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Sex-specific resource strategies mediate home range sizes of an endangered carnivore across multiple scales

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Home ranges reflect a trade-off between the costs and benefits associated with acquiring resources and are influenced by complex interactions among intrinsic and extrinsic factors. These factors can lead to different spatial and temporal patterns to acquire the necessary resources that meet energetic and reproductive needs. Identifying the drivers of these strategies concurrently across spatiotemporal scales remains rare but is essential for identifying landscape constraints on populations in rapidly changing systems. We examined spatiotemporal drivers of home range size of the federally endangered ocelot (*Leopardus pardalis*; [22 Males, 12 Females]) in the two remaining populations in the USA. Males increased home range size during reproductive periods while females constrained their home range, but increased in size to match the demands of reproduction. Habitat complexity and the associated prey diversity and abundance were related to smaller home range size. Our results suggest that home range variation is a response to environmental conditions and annual changes in life history. Sex-specific drivers of home range size across space and time—in the context of habitat loss, shifting climate patterns, and changing resource productivity—can help identify management and habitat restoration targets for small and declining populations.

Keywords Home range, *Leopardus pardalis*, Movement, Ocelot, Space use

Animals must make fundamental trade-offs between maximizing energy acquisition and minimizing energy expenditure[1]. Foraging theory predicts that individuals' behavioral decisions should maximize fitness by optimizing energetic trade-offs in the exploitation of resources[2]. The restriction of movement and space use while pursuing resources facilitates the formation of home ranges, which are defined as the area used by animals to meet life history requirements[3]. Consequently, this restriction of space use can impact many ecological processes, including the distribution and abundance of animals[4] predator-prey dynamics[5] and community dynamics[6]. Predicting spatial patterns of home ranges and space use that mediate the distribution and abundance of animals is a principal concern for species conservation in the face of environmental change[7].

Similar to energetic trade-offs animals face while foraging, the size of a home range reflects a trade-off between the costs and benefits associated with acquiring resources, such as food and mates, over a given period of time[8]. Whereas metabolic requirements for a given body size commonly drives interspecific variation in home range size[9,10] intraspecific variation can be influenced by multiple intrinsic (e.g., age or sex) and extrinsic (e.g., forage and climate) factors that maximize fitness and resource acquisition[11]. Home ranges are shaped by the distribution, predictability, and accessibility of resources, and are often smaller as resource quality and abundance increases[12–14]. Home ranges then should be spatially (e.g., patches of high habitat quality) and temporally (e.g.,

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reproductive cycles, seasonality) dynamic, influencing population-level effects as well as displaying ecosystem-level variation in time scale-specific responses[4,15].

Mammalian carnivores can have a disproportionate effect on ecosystems relative to their abundance[16,17] yet declines in their distribution and abundance have been widespread. These declines are often consequences of large spatial requirements related to diet specializations and life histories[18]. Many carnivores are territorial and exclude conspecifics from part of their home range. Thus, the size of the home range is not only constrained by environmental factors but also by social and competitive interactions that can be sex-specific[19,20]. For species that are long-lived and have low reproductive rates, an area-minimizing approach can be effective to meet energetic and reproductive needs[21]. However, the ranging behavior of polygynous male carnivores may benefit most from a resource-maximizing strategy to overlap with multiple females while also selecting for high-resource habitat patches[22]. Sex-specific fitness requirements, coupled with extrinsic factors that dictate the abundance and distribution of food, should strongly influence carnivore home range size[23–25]. For carnivores, their home range size often decreases as prey availability (e.g., productivity) and landscape connectivity increases[13,26,27]. However, variation in this response is common[28] but few studies have concurrently examined variation in sex-specific home range strategies across spatiotemporal scales and environmental variation.

Ocelots (*Leopardus pardalis*), a medium-sized solitary and territorial carnivore that are endangered in the United States, exhibit sex-specific differences in space use and strategies for maximizing reproductive success[29–31]. Generally, throughout their distribution from southern Texas, USA to southern Brazil, males have larger home ranges than females, and both sexes have been observed to change their space use in response to changes in resources[32–34]. Although the space use of ocelots has been widely studied across their broad geographic distribution[19] approaches to estimate home ranges have varied, and past studies have been limited by sample size, duration, and tracking methodologies[19,35] challenging the quantification of sex-specific patterns and responses to environmental variation. In the United States, population declines have been largely due to the loss of native woodlands that have been converted to agriculture and urban development in the 1900s[36,37]. Ocelot recovery is currently limited by available habitat and extensive fragmentation, making a better understanding of how space use and landscape conditions may influence sex-specific density paramount to help inform habitat management actions.

