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RESEARCH ARTICLE

Selection in the third dimension: Using LiDAR derived canopy metrics to assess individual and population-level habitat partitioning of ocelots, bobcats, and coyotes

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Abstract

Wildlife depends on specific landscape features to persist. Thus, characterizing the vegetation available in an area can be essential for management. The ocelot (*Leopardus pardalis*) is a federally endangered, medium-sized felid adapted to woody vegetation. Quantifying the characteristics of vegetation most suitable for ocelots is essential for their conservation. Furthermore, understanding differences in the selection of sympatric bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) can provide insight into the mechanisms of coexistence between species. Because of differences in hunting strategy (cursorial vs. ambush) and differences in use of land cover types between species, these three carnivores may be partitioning their landscape as a function of vegetation structure. Light detection and ranging (LiDAR) is a remote sensing platform capable of quantifying the sub-canopy structure of vegetation. Using LiDAR data, we quantified the horizontal and vertical structure of vegetation cover to assess habitat selection by ocelots, bobcats, and coyotes. We captured and collared 8 ocelots, 13 bobcats, and 5 coyotes in southern Texas from 2017 to 2021. We used step selection functions to determine the selection of vegetation cover at the population and individual level for each species. Ocelots selected for vertical canopy cover and dense vegetation 0–2 m in height. Bobcats selected cover to a lesser extent and had a broader selection, while coyotes avoided under-story vegetation and selected areas with dense high canopies and relatively open understories. We observed a high degree of variation among individuals that may aid in facilitating intraspecific and interspecific coexistence. Management for ocelots should prioritize vegetation below 2 m and vertical canopy cover. We provide evidence that fine-scale habitat partitioning may facilitate coexistence between sympatric carnivores. Differences among individuals may enhance coexistence among species, as increased behavioral plasticity of individuals can reduce competition for resources. By combining accurate, fine-scale measurements derived from LiDAR data with high-frequency global positioning system locations, we provide a more thorough understanding of the habitat use of ocelots and two sympatric carnivores.

Introduction

Wildlife species select habitat characteristics essential to their survival based on factors such as the locations of resources, habitat features, and mates (Powell & Mitchell, 2012). Habitat selection may shift based on annual or seasonal shifts in the availability of resources, climatic changes or interspecific interactions (Prati et al., 2021; Yamamoto et al., 2012). Despite these shifts, animals will consistently select for particular features or characteristics

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such as sources of food and water, proximity to conspecifics, and specific types of vegetation (Dumyahn et al., 2007; Leary et al., 1998; Leonard et al., 2008). Habitat features are among the most important factors in determining an individual's selection of a particular area (Anich et al., 2010). Vegetation cover is a vital characteristic for a wide range of terrestrial species, many of which adapt to specific assemblages of vegetation and cover densities (Dumyahn et al., 2007; Leonard et al., 2008; Wiley & Van Riper, 2014; Zielinski et al., 2004). Thus, characterizing the vegetation available in an area can be essential for managing specialist species. Assessments of habitat selection and coexistence among species generally assume that the gradient by which these species partition environments is accurately incorporated; however, rarely have prior studies incorporated vertical vegetation complexity into studies of terrestrial mammals. Obtaining information on vegetation cover and structure using ground surveys can be difficult and time-consuming and, particularly over large study areas, may result in inaccurate estimates (Barnes et al., 2016; Camathias et al., 2013). Remote sensing techniques can provide an effective, unbiased method for obtaining vegetation characteristics across broad scales (Andrew & Ustin, 2009), including such information as surface reflectance, precipitation, topography, and diversity of vegetation (Bradley & Fleishman, 2008).

Advancements in geospatial technology have allowed for high-resolution studies of habitat across a larger scale that may provide a better representation of local habitat availability. Light detection and ranging (LiDAR) is a remote sensing technique that can be effectively used to characterize vegetation on a landscape (Drake et al., 2003; Goetz et al., 2010). LiDAR functions by emitting light pulses from an airborne device and recording the signals reflected from the earth's surface (Seavy et al., 2009). From these signals, a digital terrain model of the surface can be created, along with a digital surface model of the vegetation (Camathias et al., 2013). By assessing differences between the two surfaces, along with the density of collected LiDAR points, the height, mass, and structure of vegetation can be effectively assessed over a large area (Hyde et al., 2006; Seavy et al., 2009). Applications of LiDAR to assess landscape characteristics have been more prevalent in forestry (Drake et al., 2003; Hyde et al., 2006; Knapp et al., 2018); however, use of this methodology for assessing habitat use by wildlife remains limited, particularly for large mammals. Several studies have examined forest structure regarding habitat for bird species such as cerulean warblers (*Setophaga cerulea*, Barnes et al., 2016), woodpeckers (*Sphyrapicus nuchalis*, Vierling et al., 2013), and spotted owls (*Strix occidentalis occidentalis*, García-Feced et al., 2011), as well as insects (Müller & Brandl, 2009), and fox squirrels (*Sciurus niger*, Nelson et al., 2005). Habitat selection using LiDAR has been evaluated for terrestrial mammals including roe deer (*Capreolus capreolus*, Ewald et al., 2014), Sitka black-tailed deer (*Odocoileus hemionus sitkensis*, Shanley et al., 2021), elk (*Cervus elaphus*, Devore et al., 2016), moose (*Alces alces*, Alston et al., 2020) and martens (*Martes caurina*, Tweedy et al., 2019). To our knowledge, this is the first application of this methodology to examine habitat selection for canids or felids and compare niche partitioning within a sympatric carnivore community. Using LiDAR technology can effectively incorporate the third dimension of vegetation structure into analyses of habitat selection and offer a novel approach to examining partitioning between species.

The ocelot is a medium-sized neotropical felid native to North and South America (Cruz et al., 2018; Di Bitetti et al., 2006). Historically, ocelots ranged across much of Texas into western Louisiana and Arkansas; however, large declines in populations have led to the species being listed as federally endangered in the United States (Haines et al., 2005). Currently, ocelots in the US are restricted to the southern tip of Texas, with approximately less than 100 individuals remaining (Jackson et al., 2005; Lombardi et al., 2021). Ocelots are typically associated with dense woody cover (Shindle & Tewes, 1998). Due to urbanization and agriculture conversion, there was a decline in woody cover in the region, which led to a decline in large woody patches (>100 ha; Lombardi, Perotto-Baldivieso, et al., 2020) and available habitat since 1982 (Veals et al., 2022). By 1986, it was estimated that <1% of this habitat type occurred in southern Texas (Tewes & Everett, 1986), but current estimates are unknown. This rapid decline in habitat, along with road mortality and historic hunting and trapping, has been responsible for declines in ocelot populations (Blackburn et al., 2021; Haines et al., 2005). Despite the decreasing availability of woody cover, research indicates an increasing selection of woody vegetation in recent decades, suggesting an increasing dependency on this specific habitat type (Veals et al., 2022). Land use projections for southern Texas suggest a continued increase in agricultural development and urbanization and a further decrease in the availability of woody vegetation (Lombardi, Perotto-Baldivieso, et al., 2020). Texas ocelots are considered habitat specialists and, as a species with narrow habitat requirements, are particularly vulnerable to habitat loss (Leonard et al., 2008). As a result, managing the remaining habitat is vital to sustaining populations of ocelots (Lombardi et al., 2021; Lombardi, Perotto-Baldivieso, et al., 2020).

