey & Kershner, 1996).

To better understand the natural history of the western spotted skunk in forested ecosystems, we studied the species' spatial ecology in the Oregon Cascade Mountains using camera traps and radio-collars. The objectives of our study were to quantify the habitat selection of the western spotted skunk at the landscape scale and at the individual home range scale and to investigate the seasonal changes in space use. We designed our analyses to reflect hypotheses related to anthropogenic disturbance and the need for resources, thermoregulation, and cover from predators (Table 1). We predicted that western spotted skunk space use would be negatively impacted by anthropogenic disturbance (Carey & Kershner, 1996), positively related to areas that provide food resources and water (Tosa et al., 2023), positively related to areas with coarse woody debris (Buskirk et al., 1989; Lesmeister et al., 2008) and lower snow fall, and driven by a need for cover from predators (Delheimer et al., 2023; Lesmeister et al., 2009, 2013; Tweedy et al., 2019) as suggested in other spotted skunk and small carnivore studies.

STUDY AREA

This study was conducted in the McKenzie River District of the Willamette National Forest and the H. J. Andrews Experimental Forest (HJA), which are located on the western slope of the Cascade Mountain Range near Blue River, Oregon (Figure 1). Elevations range from 410 to 1630 m. The maritime climate is typical of the Pacific Northwest region and consists of warm, dry summers and mild, wet winters. Mean monthly temperatures range from 1°C in January to 18°C in July. Precipitation falls primarily as rain, is concentrated from November through March, and averages 230 cm at lower elevations and 355 cm at higher elevations.

Lower elevation forests not only are dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*) but also include deciduous trees such as bigleaf maple (*Acer macrophyllum*). Upper elevation forests are dominated by noble fir (*Abies procera*), Pacific silver fir (*Abies amabilis*), Douglas-fir, and western hemlock. The understory is variable and ranges from open to dense shrubs. Common shrubs include Oregon grape (*Berberis* spp.), salal (*Gaultheria shallon*), sword fern (*Polystichum munitum*), vine maple (*Acer circinatum*), Pacific rhododendron (*Rhododendron macrophyllum*), huckleberry (*Vaccinium* spp.), and blackberry and salmonberry (*Rubus* spp.).

Before timber cutting in 1950, 65% of the HJA was covered in old-growth forest. Approximately 30% of the HJA was clear cut or shelterwood cut to create plantation forests varying in tree composition, stocking level, and age. In 1980, the HJA became a charter member of the Long Term Ecological Research network and no logging has occurred since 1985. The Willamette National Forest immediately surrounding the HJA has a similar logging history, but logging continued through the duration of our study. The HJA consisted of a higher percentage of old-growth forest than the surrounding Willamette National Forest (approximately 58% in the HJA vs. 37% in the study area; Davis et al., 2022). In addition to logging, wildfires are a primary disturbance, followed by windthrow, landslides, root rot infections, lateral stream channel erosion, and tree fall caused by heavy snow events. On 24 February 2019, near the end of the study, the Oregon Cascades experienced a large, heavy snow event that resulted in a massive tree fall event (DiGregorio, 2019; Stoelb, 2020; The White House, 2019). There were no fires during the study, but mean fire return interval of partial or complete stand-replacing fires for this area is 166 years and ranges from 20 to 400 years (Teensma, 1987; Morrison & Swanson, 1990).

METHODS

We studied the resource selection of western spotted skunks at two scales because we were interested in the spatiotemporal dynamics of the population as a whole and the responses of individual animals to their environment (Johnson, 1980; Mayor et al., 2009). To investigate the inter-seasonal and interannual variability in the spatial distribution of western spotted skunks across the study area (second-order habitat selection; Johnson, 1980), we implemented multiseason occupancy models (MacKenzie et al., 2018) using detections of spotted skunks at baited camera traps. Specifically, we were interested in the changes in occupancy between seasons and years because spotted skunks may have different habitat needs depending on their reproductive cycle and because our study was conducted in mountainous terrain where precipitation in winter can fall as rain at low elevations and heavy snow at high elevations and the weather was quite variable during the study (e.g., wet cold spring in 2017, warm dry spring in 2018, drought conditions during summer 2018, severe snow event during winter 2019). Next, we used fine-scale locations of spotted skunks from radiotelemetry and GPS data to estimate western spotted skunk home range sizes and overlap and to model western spotted skunk resource selection within home ranges (third-order habitat selection). Below, we present environmental covariates used for both scales of models, methods for field data collection, and then statistical analyses. We conducted all analyses using Program R (R Core Team, 2019) and produced figures using the *ggplot2* package (Wickham, 2016).

TABLE 1 Descriptions of candidate environmental variables used to develop occupancy and resource selection models for the western spotted skunk (*Spilogale gracilis*) in temperate rainforests in the Oregon Cascades.

Variable name	Range	Units	Description	Rationale
Disturbance				
D.ROAD[1]	0–1385	m	Euclidean distance from nearest road using rgeos::gDistance Transformations tested: linear, log	Areas closer to roads are more disturbed and exhibit more edge characteristics
P.LOGGED[1]	0–83	%	Percent within buffer that was logged within the last 100 years calculated with landscapemetrics::sample_lsm Buffer sizes tested: 0.1, 0.5, 1.0, 5.0 km	More previously logged areas, more disturbed
P.MATURE[1]	5–21	%	Percent within buffer categorized as OGSI 80 but not OGSI 200 calculated with landscapemetrics::sample_lsm Buffer sizes tested: 0.1, 0.5, 1.0, 5.0 km	More mature stands, more legacy of disturbed
P.OLDGROWTH[1]	7–92	%	Percent within buffer categorized as OGSI200 calculated with landscapemetrics::sample_lsm Buffer sizes tested: 0.1, 0.5, 1.0, 5.0 km	More old-growth stands, less disturbed
YRS_SINCE_DISTURB[1]	3–103	Year	Years since location was logged Transformations: linear, log	More time since disturbance, less disturbed
OGSI[2]	0–88		Old-growth structural index as defined by Spies and Franklin (1988)	More old-growth characteristics, less disturbed
Predation				
COVER[3]	0–1	%	Vegetation cover based on the proportion of total returns between 4 and 16 m	More cover, more visual obstruction from avian predators
CANOPY_HT[3]	2–83	m	25th percentile height for first returns (P25)	Lower canopy height, more obstruction from predators
ROUGH	0–22		Topographic roughness index (TRI) at site calculated from DEM and Raster::terrain	Rougher terrain, more opportunities to escape predators
TREE_DENSITY[2]	1–4247	trees/ha	Density of live trees, conifers, hardwoods ≥2.5 cm dbh	Lower tree density, more area between trees for avian predators
Resource				
STAND_DIVERSITY[2]	1–837		DDI = measure of the structural diversity of a forest stand, based on tree densities in different dbh classes SDI = Reineke's stand diversity index	More stand diversity, more food and rest site resources
TOPO_POS	−453-685		Topographic position index (TPI) at site calculated from DEM and Raster::terrain Buffer sizes tested: 0, 0.5, 1.0 km	Lower topographic position, more food resources
D.WATER[4,5]	0–1507	m	Euclidean distance from nearest waterbody or perennial stream using rgeos::gDistance Transformations: linear, log	Closer to water, more food resources
LANDSAT_VEG	0–5340		Landsat8 reflectance bands: 2 (blue), 3 (green), 4 (red), 5 (near-infrared), 6 (Shortwave infrared 2), 7 (Shortwave infrared 2)	Greener areas and more moist areas, more food resources
STAND_AGE[2]	1–5486	Years	Basal area weighted stand age based on field recorded or modeled ages of dominant/codominant trees	Older stand, more coarse woody debris for potential rest sites

TABLE 1 (Continued)

Variable name	Range	Units	Description	Rationale
SNAG[2]	0–310 (STPH); 1–257,697 (SBPH); 0–704 (SVPH)	trees/ha	Snag density per hectare (STPH) = Density of snags ≥25 cm dbh and ≥2 m tall Snag biomass per hectare (SBPH) snag volume per hectare (SVPH)	More snags, more potential rest sites
Thermal tolerance				
ELEVATION[3]	368–1590	m	Elevation Transformations: linear, quadratic, log	Higher elevation sites, lower ambient temperature and more snow precipitation
BASAL_AREA_SP[2]	0–2609	m²/ha	Basal area of *Abies amabilis* (ABAM), *Acer macrophyllum* (ACMA), *Pseudotsuga menziesii* (PSME), *Tsuga heterophylla* (TSHE)	More ABAM, lower temperatures and more persistent snow More ACMA, more riparian area
BASAL_AREA_TYPE[2]	0–12,004	m²/ha	Basal area of live trees, conifers, or hardwoods ≥2.5 cm dbh	Larger trees provide more insulation for rest sites
ASPECT	0–6.28	Radians	Aspect at site calculated from digital elevation model (DEM) and Raster::terrain northness = COS(Aspect); eastness = SIN(Aspect)	South-facing slopes get more sun exposure

Source: 1. USDA Forest Service; 2. GNN structure: https://lemma.forestry.oregonstate.edu/; 3. LiDAR. 4. National Hydrography Dataset; 5. Oregon Explorer, https://spatialdata.oregonexplorer.info/geoportal/; 6. Landsat 8, https://earthexplorer.usgs.gov/.