We estimated home ranges across multiple spatiotemporal scales and evaluated the effects of intrinsic and extrinsic factors on home range size in the two extant ocelot populations in the United States. We considered the intrinsic factor of sex and extrinsic factors that would influence foraging, competitive interactions, and physiological constraints, including vegetation connectivity, productivity, habitat structure, drought conditions, and temperature. We expected that both sexes would have smaller home ranges with better foraging conditions, and as productivity increased. However, we predicted that males would have larger home ranges than females, but female core ranges would have less variability and be constrained to balance the competing demands of reproduction. Consequently, we expected that males would show greater variability in their home range to maximize overlap with females and to meet energetic demands for covering greater distances. Ultimately, understanding the intrinsic and extrinsic effects on spatiotemporal variation in home range strategies offers opportunities to understand landscape constraints on populations in rapidly changing systems.

Results

We estimated 224 home ranges from 30 ocelots (19 M, 11 F) across different temporal scales – monthly ($n=167$), seasonal ($n=42$), and half-year ($n=15$) (Table 1). The monthly core area of male home ranges (2.57 km^2; 95% CI [1.77, 3.38] km^2 was approximately 3x times larger than that of females (0.76 km^2; 95% CI [0.38, 1.14] km^2, and the full home range was 2.7x larger (males: 10.55 km^2; 95% CI [7.48, 13.61] km^2 and females: 3.92 km^2; 95% CI [2.22, 5.61] km^2. Home range size was similar across temporal scales (month, seasonal, and half-year), but both sexes showed an increase (females: 12%; males: 20%) for home ranges estimated during the half-year period compared to monthly. Spatially, the full home range showed greater variability compared to core home ranges among individuals (Fig. 1). However, female home range size was less variable compared to males across temporal scales (month, seasonal, and half-year) and spatial scales (full and core home range) (Fig. 1; Table 1).

				Mean	SD	95% CI	Mean	SD	95% CI
Time	Sex	*n*	# HR	Core (50%)			Full (95%)		
Monthly	Female	11	51	0.76	0.57	0.38, 1.14	3.92	2.52	2.22, 5.61
	Male	19	116	2.57	1.67	1.77, 3.38	10.55	6.36	7.48, 13.61
Seasonal	Female	10	14	0.82	0.65	0.36, 1.29	4.27	2.46	2.5, 6.03
	Male	17	28	2.44	1.51	1.66, 3.21	10.15	5.95	7.09, 13.21
Half-year	Female	4	4	0.92	0.42	0.26, 1.59	4.42	2.24	0.86, 7.99
	Male	11	11	3.01	1.45	2.03, 3.98	12.51	5.73	8.65, 16.36

Table 1. Sample size for each time and sex for GPS location data of ocelots (*Leopardus pardalis*) in texas, USA between 2011 and 2024. Estimated home range size (km^2) using an autocorrelated kernel density estimator after fitting a continuous-time movement model from GPS location data. Home ranges were estimated at monthly (calendar months), seasonal (3-month periods), and half-year (April–September), and at the 50% (core) and 95% (full) isopleths. n – number of individuals, #HR – number of home ranges, SD – standard deviation, CI – confidence interval.