In Texas, ocelots are sympatric with two other ecologically similar carnivores, bobcats (*Lynx rufus*) and coyotes (*Canis latrans*; Lombardi, MacKenzie, et al., 2020;

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Sergeyev et al., 2022). These species overlap extensively in space use and diet (Booth-Binczik et al., 2013; Horne et al., 2009; Lombardi, MacKenzie, et al., 2020). Given the degree of overlap of the ecological niche among these three species, there exists a greater potential for interspecific competition for vital resources such as prey items or secure habitat (MacArthur, 1968; Maitz & Dickman, 2001; Smith & Remington, 1996). As generalist species, bobcats and coyotes exhibit greater plasticity in the habitats and land cover they use compared to ocelots. Bobcats select for less dense woody vegetation than ocelots (Horne et al., 2009) and use a variety of microhabitats (Kolowski & Woolf, 2002). Similarly, coyotes utilize a variety of cover types (Morey et al., 2007; Newsome et al., 2015) and have been positively linked to both open areas and dense cover (Cherry et al., 2017; Crimmins et al., 2012; Hinton et al., 2022; Stevenson et al., 2019). Furthermore, differences in hunting strategy may be driving differences in the selection of vegetation between species as well, as coyotes are cursorial predators (Kamler & Gipson, 2000; Thibault & Ouellet, 2005), while ocelots and bobcats employ an ambush style. As such, coyotes may select open areas or open understories, while bobcats and ocelots may select dense understories to facilitate stalking. Thus, fine-scale differences in the use of vegetation cover may facilitate coexistence between ocelots, bobcats, and coyotes, specifically differences in selection for the vertical dimension of vegetation. Comparison of habitat selection across concurrently monitored individuals of each species may improve our understanding of the dynamics between these three ecologically similar carnivores and provide evidence of niche partitioning.

Ocelots depend on dense vegetation cover for hunting and thermoregulation (Sergeyev et al., n.d.). Consequently, identifying the structure of vegetation selected by ocelots, as well as competing species, is essential to management and conservation. We examine selection for an often overlooked component of landscape structure, particularly for terrestrial mammals, vertical vegetation structure. Furthermore, we assess how differences in selection for vertical vegetation structure may facilitate coexistence within a carnivore community. We used high-resolution LiDAR data to assess the selection of vegetation structure by ocelots and compare the habitat selection of sympatric bobcats and coyotes. We examined differences in the selection of vertical and horizontal vegetation cover at the population and individual levels for each species to understand the mechanisms that facilitate inter- and intraspecific coexistence. We predicted selection for dense vegetation cover by ocelots and to a lesser extent by bobcats and coyotes. Further, as a specialist species, we expected less individual variation in selection by ocelots compared to bobcats and coyotes, two species with more generalist tendencies. By combining LiDAR data with high-resolution global positioning system (GPS) data, we provide a fine-scale assessment of selection for vegetation cover with greater detail than previously available. Further, we show that differences in selection for the third dimension of vegetation structure can facilitate coexistence among sympatric carnivores.

Study Area

We conducted this study on two private ranches, the East Foundation's El Sauz Ranch and the Yturria Family's San Francisco Ranch, located in Willacy and Kenedy counties in southern Texas, USA (Fig. 1). The El Sauz Ranch (113 km^2) is an operational cattle ranch that manages land for land stewardship, cattle, and the conservation of native wildlife. A variety of landscape features exist on the ranch including prairies, sand dunes, coastal estuarine wetlands, grasslands, anthropogenic water features, and patches of dense woody vegetation (Lombardi, Perotto-Baldivieso, et al., 2020). The San Francisco Ranch (25.9 km^2) is a private family ranch that manages land for the conservation of ocelots, hunting of ungulates, and land stewardship. Two conservation easements owned by the US Fish and Wildlife Service Lower Rio Grande Valley National Wildlife Refuge Complex (1.98 km^2) are found on the ranch with dense woody vegetation (Haines et al., 2006). Surrounding patches of restored native woody vegetation are managed by the Nature Conservancy of Texas. The climate is subtropical and semi-arid, with annual temperatures that range from 10 to 36°C with a mean of 23°C (Haines et al., 2006), and inconsistent precipitation in the region results in episodic drought; the mean annual rainfall is 68 cm (Haines et al., 2006; Norwine & Kuruvilla, 2007). There are diverse woody communities in these areas across different seral stages. This region contains the largest patches of native woody cover along the southern Texas Gulf Coast (Lombardi, Perotto-Baldivieso, et al., 2020) and canopy structure within these patches varies along a north-to-south gradient (Lombardi et al., 2022). In the northern parts of the study area, live oak (*Quercus virginiana*; 18–24 m height) is the dominant tree species, often reaching climax seral stages in different portions of the study area. Due to its shade-intolerant growth characteristics (Spector & Putz, 2006), live oak forests may contain various communities where understory density depends on the shade tolerance of understory species (Gommers et al., 2013). The understory of live oak forest ranges from open- to closed-canopy thornshrub species such as lime prickly ash (*Zanthoxylum fagara*; 6–7 m height) and huisache (*Acacia farnesiana*; 8–9 m height), stands of palm (*Sabal* spp.), and invasive guinea grass (*Megathyrsus maximus*; 1–3 m