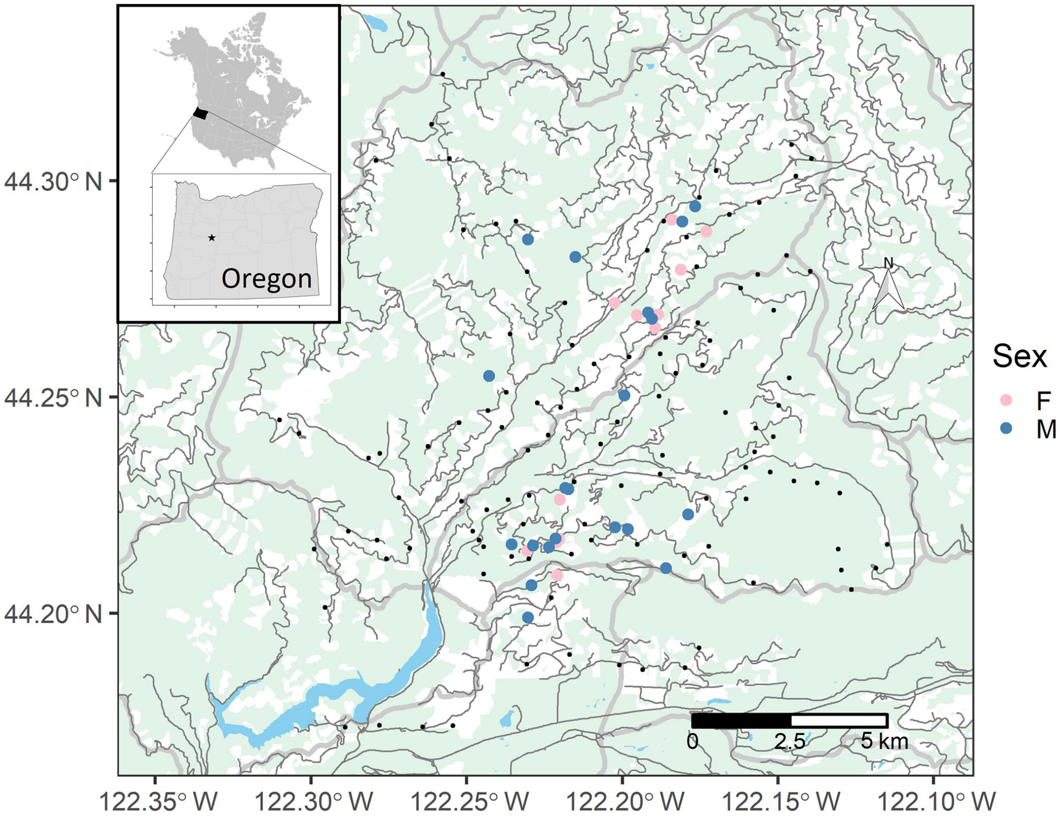

FIGURE 1 Study area and western spotted skunk (*Spilogale gracilis*) home range centroids for females and males. White areas indicate previously logged stands. Trail camera locations are shown as black circles.

Model covariates

We assessed western spotted skunk habitat at local and landscape levels with environmental covariates derived from satellite imagery, light detection and ranging (LiDAR) maps (collected from 2008 to 2016), and other maps acquired from the USDA Forest Service and Oregon Explorer (https://oregonexplorer.info/) (Table 1). We assigned each covariate to a category based on our hypotheses related to resources, predation, thermal tolerance, and disturbance. In addition to linear functional forms of each variable, we explored the quadratic form for elevation and the logarithmic form of distance to features of stream, waterbody, road, and areas logged within the last 100 years. We averaged landscape-level variables using buffer sizes of 100 m, 500 m, 1 km, and 5 km to represent minimum and mean step length traveled in 1 h when skunks were active (estimated from GPS locations), approximate core area size (also maximum step length traveled in 1 h), and home range size of a western spotted skunk (this study), respectively (McGarigal et al., 2016). To determine the appropriate scale (i.e., buffer size) and functional forms (i.e., linear, quadratic, logarithmic) of variables, we fitted single covariate models and compared models using corrected Akaike information criterion (AIC_c) for small sample size (Burnham & Anderson, 2002). For each covariate, the scale or functional form of the model with the lowest AIC_c score was identified as the most-supported scale or functional form, respectively, and was used in subsequent models. To prevent multicollinearity and confounding factors, we computed Pearson's correlation coefficients between each pair of covariates and retained the covariate with the greater average deviance explained when two or more covariates were highly correlated (i.e., $|r| \geq 0.6$) (Wan et al., 2017). All covariates were centered and scaled prior to fitting models to facilitate effect size comparisons and model convergence.

Field methods

Camera traps

We set and maintained 112 baited camera traps (HC500, Reconyx, Holmen, WI or TrophyCam, Bushnell, Overland Park, KS) between April 2017 and August 2019. Camera traps were placed ~0.3 m off the ground and ~2 m from bait to ensure detection of small carnivores. Cameras were programmed to take a burst of three photos with each trigger and had a quiet time of 1 min. We stratified placement of camera traps based on disturbance (i.e., old-growth stand characteristics) and elevation gradients. Camera traps were part of a larger biodiversity study (Frey, Hadley, & Betts, 2016; Frey, Hadley, Johnson, et al., 2016; Kim et al., 2022; Weldy et al., 2019). The camera traps located in the surrounding Willamette National Forest were deployed in May and June 2018 ($n = 58$). To increase the detection probabilities of carnivores, we baited each camera trap with a can of fish flavored cat food or sardines (partially opened), a fresh dead mouse (*Mus musculus*), and a commercially available carnivore lure (e.g., Gusto, Caven's Lure, Pennock, MN) (Avrin, Pekins, Sperry, & Allen, 2021; Avrin, Pekins, Sperry, Wolff, & Allen, 2021; Siegfried et al., 2023). Camera traps were rebaited, and lure was reapplied each month when we were able to safely access sites. We did not check or rebait cameras in unsafe road or working conditions with high snow accumulations that hindered our ability to drive the roads. We manually tagged species presence in camera trap photographs in DigiKam (V6.1.0, www.digikam.org), extracted metadata using the *exifr* package (Dunnington & Harvey, 2021), and converted western spotted skunk detections into weekly encounter histories.

Capture

We captured spotted skunks from August to May during 2017–2019 using Tomahawk live traps (Model 102 [12.7 × 12.7 × 40.6 cm] and 103 [15.2 × 15.2 × 48.3 cm], Tomahawk Live Trap Co., Hazelhurst, WI). We placed traplines of 10–30 live traps at 100–250-m intervals along accessible trails and roads near detections of western spotted skunks on camera traps. To reduce trap injuries, we modified Tomahawk traps with corrugated plastic to eliminate gaps between the trap door and floor. We also included polyester insulation in traps during winter to help trapped animals with thermoregulation. We covered traps with burlap and bark or leaf litter. We baited each trap with one or a combination of the following: sardines, a frozen dead house mouse, or commercially available carnivore lures. We checked traps daily between 0600 and 1000.

Once captured, we physically restrained and chemically immobilized skunks using an intramuscular injection of 15-mg/kg ketamine HCl (Zoetis Services LLC, Parsippany, NJ) and 40-mcg/kg dexmedetomidine HCl (Zoetis Services LLC, Parsippany, NJ). Following chemical immobilization, we determined sex, recorded mass and morphometric measurements, and examined tooth wear. We fit each skunk with two metal ear tags (Monel size 1; National Band and Tag Co., Newport, KY) and a very high frequency (VHF) radio-collar <5% of their body mass (M1545, 16 g; Advanced Telemetry Systems, Isanti, MN). We also fit four large male skunks (>550 g) with GPS collars (LiteTrack20, 20 g; SirTrack, New Zealand) during the breeding season (September–October). All capture and handling protocols were approved by the United States Department of Agriculture Forest Service Animal Care and Use Committee (USFS 2016-015) under Oregon Department of Fish and Wildlife Scientific Take Permits (ODFW 107-17, ODFW 059-18, and ODFW 081-19) and followed guidelines of the American Society of Mammalogists (Sikes et al., 2016).

Relocations

For our third order of resource selection analysis, we collected spatial data on western spotted skunks from August 2017 to August 2019 in three ways: (1) we recorded location information for any skunk that we captured in a trap, (2) we triangulated collar VHF signals from the roads nightly when skunks were more active, and (3) we used homing techniques on collar VHF signals daily to identify diurnal rest site locations. We derived skunk locations from triangulations of ≥3 signal bearings with ≥20 degrees difference within 20 min. from a hand-held 3-element Yagi antenna in the program Locate III (Nams, 2006). Conducting radiotelemetry on small-bodied animals in this montane system was challenging because of limited accessibility and topography and prevented more robust triangulation protocols. To gain finer-scale movement data, we programmed the four GPS collars to collect locations at 30-min fix intervals during the night (21:00–09:00) when skunks were more active and at 4-h fix intervals during the day (09:00–21:00) when skunks are less active (Moriarty & Epps, 2015) (Appendix S1: Text S1). We conservatively censored GPS locations where the horizontal dilution of precision was >20 ($n = 14$) (D'Eon et al., 2002).

Statistical analyses

Occupancy models

To evaluate the inter-seasonal and interannual variability in second-order selection by western spotted skunks across the landscape, we conducted dynamic occupancy analyses using camera trap data. Dynamic occupancy analyses allowed us to formally address our anecdotal observations of declines in spotted skunk detections at higher elevations during winter when there was consistent snow cover. We separated encounter histories into 17- and 18-week biologically meaningful seasons for summer (June–September), fall (October–January), and spring (February–May). Summer corresponded to the dry season in the Oregon Cascades, fall represented the wet season in the Oregon Cascades, and spring represented a period in the Oregon Cascades when there was consistent snow cover at high elevations and food resources were likely most scarce. These seasons also roughly correspond to the reproductive cycle and ontogeny of western spotted skunks where mating occurs in fall, gestation and birth occurs in spring, and rearing of young occurs in summer (Verts et al., 2001). This resulted in seven seasons (summer 2017 through summer 2019) and allowed us to investigate seasonal shifts in space use by western spotted skunks. Since it was possible for western spotted skunks to visit multiple cameras, occupancy model results should be interpreted as space use instead of occupancy of sites.