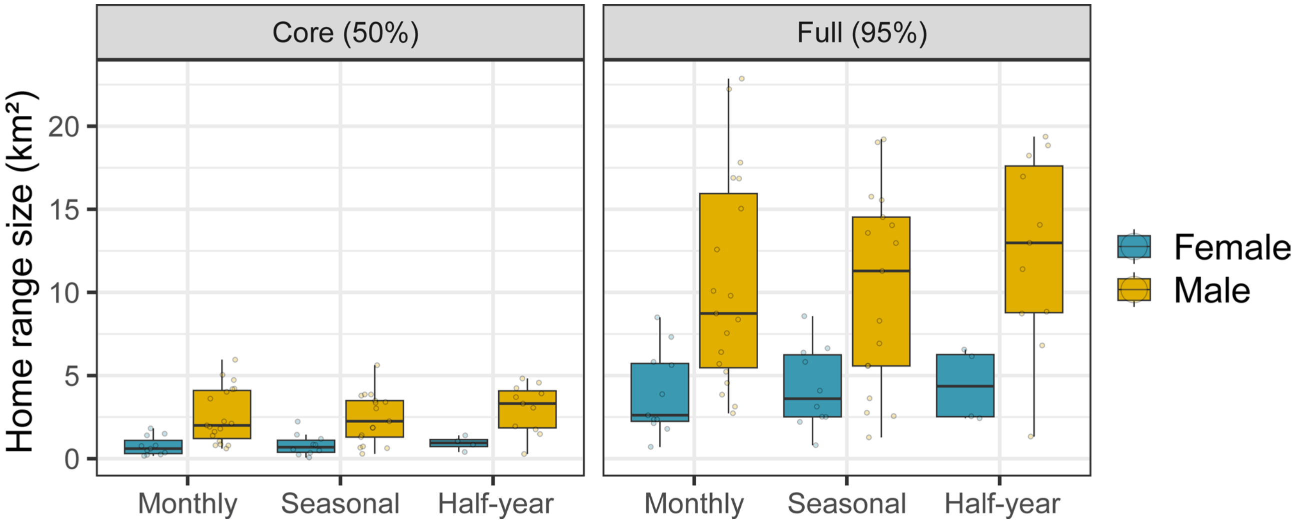

Fig. 1. Average individual home range size (km^2 for male and female ocelots in Texas, USA between 2011 and 2024. Home ranges were estimated using an autocorrelated kernel density estimator at the core (50%) and full (95%) after fitting a continuous-time movement model to monthly (calendar months), seasonal (3-month periods), and half-year (April–September) GPS location data for each individual.

For individuals with successive monthly home ranges (30 individuals), we found that location of the core home range centroid moved an average of 298 m for females and 480 m for males, while the core seasonal home ranges (11 individuals) shifted 240 m for females and 979 m for males. We found support for intra-annual variation in home range size (AIC_c *weight* = 1) with male home ranges at a minimum and female home ranges at a maximum during the summer months (Fig. 2).

We found sex-specific differences in home range size relative to multiple landscape and climate variables, and in some cases, variation between spatial scales (core vs. full). In general, males responded more strongly to landscape and climate conditions compared to females, especially at the core spatial scale (Figs. 3 and 4). For males, we found that home range size was smaller as woody cover, vegetation heterogeneity, and mean temperature increased (Fig. 3; Supplementary Information Table S1). In contrast, greater canopy cover was associated with larger home ranges for males (Fig. 3; Supplementary Information Table S1). Most landscape and climate conditions had a minimal effect on female home range size across spatial scales (Figs. 3 and 4). However, the proportion of canopy cover was likely to have a negative effect on female home range size at the 50% (pd = 97%) and 95% (pd = 89%) home range size, and the proportion of woody land cover at the 95% female home range size (pd = 100%; Figs. 3 and 4; Supplementary Information Table S1). The negative response to canopy cover of females contrasted the positive response in males across both spatial scales (Fig. 4). We found positive effects between home range size and both drought and the connectivity of woody cover for males and females (Figs. 3 and 4; Supplementary Information Table S1).

Discussion

Our study examined the effect of intrinsic and extrinsic factors on home range size across multiple spatial and temporal scales using GPS data from the only extant populations of an endangered carnivore in the United States. Concurrent analyses across spatiotemporal scales remain uncommon, but partitioning these scale-dependent processes is important for identifying mechanisms that affect variation in home range size. We found that interactions between intrinsic and extrinsic factors influenced home range size, but that relationships varied across spatial scales. In general, males responded more strongly than females to changes in environmental conditions across spatial scales (core and full home range), while female home range size generally showed a minimal response across predictors, especially in their core range. This variation in sex-specific responses may be due in part to differences in philopatry and dispersal behaviors that differentially expose males to broader landscape variation. Female carnivores often display higher philopatry and can lead to fitness benefits due to familiarity with resources within their natal home range[38]. On the other hand, males generally disperse from natal home ranges and maintain larger home ranges, likely leading to the development of behavioral plasticity to modify home ranges according to environmental conditions[39].