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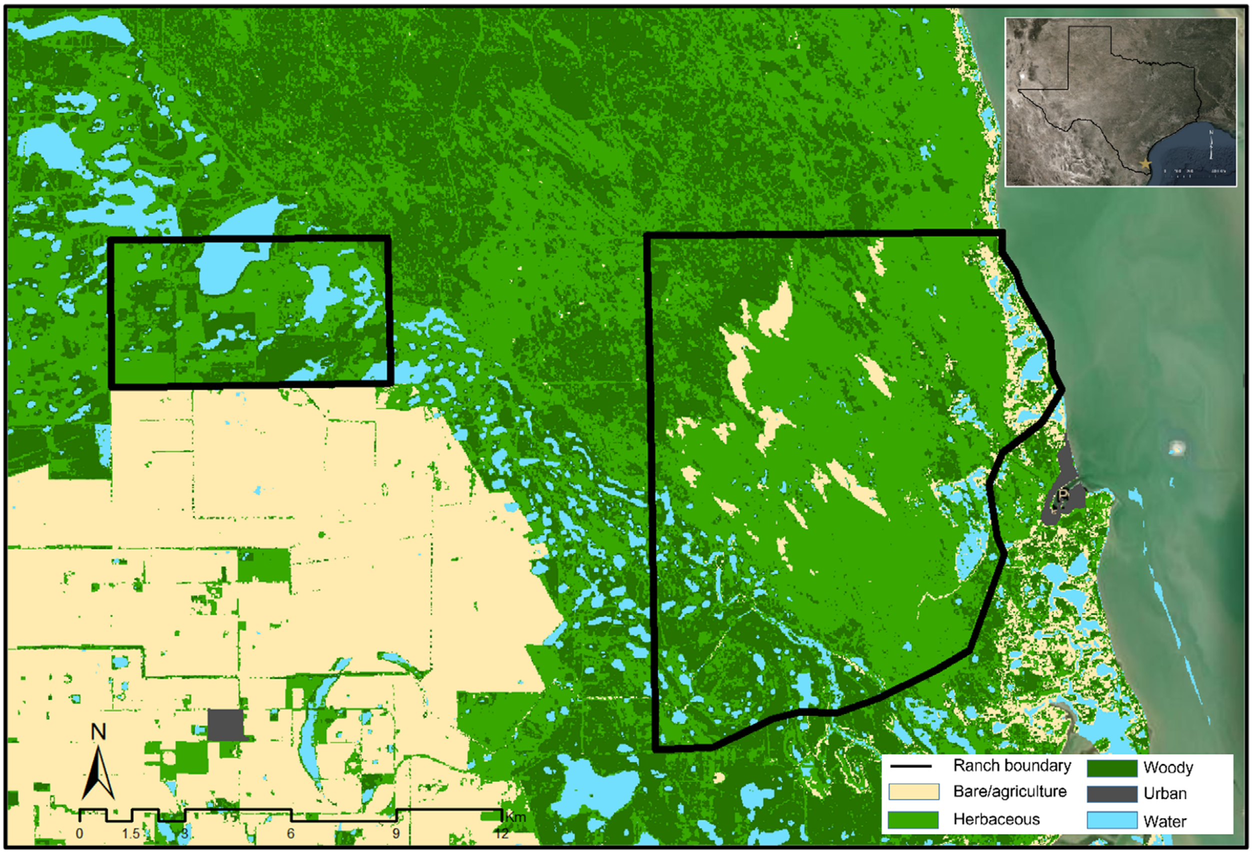

Figure 1. Map of study area to assess habitat selection of ocelots (*Leopardus pardalis*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*) in southern Texas, USA from 2017 to 2021. Left polygon denotes the boundaries of the Yturria San Francisco Ranch and the right polygon denotes the boundaries of the East Foundation's El Sauz Ranch.

height; Lombardi et al., 2022). However, closed-canopy live oak forests are characterized by open understories, with palms, and other shade-tolerant woody and herbaceous plant species and are often located near parabolic inland dunes (>30 m height). In the southern portion of the study area, the habitat transitions to primarily mesquite (*Neltuma glandulosa*), huisache, lime prickly ash, and Texas ebony (*Ebenopsis ebano*; 10 m height) dry thorn forests with varying densities of guinea grass, cordgrass (*Spartina* sp.) and diverse woody plant species (Lombardi et al., 2022). Similarly, closed canopy mesquite woodlands have more open understories, while open mesquite-ebony woodlands are characterized by dense mixed woody and herbaceous cover.

Materials and Methods

Animal capture/collaring

From January 2017 to May 2021, we captured 8 ocelots (3 males and 5 females), 13 bobcats (7 males and 6 females), and 5 coyotes (2 males and 3 females) using single-door Tomahawk box-traps (108 × 55 × 40 cm; Tomahawk Trap Co., Tomahawk, WI, USA). All collared individuals were of adult age. We baited with a live pigeon or chicken contained within a separate compartment that was inaccessible from the trap. We immobilized captured animals using a 4:1 mixture of tiletamine hydrochloride and zolazepam hydrochloride (Telazol™; Zoetis, Florham Park, NJ, USA) at a dose of 5 mg kg^{-1} in 2017 and a mixture of ketamine hydrochloride (4–5 mg kg^{-1}) and medetomidine HCl (0.05 mg kg^{-1}) and used a reversal of 5 mg of atipamezole per 1 mg medetomidine (Zoo-Pharm, Laramie, WY, USA) from 2019 to 2021 (Lombardi et al., 2021; Sergeyev et al., 2022; Shindle & Tewes, 2000). We fitted each individual with a Lotek Minitrack and Litetrack GPS radio collar (Lotek™, New Market, ON, Canada). Collars recorded locations every 30–60 min and were programmed to automatically drop after either a 4–6 month or 1-year period. Capture and handling of animals were conducted in accordance with the United States Fish and Wildlife Service permit

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(#PRT-676811), Texas Parks and Wildlife Department permit (#SP0190-600), and Texas A&M University Kingsville Institutional Animal Care and Use Committee protocols (2012-12-20B-A2, 2019-2-28A-2-28B). The sample size of locations obtained from each individual varied across individuals and species (Table S1).

Analysis of habitat selection

We downloaded LiDAR point cloud data collected by the United States Geological Survey (USGS) in 2018 from Texas Natural Resources Information System (TNRIS; Austin, TX, USA) at 70 cm resolution (USGS, 2018). We classified points into one of the following classes: water, ground, road (motorized highway), bridge decks, buildings, and vegetation at 1 m intervals at heights: 0–1 m above ground, 1–2 m, and 2–3 m, 3–4 m, 4–5 m, and >5 m (Devore et al., 2016; Ewald et al., 2014) using LP360 (GeoCue Group, Inc., Madison, AL, USA). We first manually identified any features on the landscape that were not vegetation (i.e. roads, buildings, bridges, and water). We then classified the remaining points as vegetation in different height strata using the height above the ground surface. Canopy height was obtained by calculating the difference between digital elevation models and digital surface models (Barnes et al., 2016). We calculated vegetation density based on the point density (vegetation points/cell) of the LiDAR data to quantify vertical and horizontal vegetation structure. The canopy cover variable was intended to describe the vertical structure of the vegetation, while the density at different height strata compared to the horizontal structure of the vegetation. We calculated the percent vertical canopy cover as the proportion of first-return vegetation points out of all first-return points (Korhonen et al., 2011). All raster layers were calculated at a spatial resolution of 10 × 10 m cells.