We calculated naïve occupancy for each season by dividing the number of sites where western spotted skunks were detected on baited camera traps by the total number of sites monitored during that season. We estimated each of the four parameters—detection (p), initial occupancy (ψ), colonization (γ), and extinction (ε)—as a function of environmental covariates (Table 1) using the *unmarked* package (Fiske & Chandler, 2011). Since the unmarked dynamic occupancy models require balanced encounter histories for each season, we augmented encounter histories with NA values so that each season consisted of 18 weeks. We started with the null model ($p \sim 1$, $\psi \sim 1$, $\gamma \sim 1$, $\varepsilon \sim 1$) and fit a detection only model with temporal variables: season, skunk year, and number of weeks since bait. Then, for occupancy, colonization, and extinction parameters, we fitted univariate models using environmental or temporal covariates for each hypothesis category and separately evaluated which covariates to include in each additive hypothesis model (i.e., resource model, predation model, thermal model, disturbance model, and temporal model) and ranked univariate models based on AIC_c scores (Burnham & Anderson, 2002). Only covariates from univariate models that were more supported than the null model, and those that were not highly correlated with one another ($|\text{Pearson's } r| < 0.6$) were included in each hypothesis model. We fitted a parameter model for occupancy, colonization, and extinction by combining all four hypothesis models. To prevent overparameterization and to be conservative in our biological interpretations of covariates, we removed variables with 95% CIs overlapping 0. We combined all parameter models into the final global model (Figure 2).

For our final model, we conducted a goodness-of-fit test using a parametric bootstrap with 1000 replicates and the chi-square statistic (Fiske & Chandler, 2011; Kellner et al., 2023; Kéry & Chandler, 2012). Finally, we estimated SEs of predicted occupancy in each season using a nonparametric bootstrap with 1000 replicates using the *nonparboot* function and predicted occupancy across the landscape. To explore whether occupancy probability was declining over time, we fit a post hoc linear regression to the predicted seasonal occupancy (predicted occupancy ~ season).

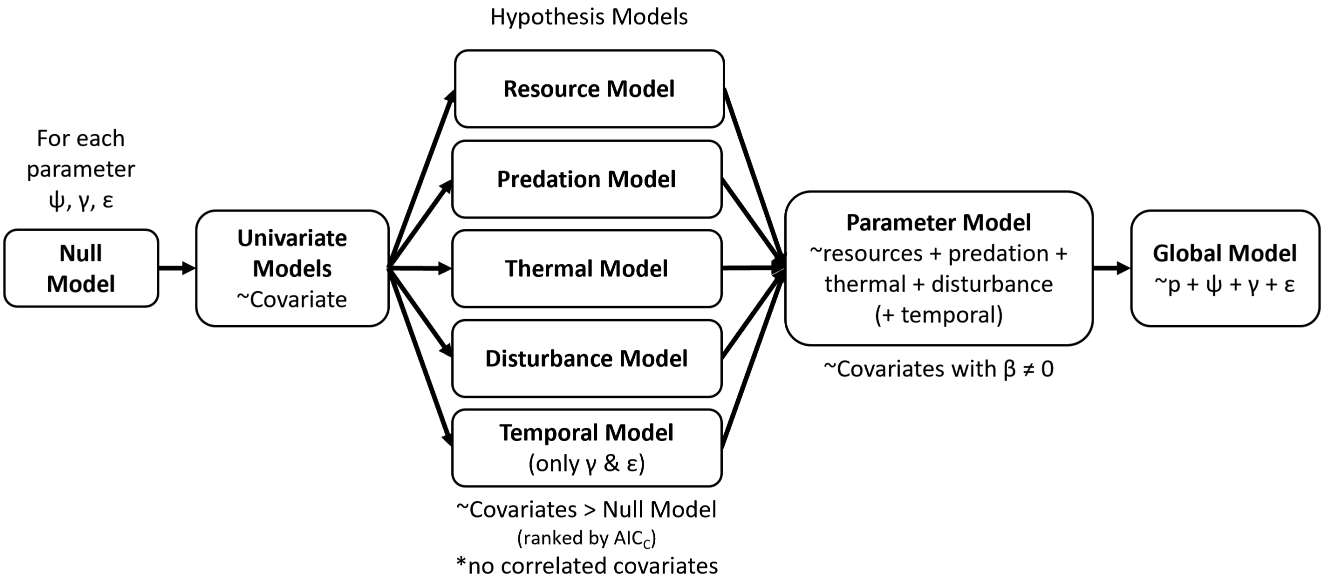

FIGURE 2 Flowchart for construction of global parameter models for each parameter, initial occupancy (ψ), colonization (γ), and extinction (ε), in the multiseason occupancy model. AIC$_c$, corrected Akaike information criterion.

Home range estimation

We calculated home range metrics using a continuous-time movement model in the *ctmm* package (Fleming & Calabrese, 2022) and incorporated all relocation data (i.e., capture, homing, telemetry, and GPS locations) and the corresponding date and time of those locations. For capture and homing locations, we assumed there was no error in location because we either had the animal in hand or were close to our physical location. For each telemetry location, we incorporated variance and covariance of 95% error ellipses. We removed outlier locations when indicated by the *outlie* function. For GPS locations, we assumed that 1 horizontal dilution of precision (HDOP) value was equivalent to 10-m error and set df to 2. Then, we estimated core range (50% isopleth) and home range (95% isopleth) for each spotted skunk with ≥5 locations using autocorrelated kernel density estimation with the *akde* function (Fleming & Calabrese, 2017). We used this method because it incorporates error in locations, performs well with low sample sizes, and allows us to combine multiple sources of location information with different fix intervals (e.g., rest sites, capture locations, VHF triangulation, and GPS locations). We calculated the degree of overlap in home ranges using the Bhattacharyya method (Bhattacharyya, 1943) in the *overlap* function to assess territoriality within and between sexes of western spotted skunks (Winner et al., 2018). In addition, because there were apparent differences in home range and core area sizes, we explored clustering within the home range sizes using the *kmeans* function ($k = 1$–5). To verify significant differences between home range sizes of groups, we ran an ANOVA and Tukey's honestly significant difference (HSD) test. Post hoc, we also explored whether the large differences in home range size we observed in males but not females could be explained by body mass, total body length, or environmental variables (i.e., mean elevation, proportion of logging, or proportion of old growth within the home range) using linear regressions.

To explore whether skunks shifted their home ranges by season, we calculated seasonal home ranges using the same methods as above. We split locations based on the same seasons used in the occupancy modeling: summer (June–September), fall (October–January), and spring (February–May). We calculated seasonal home ranges if an animal had ≥5 locations multiple seasons. Using the Bhattacharyya method in the *overlap* function, we calculated fidelity of home ranges across seasons (e.g., summer vs. fall).

Within home range resource selection

To investigate resource selection at the home range scale, we used relocation data and explored the same environmental variables from our occupancy models. Again, we tested different scales for landscape variables and linear, quadratic, and log functional forms for environmental variables with these data to determine which was the most supported. Since seasonal home range fidelity was high, we selected 25 available points for each used location within each home animal's overall home range to estimate resource selection (Appendix S1: Figure S1). We fitted a binomial generalize linear mixed effects regression to used and available points within the home range and included individual as a random intercept in the *blme* package (Chung et al., 2013). To determine which variables to include in the global model, we fitted univariate models to used and available points. We ranked univariate models against the null model using $\mathrm{AIC_c}$ and included any variables with a univariate model that ranked higher than the null and were not correlated with one another ($|\text{Pearson's } r| < 0.6$) in an additive global model. Similar to the dynamic occupancy analysis, we fit additive hypothesis models for resources, predation, thermal, and disturbance and combined all hypothesis models into the final global model. We took this approach for the resource selection analysis because our analysis was largely exploratory, and a global model would better reflect relationships of western spotted skunks with variables of interest for forest management such as amount of logging. We excluded skunks with <25 used locations from this analysis because of model convergence issues.

From observations in the field, we suspected that some western spotted skunks had opposite relationships with some environmental variables, specifically elevation, percentage of area logged, and percentage of area mature. To test this, we added a random slope by individual term for one environmental covariate at a time to the final global model and ranked these models using $\mathrm{AIC_c}$. We only added a random slope by individual term for one environmental covariate at a time to prevent overparameterization and facilitate model convergence.

RESULTS

Over the course of 7970 trap nights, we captured 31 western spotted skunks (12 female, 19 male) 177 times (2.2% capture success) and tracked 25 of those individuals (9 female, 16 male) for various durations between October 2017 and August 2019 (Appendix S1: Figure S2). Males weighed 1.5 times more ($\text{mass}_{\text{male}} = 595.3 \pm 22.3$ g, $\text{mass}_{\text{female}} = 392.4 \pm 11.2$ g; $F_{1,29} = 47.2$, $p < 0.001$) and total body lengths were 4.5 cm longer ($\text{length}_{\text{male}} = 42.2 \pm 0.5$ cm, $\text{length}_{\text{female}} = 37.7 \pm 0.5$ cm; $F_{1,29} = 36.7$, $p < 0.001$) than females. We recorded 170 skunk capture events, 293 rest site uses, 1011 telemetry locations, and 109 GPS locations. We excluded 34 reuses of a single site by a female (SG-008) during summer that we suspect was used for denning and rearing kits. During the spring of 2019, many of our VHF collars failed because the VHF antenna broke off the collars within 1 month of deployment. We recovered location data from 2 GPS collars (one SWIFT fix and one standard fix): the SWIFT fix collar recorded 121 points and 107 points met our error threshold criteria (11.0% fix success rate; Appendix S1: Figure S3), whereas the standard fix collar only recorded two successful locations, both of which met the error threshold criteria (0.8% fix success rate).