Regardless of spatiotemporal scale, male ocelots had larger and more variable home ranges than females. Beyond body size differences, the larger home ranges of males are common among mammalian taxa and are often attributed to a behavioral response to overlap with multiple females during reproductive periods[40]. Ocelots can reproduce year-round, and in this system, parturition is thought to occur more frequently with wetter conditions in the spring and fall[41]. We found some support for males reducing their home ranges during summer months when females were more likely to be with offspring and anestrus, therefore reducing the value of larger home ranges that would contact multiple females. Concomitant with the decrease in male home ranges, females showed an increase in home range size during summer months, potentially due to behavioral and energetic

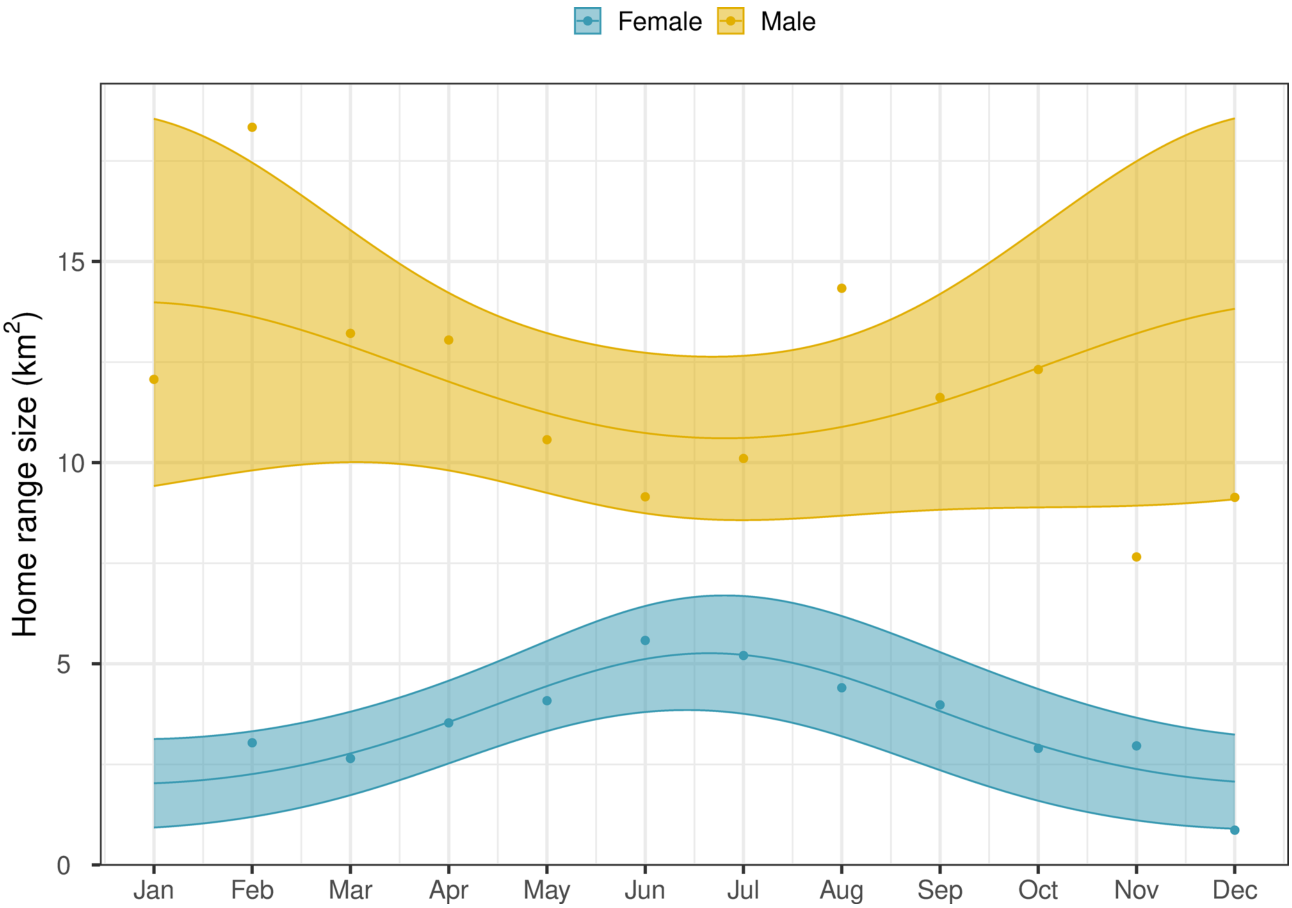

Fig. 2. Intra-annual variation in the full (95%) home range size for male and female ocelots (*Leopardus pardalis*) in Texas, USA between 2011 and 2024. Shaded areas show the 95% confidence intervals and points represent individual home range size. Home ranges were estimated using an autocorrelated kernel density estimator after fitting a continuous-time movement model to monthly GPS locations.

requirements that change with dependent offspring. Two strategies have been hypothesized to influence home range size: resource maximization, which would promote acquiring more resources that lead to larger home range, and area minimization, which meets a minimum resource threshold for survival and reproduction in the smallest possible unit area[42]. Males appeared to employ a resource maximization strategy during reproductive periods while females constrained their home range in an area-minimizing approach, only increasing in size to match the demands of reproduction[24].