We used a step selection framework to assess habitat selection (Muff et al., 2019). The case–control design employed in step selection functions mitigates the temporal autocorrelation inherent in telemetry data, especially at high position acquisition rates (Thurfjell et al., 2014). Additionally, the use of random slopes and intercepts to represent individual identification can effectively incorporate variation between individuals (Muff et al., 2019). Step selection functions have been used to model the movement of wildlife with respect to roads (Roever et al., 2010), identify movement barriers and corridors (Meyer et al., 2020; Panzacchi et al., 2016), and evaluate habitat selection (Avgar et al., 2016; Thurfjell et al., 2014). However, these methods have not been applied to evaluate the habitat selection of ocelots and may provide a more detailed description of the use of thornshrub vegetation by ocelots. Step selection functions compare case-controlled, randomly generated steps to the true steps obtained to evaluate the probability of selection. We generated 10 random steps for each observed location and used mixed-effects conditional logistic regression models in the 'survival' package in R (Muff et al., 2019). We executed species-specific step selection functions including the density of vegetation in 1 m height increments (0–1, 1–2, 2–3, 3–4, 4–5, >5 m; vegetation points/cell) and the percent vertical canopy cover to evaluate selection for horizontal and vertical cover as predictors. All variables were standardized in the model; Table S2 provides the correlation between variables. A random intercept for animal ID was incorporated in every population-level model. We elected to only examine vegetation-oriented variables (1) to specifically examine how vertical structure influences selection and (2) because within our study area vegetation is often the main driver of selection as there is little anthropogenic development aside from roads and minimal change in elevation across the landscape. We compared this same model at a population level for each species (ocelots, bobcats, and coyotes). To examine the selection of each individual during the day and night, we fitted the same model again at the individual level to assess variation among individuals. We compared selection between daytime (sunrise–sunset) and nighttime (sunset–sunrise) for each species by fitting a model for daytime selection and a model for nighttime selection. Sunrise and sunset times were obtained using the 'suncalc' package in R. We calculated a coefficient of variation of the selection coefficients (expressed as a percentage) for each species to quantify the differences in selection among individuals using the cv() function in the 'raster' package in R (Hijmans & van Etten, 2012).

Results

We evaluated population- and individual-level habitat selection of each species and compared diurnal and nocturnal selection; any trends in habitat selection are reported at $\alpha = 0.05$ unless otherwise stated. Ocelots showed strong selection for vertical canopy cover, such that a one standard deviation increase in canopy cover resulted in 111% greater odds of use during the day (odds ratio [OR] = 2.11, 95% CI [2.01, 2.22]) and 75% at night (OR = 1.75, 95% CI [1.68, 1.83]). Ocelots selected for vegetation 0–2 m in height throughout the diel cycle (Fig. 2; Table 1), such that a one standard deviation increase in 0–1 m vegetation and 1–2 m vegetation resulted in 57% (OR = 1.57, 95% CI [1.54, 1.61]) and 17% (OR = 1.17, 95% CI [1.14, 1.20]) greater odds of use during the day and 44% (OR = 1.44, 95% CI [1.41, 1.47]) and 14% (OR = 1.14, 95% CI [1.11, 1.17]) respectively at night. Ocelots used 2–3 m vegetation as available

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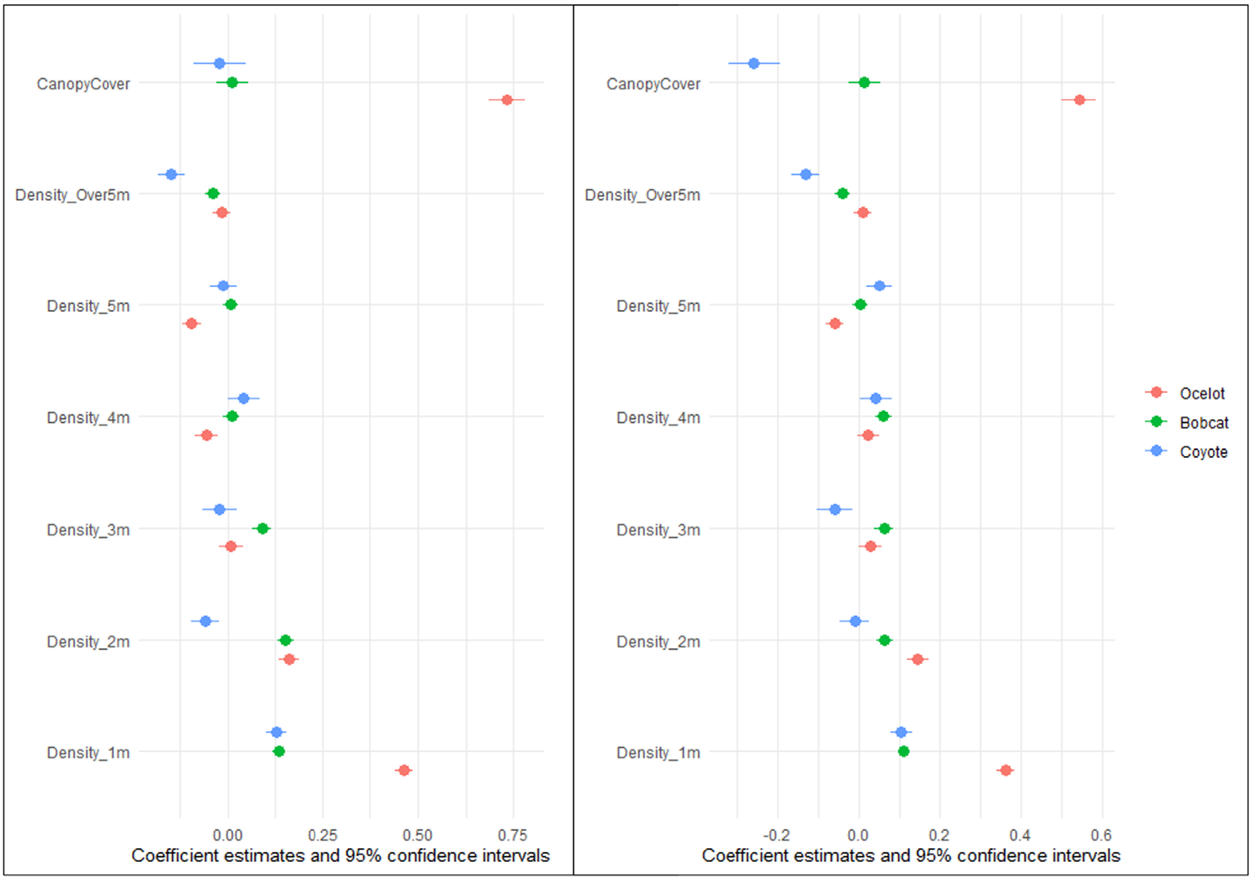