The western spotted skunks in this study had relatively large home ranges relative to their body mass compared with other mammalian carnivores (Figure 3). One skunk (SG-001) had two distinct home ranges, suggesting the spotted skunk dispersed on 10 May 2018 (Appendix S1: Figure S4). Therefore, we treated the two home ranges as separate for the remainder of the analysis. *K*-means clustering revealed two groups of home ranges ($F_{2,22} = 15.2$, $p < 0.001$): a smaller home range consisting of females ($\text{mean} = 10.93\ \text{km}^2$, 95% $\text{CI} = 6.63\text{–}16.86$) and males ($\text{mean} = 16.38\ \text{km}^2$, 95% $\text{CI} = 12.83\text{–}20.49$) and a distinctly larger home range consisting of males ($\text{mean} = 35.83\ \text{km}^2$, 95% $\text{CI} = 31.52\text{–}40.40$) (Table 2). Home range size and clustering were independent of the number of locations used to calculate the home range ($\beta_{\text{total locs}} = -0.05$, $p < 0.56$; Appendix S1: Figure S5), length or body mass of the skunk ($\beta_{\text{length}} = 2.21$, $p = 0.23$, $\beta_{\text{mass}} = 0.05$, $p = 0.09$), and other environmental variables including mean elevation within the home range, percent of forest logged, or percent old growth (Appendix S1: Figure S6). Females had similar home range size across seasons, and male home range sizes differed by season, but there was no consistent trend among individuals (Figure 4A). Some males had larger home ranges during spring, whereas other males had larger home ranges during fall (Figure 4A). Home range overlap between neighboring skunks was high regardless of sex (Table 3; Appendix S1: Figure S7), and individual home range fidelity was high across seasons (fall–spring overlap: 87.6 ± 2.6%, fall–summer overlap: 80.2 ± 4.5%, spring–summer overlap: 82.0 ± 5.8%; Figure 4B).

Occupancy models

We detected western spotted skunks at 80 of 112 camera sites (naïve occupancy = 71.4%; Appendix S1: Figure S8). The final multiseason occupancy model revealed that detection probability declined with more weeks since bait ($\beta_{\text{bait}} = -0.09 \pm 0.01$) (Figure 5; Appendix S1: Table S2). Detection probability was highest in fall and in 2019 and lowest in summer and in 2017 ($\beta_{\text{p.SPRING}} = -0.56 \pm 0.10$, $\beta_{\text{p.SUMMER}} = -1.03 \pm 0.10$, $\beta_{\text{p.2018}} = 0.25 \pm 0.08$, $\beta_{\text{p.2019}} = 0.36 \pm 0.23$). Initial occupancy was also higher when there was more mature forest in the landscape ($\beta_{\text{P.MATURE.5KM}} = 0.99 \pm 0.67$), in local valley bottoms ($\beta_{\text{TOPO\_POS.1KM}} = -0.71 \pm 0.45$), and areas with dense vegetation ($\beta_{\text{B4}} = -1.23 \pm 1.19$). Colonization probability was

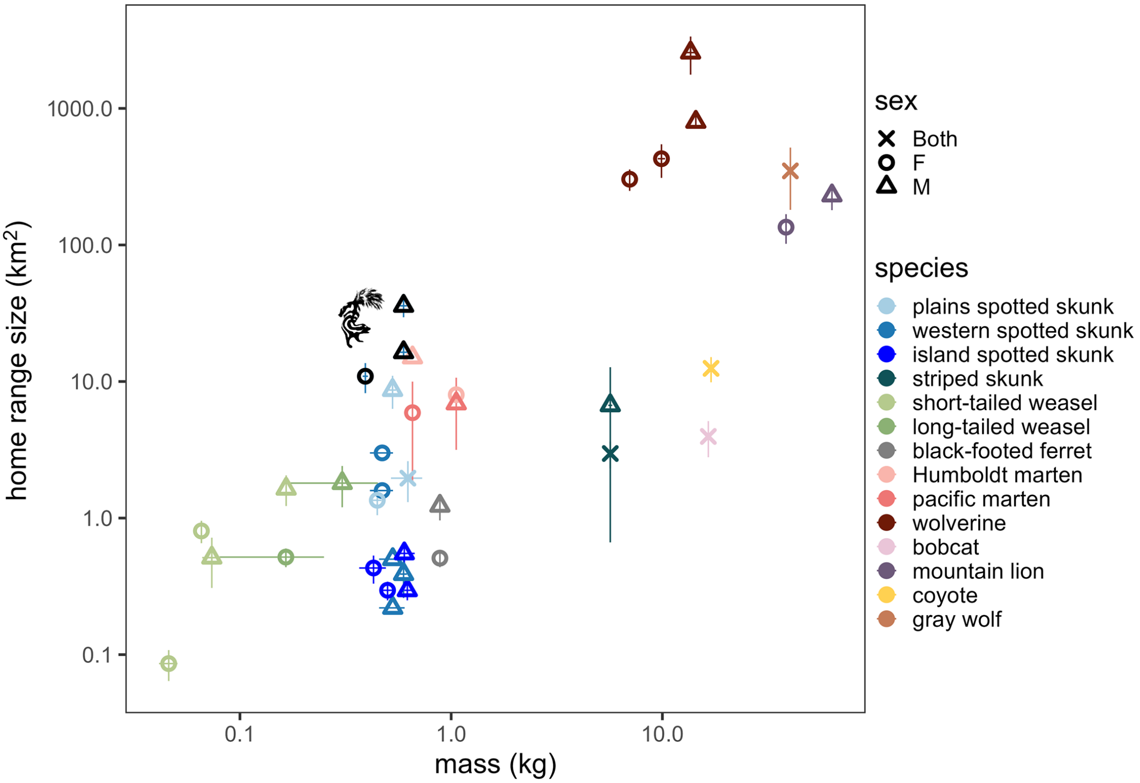

FIGURE 3 Comparison of mean home range sizes and mean body mass of mammalian carnivores in North America. Lines represent SE or range of values presented in study. Values from Crooks and Van Vuren (1995), Lisgo (1999), Carroll (2000), Doty (2003), Gehring and Swihart (2004), Jachowski (2007), Jones et al. (2008), Lesmeister et al. (2009), Dawson et al. (2010), Inman et al. (2012), Linnell et al. (2017, 2018), Mastro et al. (2019), Orning (2019), Martin et al. (2021), and Schmidt et al. (2023). Values from this study appear in black. Note mass and home range size axes are on $\log_{10}$ scale.

TABLE 2 Western spotted skunk (*Spilogale gracilis*) home ranges (95% utilization distributions) and core areas (50% utilization distributions) estimated using continuous-time movement models in the Willamette National Forest, Oregon during August 2017–August 2019 (mean with 95% CI in parentheses).

Group	Core area (km^2)	Home range (km^2)
Female	2.52 (1.55–3.83)	10.93 (6.63–16.86)
Male (small)	3.55 (2.68–4.60)	16.38 (12.83–20.49)
Male (large)	6.81 (6.00–7.69)	35.83 (31.52–40.40)

higher in areas with more moisture ($\beta_{B6} = -0.69 \pm 0.26$), areas with rougher topography ($\beta_{ROUGH} = 0.25 \pm 0.20$), and areas with lower basal area of Pacific silver fir ($\beta_{ABAM} = -0.53 \pm 0.32$) (Figure 6). Extinction probability was higher at low and high elevations ($\beta_{ELEVATION} = -5.14 \pm 1.53$, $\beta_{ELEVATION2} = 5.76 \pm 1.67$), at ridge tops ($\beta_{TOPO\_POS.0.5KM} = 0.45 \pm 0.19$), and in areas with more Pacific silver fir ($\beta_{ABAM} = 0.65 \pm 0.46$). Extinction probability was also higher immediately following a disturbance ($\beta_{YRS\_SINCE\_DIST} = 0.88 \pm 0.76$, $\beta_{LOG(YRS\_SINCE\_DIST)} = -1.47 \pm 0.92$) and in areas with less mature forest in the landscape ($\beta_{P.MATURE.5KM} = -0.41 \pm 0.20$). Probability of colonization was highest between summer and fall ($\beta_{\gamma.SUMMER} = 1.70 \pm 0.51$), and probability of extinction was highest between spring and summer ($\beta_{\varepsilon.SPRING} = 1.10 \pm 0.43$) and between 2018 and 2019 ($\beta_{\varepsilon.2018} = 1.04 \pm 0.35$). After accounting for detection, colonization, and extinction, predicted seasonal occupancy was highest during the fall of 2017 (63.7 ± 5.3%) and lowest during the summer of 2019 (19.9 ± 4.3%) following the severe heavy snow event (Figure 7). Overall, predicted occupancy declined by 30.3% between summer 2017 and summer 2019, and seasonal occupancy had a declining trend over the duration of the study ($\beta_{season} = -0.05 \pm 0.02$, $p = 0.038$), but this trend was primarily driven by the low predicted occupancy rate during summer 2019.