Increasing vegetation heterogeneity, our proxy for prey diversity, was related to smaller home range sizes. Mechanistic and empirical models have found that resource aggregation (i.e., increasing patchiness of resources across space) dictates the shape and spatial distribution of home ranges and tends to lead to greater movement and larger individual home ranges[12,42]. However, in some cases, greater habitat heterogeneity can increase availability of resources within a smaller area, thereby reducing the need for extensive movements[43]. In this system, vegetation heterogeneity may be associated with a more uniform distribution of prey and foraging opportunities, particularly for dietary generalists and opportunistic foragers like ocelots[44–46]. Similarly, the home range size was smaller with greater amounts of woody cover. The response to woody cover in the region is consistent with previous work that found resource selection and even spatial partitioning of sympatric carnivores were affected by structural complexity of the vegetation[47]. Selection for woody cover likely provided access to mates, protection from interspecific competitors, and greater prey availability[48–50] that reduces the space needed to meet energetic demands.

Contrary to our hypothesis, we observed a minimal effect of productivity on home range size for both sexes. Productivity (e.g., NDVI) as a measure of prey availability has been commonly used to test expectations on home range size, with responses often varying by individuals, populations, and species[12,28,51]. The lack of seasonal changes (e.g., wet and dry seasons) in ocelot home range size has been observed in other portions of their range[33] as well as other felids and carnivores[28,52,53]. However, the degree of seasonality in a system may interact with productivity to shape home ranges of carnivores[28]. Most of our home ranges were estimated between April and September, representing both wet and dry periods, but relatively few samples came from the coldest months. In this system, plant flowering and fruiting can occur year-round, even in colder months[54] which may have dampened any response of home range size to productivity. Further, carnivores such as ocelots that are dietary