Figure 2. Population level estimates of habitat selection of ocelots (*Leopardus pardalis*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*) in southern Texas, USA from 2017 to 2021 during the day (left panel) and at night (right panel). We examined selection of vertical canopy cover and vegetation density in 1 m increments above the ground (0–1 m = Density_1m, 1–2 m = Density_2m, 2–3 m = Density_3m, 3–4 m = Density_4m, 4–5 m = Density_5m, >5 m = Density_Over5m). The vertical zero line represents no selection, positive estimates denote selection and negative estimates signify avoidance. Horizontal bars represent 95% confidence intervals.

during the day and avoided 3–4 m vegetation (OR = 1.01, 95% CI [0.98, 1.04] and 0.94, 95% CI [0.91, 0.97] for 3–4 m vegetation respectively) but showed greater use of these areas at night (OR = 1.03, 95% CI [1.00, 1.06] for 2–3 m vegetation [$\alpha = 0.07$], 1.01, 95% CI [0.99, 1.04] for 3–4 m vegetation). Ocelots avoided the upper canopy (4–5 m) during day and night (OR = 0.91, 95% CI [0.89, 0.93] during the day and 0.95, 95% CI [0.92, 0.97] at night). Ocelots showed no selection or avoidance of vegetation over 5 m in height. Concordance values for population-level models were 0.691 and 0.657 for the models of daytime and nighttime selection respectively. At the individual level, all ocelots selected for vertical canopy cover and vegetation 0–1 m and all but one selected 1–2 m vegetation and coefficients of variation were the lowest for these variables (Fig. 3; Table 2). Selection for these landscape characteristics tended to be higher during the day for most individuals. Variation among individuals was greater for selection for vegetation above 2 m such that some individuals selected for taller vegetation while others avoided these areas or exhibited no selection; coefficients of variation were larger above 2 m than for vegetation 0–2 m. No ocelots were selected for 4–5 m vegetation.

Bobcats selected for vegetation 0–3 m during the day (OR = 1.15, 95% CI [1.13, 1.16] for 0–1 m, 1.16, 95% CI [1.14, 1.19] for 1–2 m, and 1.09, 95% CI [1.06, 1.12] for 2–3 m) and 0–4 m at night (OR = 1.12, 95% CI [1.10, 1.13] for 0–1 m, 1.07, 95% CI [1.05, 1.10] for 1–2 m, 1.06, 95% CI [1.04, 1.08] for 2–3 m, and 1.07, 95% CI [1.04, 1.09] for 3–4 m; Fig. 2; Table 3). Bobcats avoided vegetation above 5 m throughout the diel cycle, such that a one standard deviation resulted in ~4% lower odds of use (OR = 0.96, 95% CI [0.94, 0.98] during the day and [0.95, 0.98] at night), and showed neither avoidance nor selection vegetation 4–5 m (OR = 1.00, 95% CI [0.98,

Table 1. Model summary of conditional logistic regression model evaluating habitat selection of ocelots (*Leopardus pardalis*) at the population level ($n = 8$) in southern Texas, USA from 2017 to 2021.

	Coef.	exp(Coef.)	SE	*P*-value
Day				
Density 0–1 m veg	0.4555	1.5770	0.0110	<0.001
Density 1–2 m veg	0.1578	1.1709	0.0138	<0.001
Density 2–3 m veg	0.0066	1.0066	0.0157	0.674
Density 3–4 m veg	−0.0596	0.9421	0.0150	<0.001
Density 4–5 m veg	−0.0934	0.9108	0.0128	<0.001
Density >5 m veg	−0.0168	0.9833	0.0121	0.164
Canopy cover	0.7490	2.1148	0.0248	<0.001
Night				
Density 0–1 m veg	0.3650	1.4404	0.0109	<0.001
Density 1–2 m veg	0.1339	1.1432	0.0130	<0.001
Density 2–3 m veg	0.0262	1.0266	0.0143	0.068
Density 3–4 m veg	0.0142	1.0143	0.0134	0.288
Density 4–5 m veg	−0.0553	0.9462	0.0116	<0.001
Density >5 m veg	−0.0059	0.9941	0.0109	0.589
Canopy cover	0.5616	1.7534	0.0213	<0.001

We examined selection for density of vegetation at 1 m increments above the ground and percent canopy cover to encompass horizontal and vertical structure of vegetation and compared selection during daytime (sunrise–sunset) to nighttime (sunset–sunrise). The exp(Coef.) is the odds ratio for that variable.

1.02] during the day and [0.99, 1.03] at night). Bobcats used vertical canopy cover in proportion to availability (OR = 1.03, 95% CI [0.98, 1.07] during the day and 1.00, 95% CI [0.96, 1.04] at night). Concordance values for population-level models were 0.572 and 0.553 for models of daytime and nighttime selection. At the individual level, all but one bobcat selected for 0–1 m vegetation during day and night and all but one showed selection for 1–2 m vegetation for at least part of the diel cycle (i.e. either day, night or both; Fig. 3; Table 2). As with ocelots, variation was greater in selection for vegetation above 2 m. Several individuals showed a stronger selection for upper-story vegetation at night, however, the opposite pattern was observed in other individuals as well.

Coyotes selected 0–1 m vegetation during the day and night (OR = 1.14, 95% CI [1.11, 1.17] in daytime and 1.11, 95% CI [1.08, 1.14] at night). Coyotes avoided 1–2 and 2–3 m vegetation during the day (OR = 0.95, 95% CI [0.91, 0.98] and 0.96, 95% CI [0.92, 1.00] [$\alpha = 0.10$] respectively) and 2–3 m vegetation at night (OR = 0.96, 95% CI [0.92, 1.00], $\alpha = 0.07$; Fig. 2; Table 4). Coyotes selected for 3–4 m vegetation during the day (OR = 1.04, 95% CI [1.00, 1.08]) and 3–4 and 4–5 m vegetation at night (OR = 1.05, 95% CI [1.01, 1.09] and 1.06, 95% CI [1.02, 1.09] respectively). Coyotes avoided vegetation above 5 m during day and night (OR = 0.85, 95% CI [0.82, 0.88] and 0.89, 95% CI [0.86, 0.92] respectively). Coyotes avoided canopy cover at night (OR = 0.74, 95% CI [0.69, 0.79]) but showed no response during the day (OR = 1.00, 95% CI [0.94, 1.08]). Concordance values for population-level models were 0.552 and 0.561 for models of daytime and nighttime selection. Selection among individuals varied greatly; however, selection for 0–1 m and 3–4 m vegetation was consistent with the exception of one individual during the night and day respectively (Fig. 3; Table 2). Across all species, variation among individuals was high and we did not observe any discernible patterns across individuals or sexes.