Home range resource selection

We censored five skunks from the resource selection analysis due to small sample size ($n < 25$). Used locations

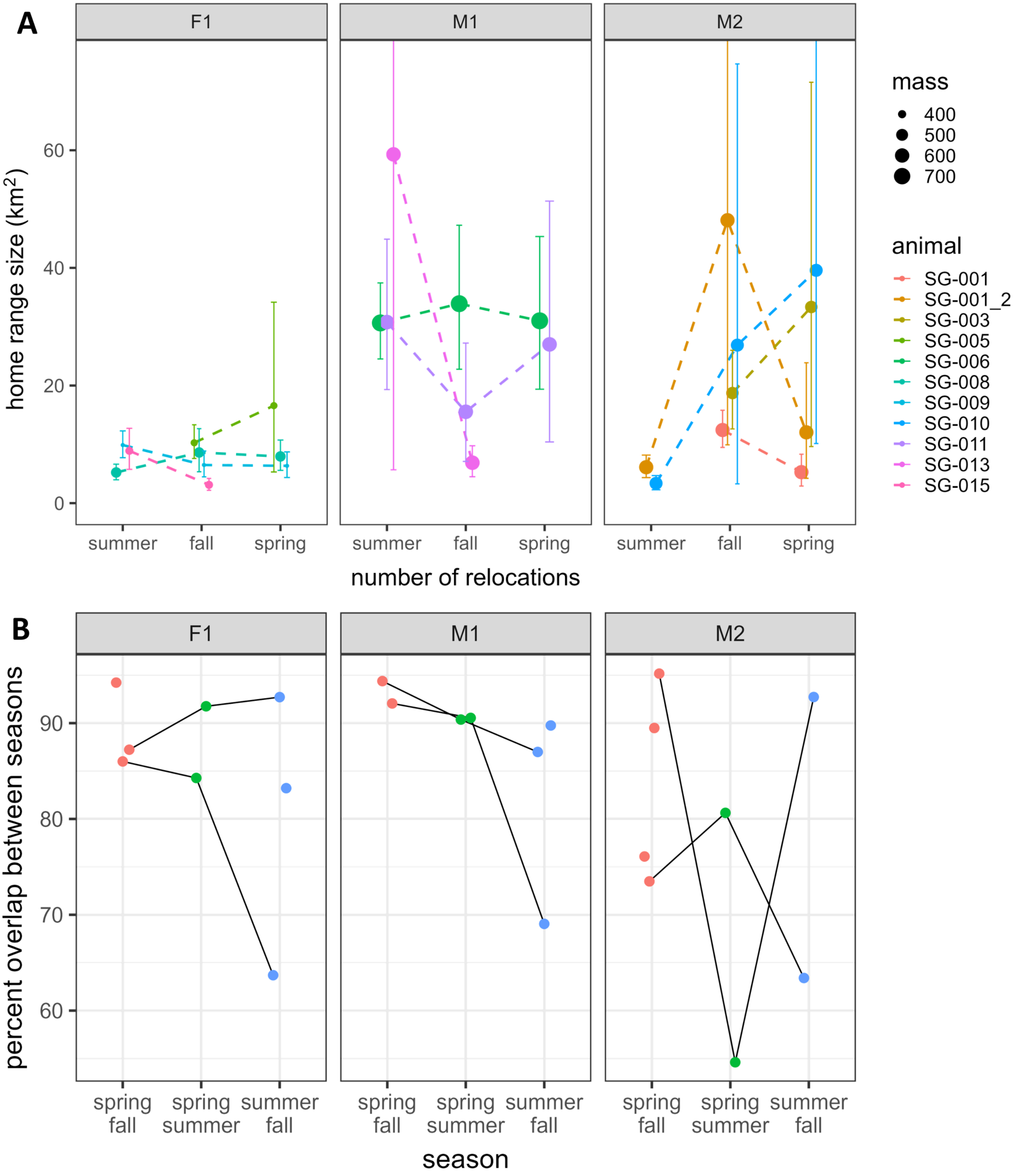

FIGURE 4 (A) Changes in seasonal home range size estimates and (B) fidelity of home ranges across seasons (spring: February–May, summer: June–September, fall: October–January) of western spotted skunks (*Spilogale gracilis*). Point size in (A) represents body mass size of skunk. Points connected with lines represent the same animal.

within the western spotted skunk home range were best predicted by disturbance variables, followed by predation, resource, and thermal variables (Appendix S1: Table S3). The best performing model was one that included a term for random slope by individual on elevation (Appendix S1: Table S4). When we fitted the global model with random slopes for each skunk, we found that each skunk had distinct responses to elevation where some individuals selected for low elevations whereas other selected for intermediate elevations (Appendix S1: Figure S9). Coefficients for covariates were similar between the global model that only included random intercepts by individuals (Appendix S1: Table S5) and the global model that included random intercepts and random slopes for elevation by individuals (Appendix S1: Table S6). Overall, spotted skunks selected for resources such as local valley bottoms ($\beta_{\mathrm{TOPO\_POS.1KM}} = -0.29 \pm 0.04$), areas near streams ($\beta_{\mathrm{DIST.STREAM}} = -0.10 \pm 0.05$, $\beta_{\mathrm{LOG(DIST.STREAM)}} = 0.02 \pm 0.05$), and wetter areas ($\beta_{\mathrm{B4}} = -0.10 \pm 0.04$) (Figure 8) and variables related to predation avoidance including shorter understory canopy ($\beta_{\mathrm{CANOPY\_HT}} = -0.13 \pm 0.03$) and flatter terrain ($\beta_{\mathrm{ROUGH}} = -0.22 \pm 0.03$) (Figure 9). Spotted skunks also selected for variables related to thermal tolerance including northerly aspects ($\beta_{\mathrm{NORTH}} = 0.30 \pm 0.04$), intermediate elevations ($\beta_{\mathrm{ELEVATION}} = 0.02 \pm 0.15$, $\beta_{\mathrm{ELEVATION2}} = -0.39 \pm 0.13$), and more disturbed areas such as locations closer to roads ($\beta_{\mathrm{DIST.ROAD}} = -0.14 \pm 0.06$, $\beta_{\mathrm{LOG(DIST.ROAD)}} = -0.15 \pm 0.03$) and locations with more previously logged areas in the landscape ($\beta_{\mathrm{P.LOGGED.1KM}} = 0.17 \pm 0.04$).

TABLE 3 Home range overlap between western spotted skunk (*Spilogale gracilis*) estimated using continuous-time movement models and the Bhattacharyya coefficient (mean with 95% CI in parentheses).

Dyad	Home range overlap
Female–Female	0.78 (0.67–0.86)
Male–Female	0.76 (0.61–0.89)
Male–Male	0.83 (0.65–0.94)

Note: Values range between 0 and 1, where 0 indicates no shared areas and 1 indicates identical distributions of 95% utilization distributions.

DISCUSSION

This study provides the first detailed movement and habitat analysis of western spotted skunks in temperate

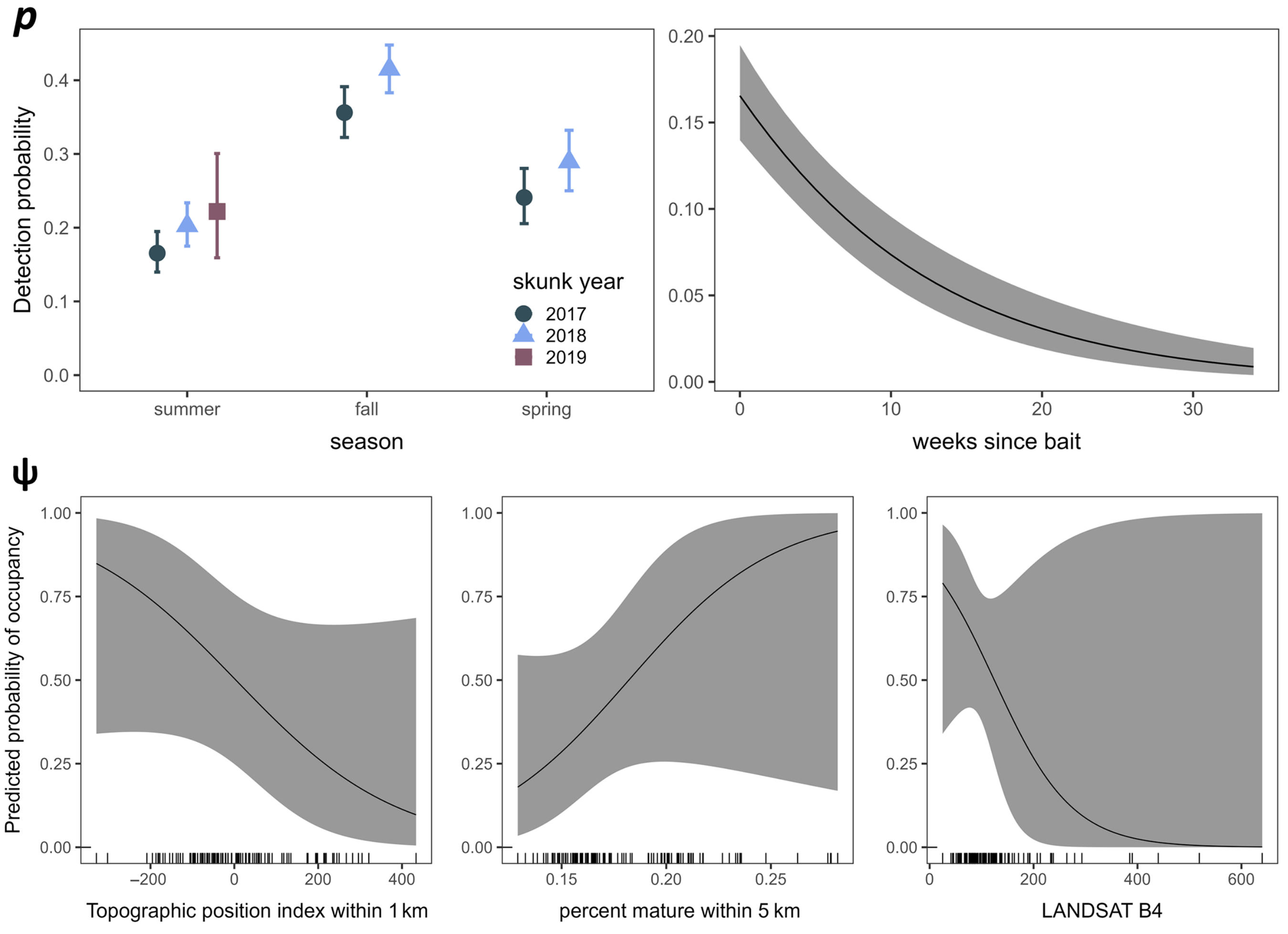

FIGURE 5 Marginal plots (mean and 95% confidence intervals) for detection (p) and initial occupancy (ψ) from multiseason occupancy models of western spotted skunks (*Spilogale gracilis*) in the Oregon Cascades from 2017 to 2019. Note differences in scales.

rainforests of the Pacific Northwest. By studying habitat selection at multiple spatial and temporal scales and with multiple methods, we found that responses to some environmental variables, such as complex forest structure, were scale specific, whereas responses to other environmental variables, such as topographic position index, were consistent at all scales. Given that there is little information available on the natural history of the western spotted skunk, these results provide evidence for key aspects of their ecology to focus monitoring efforts and may be beneficial to understand and identify potential threats (e.g., forest management, severe snow events, or wildfires) to this species.