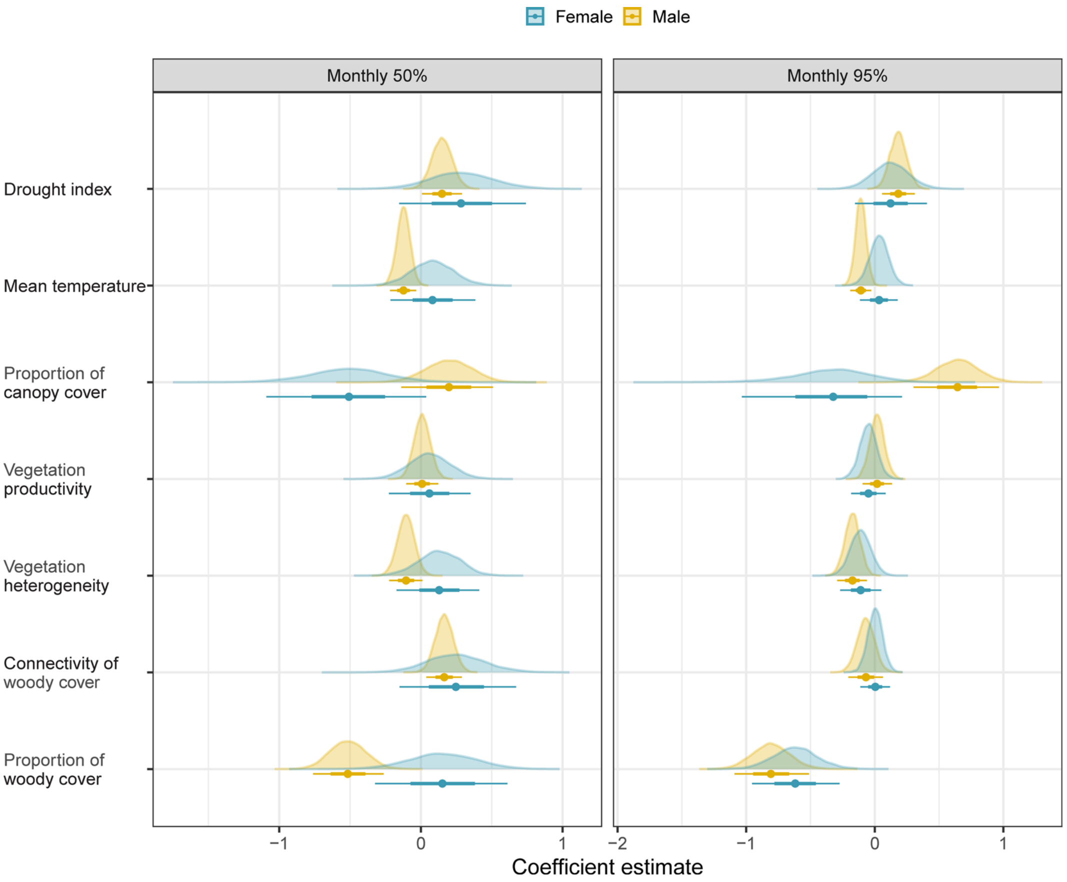

Fig. 3. Beta coefficient estimates of landscape effects on ocelot home range size in Texas, USA between 2011 and 2024. Generalized linear mixed effects models with a gamma distribution and log link were fitted to test the effect of landscape variables on the monthly core (50%) and full (95%) home range size for males and females. Home range size was estimated using an autocorrelated kernel density estimator after fitting a continuous-time movement model from GPS location data for each individual.

generalists may be able to maintain stable home ranges despite seasonal changes in productivity due, in part, to wide diet variation[28].

The home range size of males and females responded differently to horizontal and vertical habitat structure. Male home range size was greater as canopy cover increased, as more structural complexity in vegetation within a home range may provide the necessary cover to access additional hunting opportunities or explore new areas for food or mates. On the other hand, female home range size decreased as canopy cover increased. This contradictory effect may be tied to differences in behavioral strategies to balance the energetic costs of reproduction and vulnerability of young (e.g[55].,. Many female carnivores with young reduce their movements to account for greater energetic demands and select for structural complexity that provides stable thermal properties and protection from weather and predators[40,56,57]. Consequently, female space use and ranging behavior can have impacts on juvenile survival and reproductive success that influence population dynamics[58,59].

Considering multiple spatial and temporal scales when defining a home range is critical to evaluate mechanisms that might directly or indirectly affect ranging behavior[60] (Fieberg and Börger 2012). Despite our coarse resolution of weather predictors, we captured variation in weather conditions across 12 years of ocelot home ranges; however, the effects of temperature and drought had a minimal effect on home range size. This suggested that indirect predictors, like weather conditions, were less important than direct predictors like habitat composition and configuration at monthly timescales to influence home range size. Weather conditions have been shown to influence short temporal scales (e.g., days and weeks[11], and although we examined environmental conditions across multiple spatial and temporal scales, their impact may be more pronounced over shorter time frames or finer movement behaviors, such as daily distance traveled or resource selection within a home range. For example, drought may reduce the density of prey, but not the distribution within the home range, leading to decreased encounters that require greater daily movements within the home range to acquire enough prey. Alternatively, we may not have captured changes that would influence prey abundance and distribution using the short-term drought metric (3-month SPEI), even though it captures changes in vegetation productivity. In addition, weather conditions interact with vegetation composition and structure and this interaction may mediate space use during periods of high temperature and drought[61].