Discussion

Understanding the habitat selection of a species is an essential component of management, particularly for endangered species with narrow habitat requirements. Further, identifying differences in habitat selection between potential competitors can provide insight into mechanisms of coexistence and niche partitioning between species and guide habitat management for the benefit of the overall carnivore community. We assessed the selection for vertical vegetation structure, an often-overlooked component of the landscape in many studies of terrestrial mammals and examined how this three-dimensional gradient can facilitate fine-scale habitat partitioning between species. We observed differences in habitat selection between ocelots, bobcats, and coyotes that provide evidence of fine-scale habitat partitioning at the population level. At the individual level, we observed a high degree of intraspecific variation in habitat selection. Variation in selection among individuals might be more expected for generalist species such as bobcats and coyotes, however, we unexpectedly observed intraspecific variability in the habitat selection of ocelots, a specialist species considered strongly tied to dense woody vegetation (Harveson et al., 2004; Shindle & Tewes, 1998). We found consistent selection among ocelots for dense vegetation 0–2 m in height, supporting the idea that ocelots strongly select for dense thornshrub cover (Horne et al., 2009; Jackson et al., 2005; Sergeyev et al., n.d.). While Shindle and Tewes (1998) suggested a minimum of 2 m canopy height to be considered ideal habitat for ocelots, our results emphasize a strong selection for lower story vegetation, likely to allow for denning (Laack et al., 2005), resting, foraging or movement forays (Lombardi et al., 2022; Sergeyev et al., 2022). We observed selection for areas of greater percent vertical canopy cover throughout the diel cycle, supporting prior findings of ocelots selecting dense canopy cover (Horne et al., 2009; Sergeyev et al., n.d.; Sergeyev et al., 2022; Shindle & Tewes, 1998). Selection for cover was stronger during the day, potentially as ocelots used these areas of cover when resting

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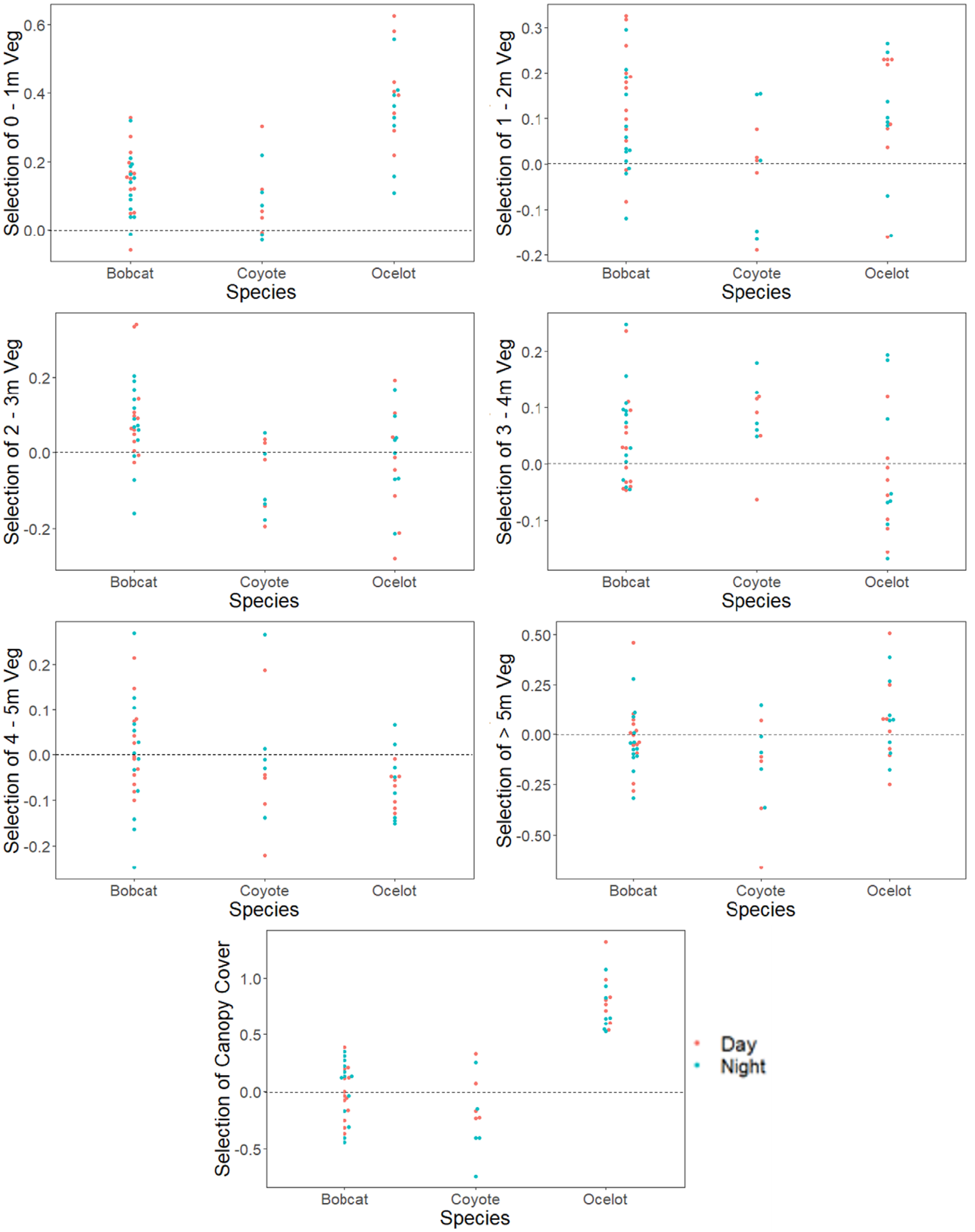

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Figure 3. Selection coefficients for vegetation cover by individual ocelots (*Leopardus pardalis*), bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) in southern Texas, USA from 2017 to 2021. Panels show selection of 0–1 m vegetation (top left), 1–2 m vegetation (top right), 2–3 m vegetation (middle left), 3–4 m vegetation (middle right), 4–5 m vegetation (lower left), >5 m vegetation (lower right) and percent canopy cover (bottom middle) during the day (red) and night (blue). The horizontal zero line represents no selection, positive estimates signify selection and negative estimates denote avoidance.

Table 2. Coefficients of variation associated with the individual selection coefficients of ocelots (*Leopardus pardalis*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*) in southern Texas from 2017 to 2021.

	Ocelots Daytime	Ocelots Nighttime	Bobcats Daytime	Bobcats Nighttime	Coyotes Daytime	Coyotes Nighttime
0–1 m veg	30.84	48.57	60.04	63.65	87.06	107.76
1–2 m veg	75.38	99.88	82.04	113.15	165.77	122.32
2–3 m veg	122.81	145.98	101.19	111.67	123.73	103.41
3–4 m veg	102.30	125.15	137.01	104.18	87.53	59.37
4–5 m veg	66.14	107.54	136.18	131.51	117.70	153.04
>5 m veg	135.25	119.22	150.13	137.08	83.48	118.77
Canopy cover	47.40	21.01	121.94	120.23	126.91	97.97

Variables included density of 0–1 m vegetation, 1–2 m vegetation, 2–3 m vegetation, 3–4 m vegetation, 4–5 m vegetation, >5 m vegetation, and % canopy cover. Coefficients were estimated from conditional logistic regression models in a step selection framework.