We found that western spotted skunks were widely distributed across our study area (seasonal occupancy up to 63.7 ± 5.3%) and highly detectable (weekly detection probability = 41.2%), suggesting that populations are common in the Willamette National Forest. We also found that western spotted skunks exhibited sexual dimorphism in body mass, body length, and home range size. Females were consistently lighter and smaller and had smaller home ranges. Some male western spotted skunks had relatively small home range sizes (16.38 km^2) that were similar to female western spotted skunks (10.93 km^2), but other males had home ranges that were 2.4-fold larger (35.83 km^2). The differences in male home range size were independent of the physical characteristics of the individuals, proportion of forest type, elevation, or the number of relocations we were able to collect (Appendix S1: Figure S6). The home ranges of western spotted skunks in our study were considerably larger than those previously reported for other western spotted skunk populations (0.50 km^2 for males, 1.59 km^2 for females; Carroll, 2000), and for island spotted skunks (0.29–0.61 km^2; Crooks & Van Vuren, 1995; Jones et al., 2008). We also found that this population of western spotted skunks had larger home ranges than other similarly sized or closely related carnivores (Doty, 2003; Gehring & Swihart, 2004; Jachowski, 2007; King & Powell, 2007; Lindstedt et al., 1986) (Figure 3).

Western spotted skunk occupancy was higher in local valleys and areas with wetter areas and close to streams, which typically corresponded to areas near ephemeral creeks and was consistent with previous studies (Brown, 1985; Carey & Kershner, 1996; Crooks & Van Vuren, 1995). These areas likely provide spotted skunks with food resources such as invertebrates (e.g., wasps, millipedes, and beetles) (Tosa et al., 2023). Occupancy was also higher in areas surrounded by higher proportions of mature forests, not of old-growth forest, at the 5-km buffer scale, which was not aligned with our predictions given a past study that suggested that spotted skunks were associated with old-growth forest (Carey & Kershner, 1996).

Seasonal occupancy (i.e., landscape use) estimates were highest during fall, which may have been driven by higher movement rates by males during the breeding season. This could have resulted in individual western spotted skunk detections on multiple camera traps. Lesmeister et al. (2009) found that the highest movement rates of plains spotted skunks occurred during spring when males quested for reproductive females. Because seasonal home range fidelity of western spotted skunks was high (>80%), increases in seasonal occupancy rates during fall may also have been due to birth and dispersal events. Conversely, we suspect decreases in seasonal occupancy rates during spring may be due to increased mortality in winter.

Seasonal extinction probabilities appear to reflect sensitivity to recent forest harvest (harvest within 25 years) and thermal tolerance of western spotted skunks. Extinction probability was highest in areas with a recent disturbance but dropped off sharply thereafter (Figure 6; Appendix S1: Figure S10). Extinction probability was also higher at higher elevations, on ridges, and in areas with more Pacific silver fir. These attributes represent areas that experience greater volumes of precipitation in the form of snow, consistent snow cover, especially during spring, and prolonged snowmelt. This was especially apparent when we mapped predicted extinction probabilities across our study area (Appendix S1: Figure S12). Western spotted skunk sensitivity to snow and cold temperatures was apparent when we observed the greatest decline in seasonal occupancy between spring and summer 2019 following the severe wet snow event that occurred in February 2019 (Figure 7). Not only did this event provide a downfall of heavy, wet snow, but also it caused widespread tree damage, tree falls, and landslides (Stoelb, 2020). Therefore, declines in spotted skunk occupancy may have resulted from tree mortality or ground movement (e.g., landslides). It remains uncertain what population-level impact these extreme events may have on western spotted skunks, but this warrants further investigation given extreme weather events are projected to increase in frequency and severity with climate change (Seneviratne et al., 2022).

Other similarly sized carnivores are also sensitive to snow and cold temperatures because of their morphology, high metabolic demands, and limited energy reserves (Buskirk & Harlow, 1989). For example, long-tailed weasels (*Neogale frenata*) may be limited in their northward distribution because of snow cover (Simms, 1979). Other species such as ermine (*Mustela erminea*) and American marten (*Martes americana*), however, may be better suited to these conditions

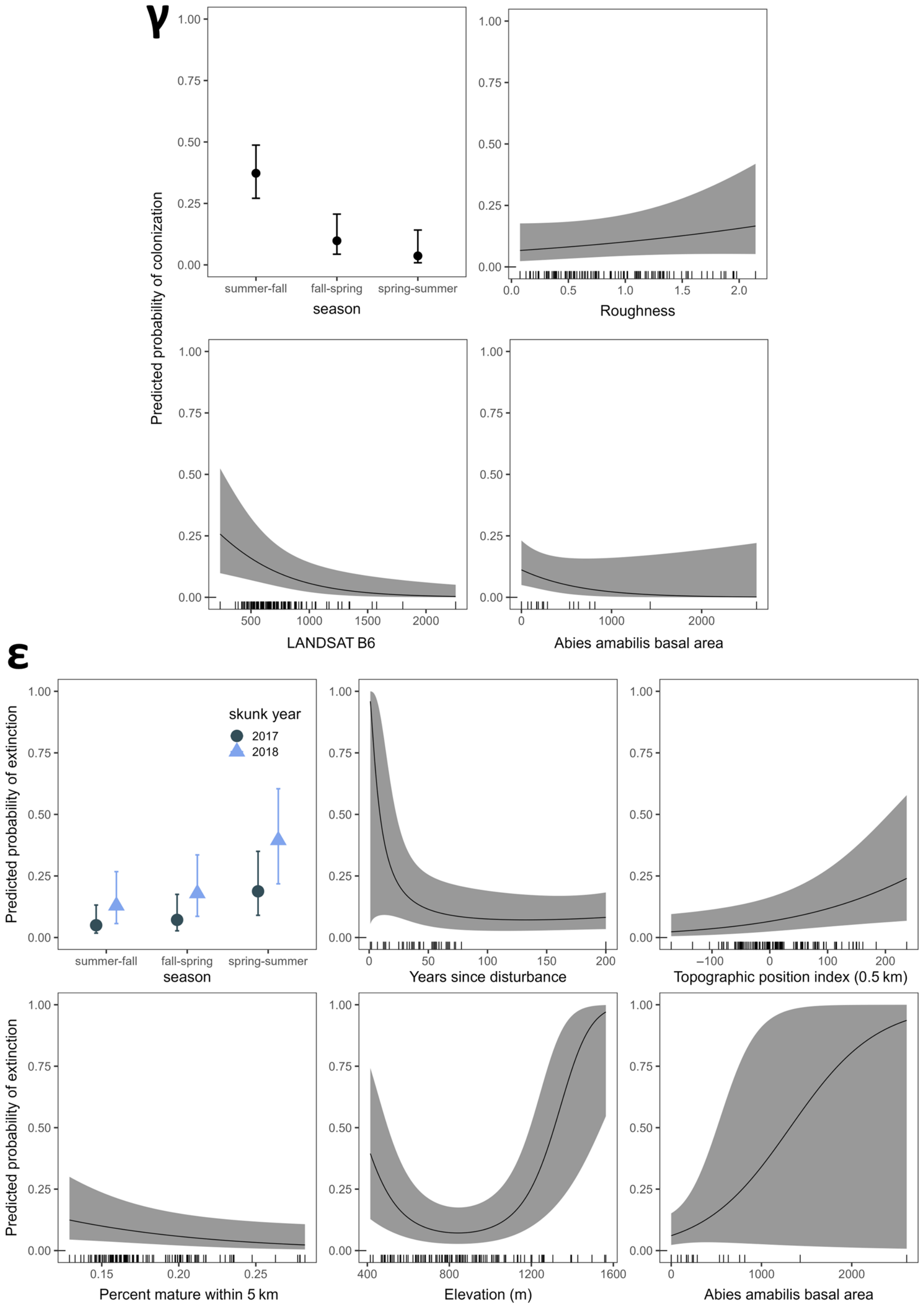

FIGURE 6 Marginal plots (mean and 95% confidence intervals) for colonization (γ) and extinction (ε) from multi-season occupancy models of western spotted skunks (*Spilogale gracilis*) in the Oregon Cascades from 2017 to 2019.

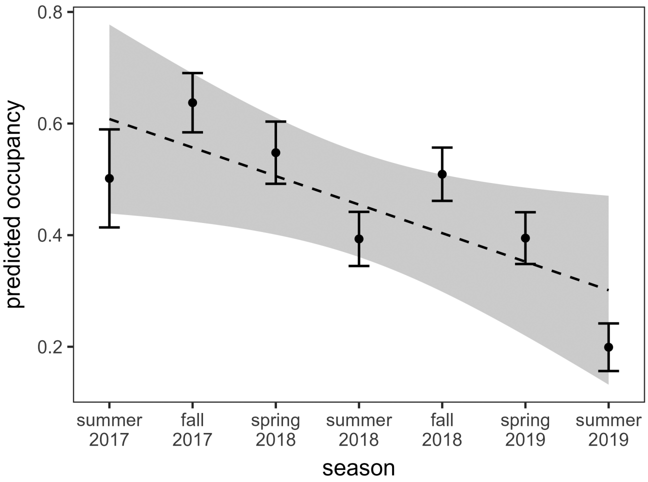

FIGURE 7 Predicted seasonal occupancy of western spotted skunks (*Spilogale gracilis*) in the Willamette National Forest for each season during 2017–2019 (mean ± SE).

through behavioral adaptations. Ermines are highly adept predators that can balance their energetic demands by hunting voles in the subnivean zone (Simms, 1979). American marten behaviorally cope with colder temperatures and heavy snow by selecting subnivean rest sites (Buskirk et al., 1989; Wilbert et al., 2000). Although we were generally unsuccessful in tracking western spotted skunks when there was deep snow cover, we regularly detected spotted skunks in camera trap photos walking on top of the snow, which suggests that spotted skunks were not restricted to the subnivean zone, at least when active.

While dynamic occupancy models revealed general patterns of space use by western spotted skunks, resource selection at the home range scale revealed more detailed responses to environmental variables. In both models, predicted use by western spotted skunks was higher in local valleys and in wetter areas. Use of wetter areas was further supported by the greater use of northerly aspects, which typically remained moister, compared with southerly aspects. Our hypotheses about spotted skunk use of local valleys were further refined by the home range scale analysis that showed use was higher with less bigleaf maple basal area and lower canopy height. Spotted skunks may have avoided lowland riparian forests prone to flooding. Western spotted skunks are susceptible to predation by barred owls (*Strix varia*) (Tosa et al., 2022), which may be a driving factor for selecting areas with more shrubby vegetation that could reduce predation risk (Figure 9). Selection for vegetative cover to reduce predation risk is consistent with other studies on plains spotted skunks and eastern spotted skunks (Eng & Jachowski, 2019; Lesmeister et al., 2009; Sprayberry & Edelman, 2018).

At the home range scale, western spotted skunk use was greater in locations surrounded by more logged area at the 1-km scale, also contrary to the observations by Carey and Kershner (1996). This was also counter to our findings in the landscape-level occupancy analysis where occupancy was higher in areas surrounded by more mature forest at the 5-km scale and extinction probability was higher in areas with recent disturbances. A possible reason for selection for previously logged forest could be because light is able to penetrate through the canopy and create denser shrub cover (Bunnell, 1990), which in turn could provide more cover from predators.

In addition, we found that individuals had different responses to environmental variables, especially elevation. Most skunk home ranges were at intermediate elevations, but some individuals selected low elevation sites and one individual selected high elevation sites (Appendix S1: Figure S9). This suggests that western spotted skunks exhibit high plasticity and can employ a variety of strategies to survive in the forests of the Pacific Northwest. Conflicting selection of resources by individuals has also been noted by a previous study on island spotted skunks, where one individual preferred a vegetation type that was avoided by all other monitored animals (Crooks & Van Vuren, 1995). Although spotted skunks may be highly adaptable to their environmental, they may experience varying mortality risks in these different environments (Lesmeister et al., 2010). Together, our results suggest that western spotted skunks are a common, habitat generalist species.

Although spotted skunks have been described as having more of an "area of familiarity" instead of a home range (Crabb, 1948), we found that western spotted skunks generally used the same area over the course of the study, apart from one dispersing skunk. We found that western spotted skunk home ranges of both males and females overlapped considerably, suggesting that western spotted skunks are not territorial, unlike other solitary small carnivores (Inman et al., 2012; Moriarty et al., 2017; Powell, 1979). There were no obvious correlations between seasonal male home range sizes and body mass or body length (Appendix S1: Figure S6). Male spotted skunk home ranges appear to be driven by the size of their summer home ranges where males with large summer home ranges had large overall home ranges, whereas male skunks with small summer home ranges had small overall home ranges. Male home ranges in fall and spring were similar (Figure 4A). Since food resources are most abundant during summer, male skunks with large home ranges may require larger home ranges to acquire enough food resources to meet their energetic requirements. Female western spotted skunk home ranges, on the other hand, were small overall and consistently small across all seasons.

The montane temperate rainforests of the Pacific Northwest can be a challenging landscape to conduct animal GPS and VHF tracking studies. Dense canopy cover in valley bottoms are known to hinder communication between GPS devices and satellites and may prevent fixes from occurring in those location (Moriarty & Epps, 2015) (Appendix S1: Figure S3). VHF signal strength was limited by mass of the battery in comparison to the small body size of the western spotted skunk and prevented us from locating animals far from roads or if the animal was inside a dense structure (Frair et al., 2010). Therefore, our sample of locations may be biased, so the apparent selection of areas close to roads by spotted skunks may be artificial. Still, many carnivores take advantage of road networks for traveling and hunting because there are fewer obstructions. Furthermore, we found that western spotted skunks consistently selected areas of low topographic position index, even with these biases, suggesting that selection for these areas may be higher than quantified in our analyses.

Although the use of bait at cameras may bias the detection rates and occupancy rates by increasing detection rates for western spotted skunks, this method was necessary to obtain adequate observations of our focal species. Other studies were not able to detect spotted skunks without bait, whereas those with bait in the same area were able to detect spotted skunks (Kelly & Holub, 2008; Siegfried et al., 2023; Thorne et al., 2017).

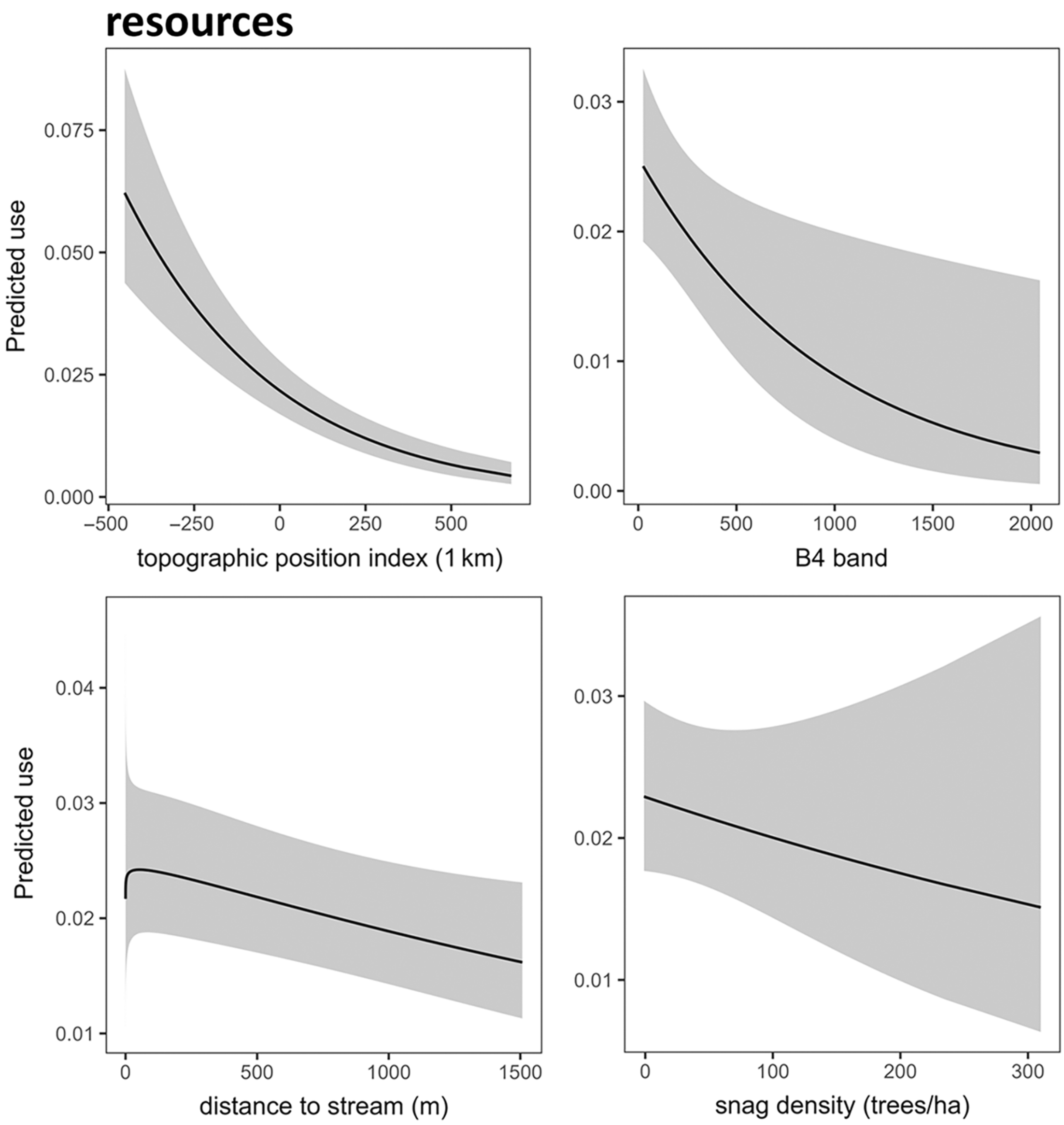

FIGURE 8 Predicted marginal plots (mean and 95% confidence intervals) of resource and thermal tolerance variables for home range level resource selection by western spotted skunks (*Spilogale gracilis*) in the Oregon Cascades from 2017 to 2019. Note differences in scales.