Table 3. Model summary of conditional logistic regression model evaluating habitat selection of bobcats (*Lynx rufus*) at the population level (n = 13) in southern Texas, USA from 2017 to 2021.

	Coef.	exp(Coef.)	SE	*P*-value
Day				
Density 0–1 m veg	0.1370	1.1468	0.0078	<0.001
Density 1–2 m veg	0.1522	1.1644	0.0109	<0.001
Density 2–3 m veg	0.0850	1.0888	0.0130	<0.001
Density 3–4 m veg	0.0041	1.0041	0.0117	0.727
Density 4–5 m veg	0.0053	1.0053	0.0102	0.605
Density >5 m veg	−0.0440	0.9570	0.0102	<0.001
Canopy cover	0.0271	1.0274	0.0214	0.206
Night				
Density 0–1 m veg	0.1118	1.1183	0.0073	<0.001
Density 1–2 m veg	0.0722	1.0748	0.0103	<0.001
Density 2–3 m veg	0.0586	1.0604	0.0120	<0.001
Density 3–4 m veg	0.0651	1.0673	0.0105	<0.001
Density 4–5 m veg	0.0078	1.0078	0.0093	0.403
Density >5 m veg	−0.0368	0.9638	0.0092	<0.001
Canopy cover	0.0015	1.0015	0.0195	0.940

We examined selection for density of vegetation at 1 m increments above the ground and percent canopy cover to encompass horizontal and vertical structure of vegetation and compared selection during daytime (sunrise–sunset) to nighttime (sunset–sunrise). The exp(Coef.) is the odds ratio for that variable.

Table 4. Model summary of conditional logistic regression model evaluating habitat selection of coyotes (*Canis latrans*) at the population level (n = 5) in southern Texas, USA from 2017 to 2021.

	Coef.	exp(Coef.)	SE	*P*-value
Day				
Density 0–1 m veg	0.1299	1.1387	0.0136	<0.001
Density 1–2 m veg	−0.0548	0.9467	0.0190	0.004
Density 2–3 m veg	−0.0404	0.9604	0.0228	0.077
Density 3–4 m veg	0.0398	1.0407	0.0210	0.058
Density 4–5 m veg	−0.0139	0.9862	0.0179	0.436
Density >5 m veg	−0.1598	0.8523	0.0178	<0.001
Canopy cover	0.0081	1.0082	0.0344	0.813
Night				
Density 0–1 m veg	0.1069	1.1129	0.0139	<0.001
Density 1–2 m veg	−0.0034	0.9966	0.0181	0.849
Density 2–3 m veg	−0.0402	0.9606	0.0220	0.068
Density 3–4 m veg	0.0474	1.0485	0.0201	0.018
Density 4–5 m veg	0.0540	1.0555	0.0165	0.001
Density >5 m veg	−0.1181	0.8886	0.0176	<0.001
Canopy Cover	−0.2999	0.7408	0.0334	<0.001

We examined selection for density of vegetation at 1 m increments above the ground and percent canopy cover to encompass horizontal and vertical structure of vegetation and compared selection during daytime (sunrise–sunset) to nighttime (sunset–sunrise). The exp(Coef.) is the odds ratio for that variable.

(Sergeyev et al., 2022) or as a thermal refuge (Sergeyev et al., n.d.). Further, ocelots in the region are nocturnal and use less vegetated areas when traveling compared to resting (Sergeyev et al., 2022), supporting our findings of differences between diurnal and nocturnal selection. While our findings support the idea of ocelots as heavily tied to dense cover, we show a surprising amount of variation in selection among individuals, particularly for density of overstory vegetation. In areas with greater upperstory vegetation, a dense canopy may crowd out shade-

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intolerant species below, resulting in a dense overstory but areas devoid of vegetation underneath (Gommers et al., 2013). We observed instances of both selection and avoidance of these areas by individual ocelots while others used these areas in proportion to availability. Ocelots are considered an adaptable predator and used a variety of vegetation types in more central portions of their range (Boron et al., 2020; Lombardi et al., 2022; Moreno-Sosa et al., 2022; Paolino et al., 2018; Wang et al., 2019). This variation among individuals may play an important role in facilitating both intraspecific and interspecific coexistence.

We observed differences in habitat selection of bobcats and coyotes compared to ocelots, providing evidence of fine-scale habitat partitioning. While ocelots exhibited a strong selection for percent vertical canopy cover, bobcats used cover proportionately as available, as did coyotes during the day but showed avoidance of cover at night supporting previous findings of bobcats and coyotes using less vegetated areas than ocelots (Crimmins et al., 2012; Horne et al., 2009; Koehler & Hornocker, 1991; Sergeyev et al., 2023). While all three species were selected for 0–1 m of vegetation, coyotes avoided 1–3 m of vegetation, likely dominated by thornshrub vegetation, areas that bobcats and ocelots selected. We observed individual bobcats predominately select for greater vegetation densities across multiple height strata (0–4 m) except for heights greater than 5 m. Across their range, bobcats have wide habitat preferences and have been strongly linked to open, herbaceous, shrub, and deciduous forest (Donovan et al., 2011; Horne et al., 2009; Kolowski & Woolf, 2002; McNitt et al., 2020). Bobcats also have been connected to dense herbaceous cover, especially on the edges of woody vegetation, because these areas are likely to hold an increased abundance of small rodents (Godbois et al., 2003). In our study system, the diversity of understory communities that shifts from dense guinea grass and cordgrass to greater densities of low shrubs (<4 m) likely facilitates foraging and denning, while providing movement cover for bobcats (McNitt et al., 2020; Sergeyev et al., 2022). Coyotes selected open areas and herbaceous cover (Sergeyev et al., 2023), and as such are likely using 0–1 m vegetation in open habitats as opposed to thornshrub. During the day, ocelots avoided areas with dense upper canopy (3–5 m), likely avoiding areas with open understories (Gommers et al., 2013), while bobcats and coyotes were selected for these areas. Use of areas with low vegetation densities at different height strata may reflect tendencies of forest-dwelling coyotes to select more open areas to accommodate their cursorial foraging strategies (Kamler & Gipson, 2000; Thibault & Ouellet, 2005). An overstory taller than 5 m, areas likely dominated by taller thornshrub and live oak forests, was used proportional to availability by ocelots but avoided by bobcats and coyotes during day and night, suggesting ocelots are tied to areas of increased forested cover (Lombardi et al., 2021; Veals et al., 2022; Wang et al., 2019), and may use areas of closed canopy forests with open understories as movement corridors between patches of mixed-dense low shrub cover. Overall, we found a strong selection for vegetation cover by ocelots and broader selection preferences among bobcats and coyotes, supporting prior ideas of these two species utilizing a wider array of cover types as habitat generalists in comparison to ocelots (Crimmins et al., 2012; Horne et al., 2009; Koehler & Hornocker, 1991; Kolowski & Woolf, 2002; Newsome et al., 2015; Robertson et al., 2015). One caveat to note, sample sizes across individuals did vary (Table S1) and may have influenced the population-level results.