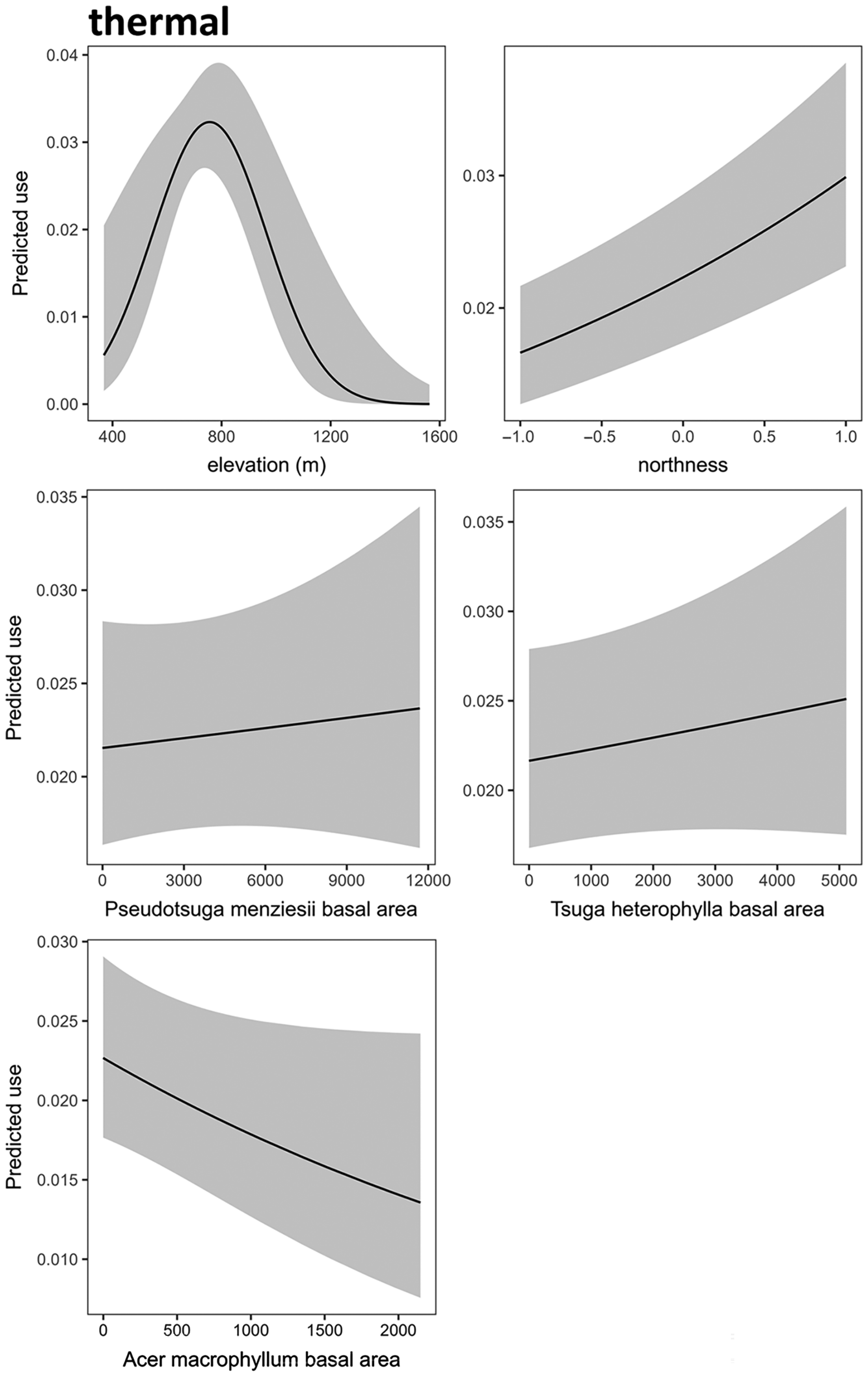

FIGURE 8 (Continued)

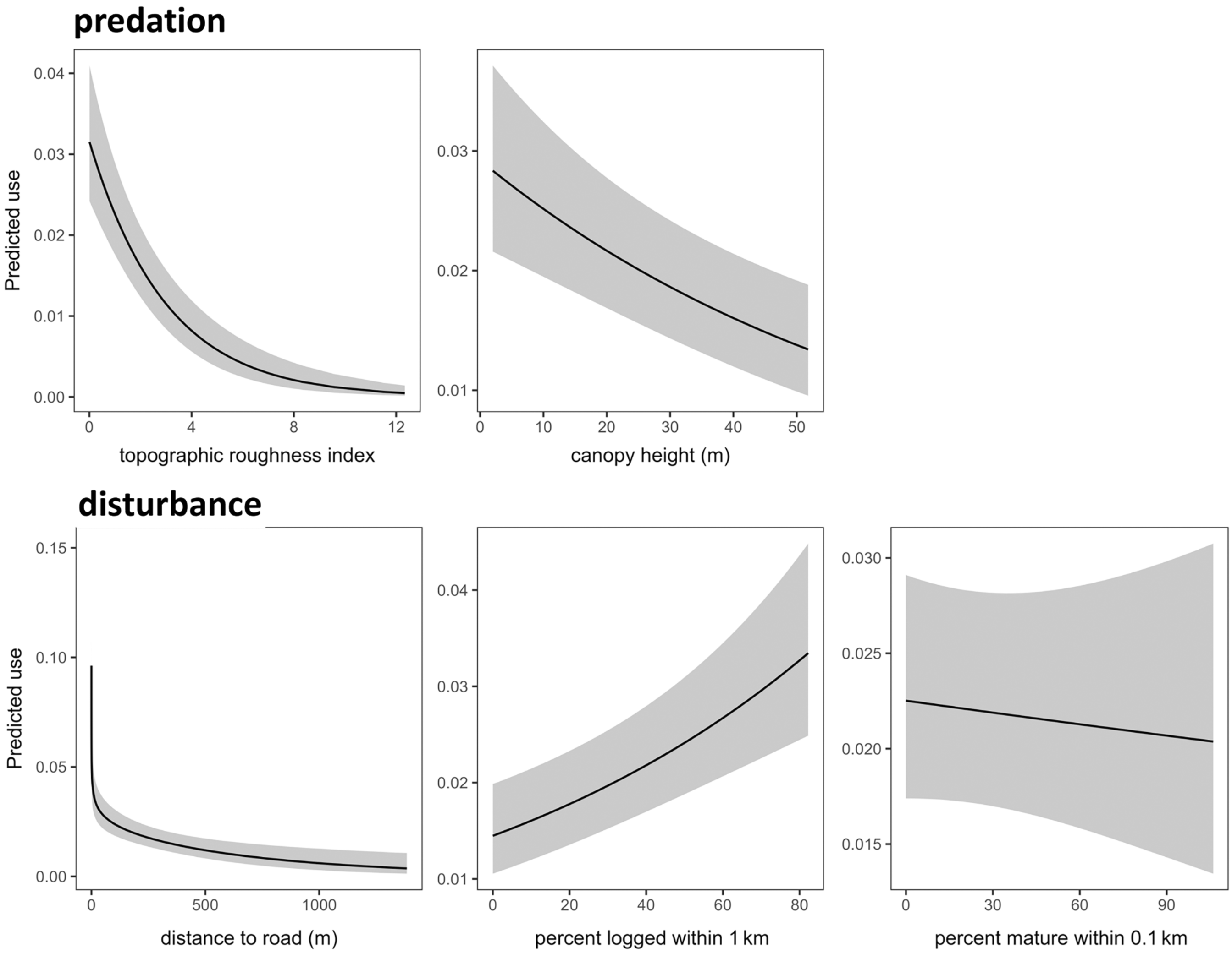

FIGURE 9 Predicted marginal plots (mean and 95% confidence intervals) of predation and disturbance variables for home range level resource selection by western spotted skunks (*Spilogale gracilis*) in the Oregon Cascades from 2017 to 2019. Note differences in scales.

Moreover, when Siegfried et al. (2023) compared detection rates and activity rates of carnivores at sites with and without bait, they found increased detection rates of most carnivores with bait, but general activity patterns remained similar to when there was no bait.

Forest stand age was not an important predictor of western spotted skunk space use or resource selection at any scale as it was for plains spotted skunks (Lesmeister et al., 2013). This may be because forest structure and understory complexity are not strictly correlated with forest age in the Pacific Northwest. Most federally managed forest, regardless of age, typically consist of complex vegetation structure that can provide ample rest sites and protection from predators. Stands in the stem-exclusion stage, however, have simple structure and may lack the necessary resources and protection needed for stable occupancy. Thorne et al. (2017) found that for eastern spotted skunks, occupancy was high in both young-aged forest and mature stands that had complex forest structure. If we had not studied western spotted skunks in old-growth stands that have high vegetation complexity and structure, we may have concluded that western spotted skunks favor young stands. Therefore, studying western spotted skunk spatial ecology in a variety of forest types provides important conservation and forest management information.

As small carnivore populations face anthropogenic threats and changes to their environmental conditions, it is increasingly important to understand species' habitat requirements. This study adds to our knowledge about a relatively common small carnivore in Pacific Northwest coniferous forests. Western spotted skunks had disproportionately large home ranges relative to their body mass that overlapped neighboring individuals, regardless of sex, indicating that western spotted skunks were not territorial. Our results suggest that western spotted skunks navigate their environment by balancing their needs for food resources, cover from predators, and thermal tolerance with the effects of anthropogenic disturbance. Multiple lines of evidence suggested that western spotted skunks selected against, and were negatively affected by, snowpack. Otherwise, western spotted skunks were a widely distributed habitat generalist throughout lower to mid-elevation sites in this montane, coniferous forest. Future studies of western spotted skunks should explore co-occurrence patterns with other species and finer scales of selection, such as the characteristics and availability of rest sites, which may limit spotted skunk distribution (Lesmeister et al., 2008).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Tosa et al., 2024) are available from Zenodo: https://zenodo.org/doi/10.5281/zenodo.12804911.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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