In addition to differences between species observed at the population level, we saw extensive variation in individual selection that was masked at the population level. The extensive variation between individuals may aid in facilitating coexistence both within and across species. Competition is greatest when overlap among niches is the highest (MacArthur, 1968). Given the extensive spatial overlap of these species in southern Texas (Horne et al., 2009; Lombardi, MacKenzie, et al., 2020; Sergeyev et al., 2022), the potential for competition is high. Through variability in behavioral decision-making, members of the same species can minimize intraspecific competition (Prati et al., 2021; Svanbäck & Bolnick, 2007). Furthermore, variation among individuals can similarly mitigate interspecific competition through behavioral plasticity (Svanbäck & Bolnick, 2007). To our knowledge, individual variation in habitat use by ocelots has not been assessed previously but has been documented in both bobcats and coyotes. Bobcats have previously shown a high degree of variation in use of micro-habitat features such as vegetation cover and rocky outcroppings (Kolowski & Woolf, 2002). Coyotes have also previously shown individual variation in the use of anthropogenic resources (Newsome et al., 2015) and spatial and temporal variation in the diet of individuals (Morey et al., 2007). Extensive individual variation has been documented among other felid and canid species such as the Geoffroy's cat (*Leopardus geoffroyi*; Castillo et al., 2019) and wolves (*Canis lupus* and *C. lycaon*; Benson & Patterson, 2015), as well as other species such as European badgers (*Meles meles*; Robertson et al., 2015), moose (*Alces alces*; Gillingham & Parker, 2008) and brown bats (*Myotis lucifugus*; Nelson & Gillam, 2017). Examining selection at a population level may obscure avoidance and selection at the individual level. We recommend that, when possible, the selection of individuals be considered to elucidate patterns masked at a population scale (Wirsing & Heithaus, 2014).

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Vegetation is often among the most important factors in influencing the habitat use of wildlife; however, few studies have quantified the horizontal and vertical structure of vegetation in assessments of habitat selection. Particularly in our study area, vegetation is often the main driver of habitat selection as this area has little variation in elevation and low anthropogenic impact. Using LiDAR provided a reliable and accurate method for obtaining landscape characteristics across a large area (Hyde et al., 2006) and quantified the vertical component of the vegetation. Ground estimates at this scale would have been costly, labor-intensive, and less accurate (Barnes et al., 2016; Camathias et al., 2013). Furthermore, previously available remotely sensed imagery of canopy cover in the area is coarse and has poor accuracy. However, LiDAR-derived metrics provided high-resolution measurements of the characteristics of vegetation across the entire study area (Vogeler & Cohen, 2016). Further, characterizing the inner structure of the vegetation would not have been possible using other remote sensing techniques as LiDAR has the ability to penetrate the upper canopy through several layers of vegetation and describe the inner structure as opposed to strictly the surface (Devore et al., 2016; Ewald et al., 2014). Prior studies have used LiDAR data to assess forest composition (Hill & Thomson, 2011; Hyde et al., 2006), model habitat suitability (Barnes et al., 2016; Hagar et al., 2020; Vierling et al., 2013), create species richness models (Camathias et al., 2013), and determine resource selection of wildlife (Devore et al., 2016; Tweedy et al., 2019). Similarly, we used LiDAR-derived canopy metrics to compare fine-scale habitat selection for vertical vegetation structure by ocelots, bobcats, and coyote. By combining high-frequency GPS data with these fine-scale metrics, we provide a more precise and detailed examination of the habitat selection of three sympatric carnivores and show differences in diurnal and nocturnal selection for vertical vegetation structure, at the population and individual level, which may facilitate intraspecific and interspecific coexistence. One caveat worth noting is the issue of scale. We examined habitat selection using fine-scale data and step selection functions to examine selection for vegetation structure at a detailed level; however, these patterns may change across scales (Sergeyev et al., 2023).

Ocelots have shown an increasing selection for woody cover in recent decades (Veals et al., 2022), despite the availability of this cover type decreasing sharply (Harveson et al., 2004). Identifying desirable attributes of preferred habitats can guide habitat management and restoration. By combining LiDAR data with high-frequency GPS locations, we provide a detailed assessment of habitat selection by ocelots and two potential competitor species. We examine an often overlooked component of landscape complexity, vertical vegetation structure, and show how this three-dimensional gradient can facilitate coexistence among sympatric carnivores. Ocelots exhibited a strong selection for vertical canopy cover and dense vegetation 0–2 m in height. Bobcats showed similar selection to ocelots but selected cover to a lesser degree, while coyotes avoided under-story vegetation and selected areas of upper canopy with open understories. We observed fine-scale habitat partitioning between ocelots, bobcats, and coyotes and a high degree of individual variation that may facilitate coexistence within and across species. Management for ocelots should prioritize dense cover 0–2 m above the ground and vertical canopy cover. Furthermore, heterogeneity in vegetation communities may improve management by providing more variable habitats to accommodate differences in selection by individuals, as well as benefiting sympatric species such as bobcats and coyotes. Our results support prior notions of ocelots as a species strongly tied to dense cover and provide a fine-scale assessment of habitat characteristics selected by ocelots through the use of LiDAR-derived canopy metrics. In addition, we provide the first description of individual variation in habitat selection by ocelots and suggest that coexistence with sympatric bobcats and coyotes may be facilitated by plasticity in habitat use, wherein individuals may adapt to alter their habitat use to avoid conspecifics or competitor species.

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Author Contributions

M.S. – manuscript writing, formal analysis, data acquisition, conceptualization, D.A.C. – formal analysis, review and editing, J.D.H. – conceptualization, formal analysis, J.V.L. – data acquisition, conceptualization, funding, M.E.T. – project administration, funding, conceptualization, T.A.C. – project administration, funding, conceptualization.

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Supporting Information

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

Table S1. Number of locations obtained from each GPS collared individual (ocelots, bobcats, and coyotes), in South Texas, USA from 2017 to 2021.

Table S2. Correlation values between predictor variables for modeling habitat selection of ocelots, bobcats and coyotes in southern Texas from 2017 to 2021. Variables include the density of vegetation in 1 m increments above the ground as well as vertical canopy cover. Variables were derived using aerial LiDAR data.

Figure S1. Distribution of vegetation cover within the study area in South Texas, USA. Variables were derived using LiDAR data flown by the USGS.

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