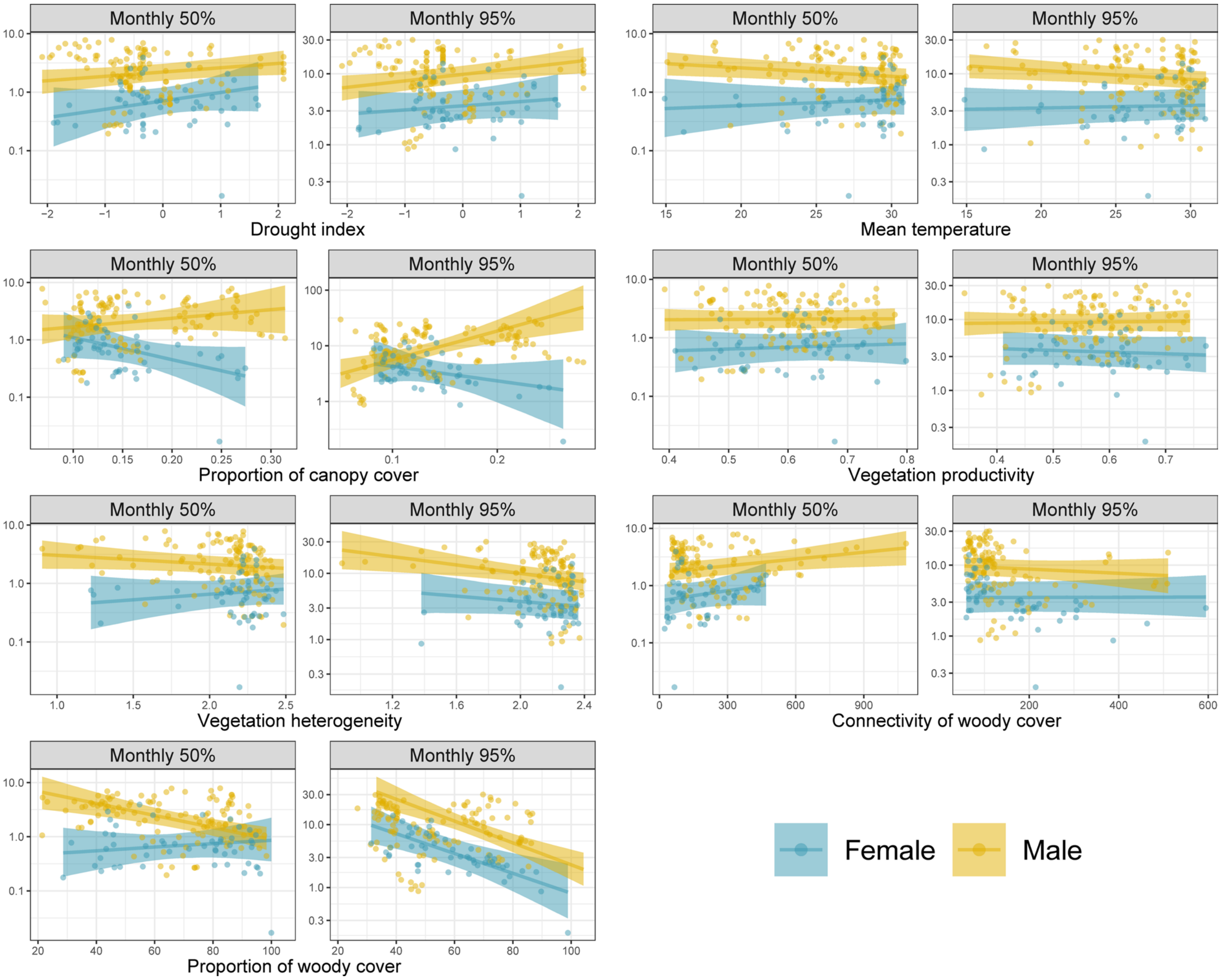

Fig. 4. Conditional effects of covariates on the monthly core (50%) and full (95%) home range size of male and female ocelots in Texas, USA between 2011 and 2024. Separate generalized linear mixed effects models with a gamma distribution and log link were fit for males and females for 50% and 95% home range size. Home range size was estimated using an autocorrelated kernel density estimator after fitting a continuous-time movement model from GPS location data for each individual. The y-axis was scaled logarithmically to improve visualization.

Understanding sex-specific variation and multiscale drivers of home range variation has important implications for species management and conservation. Recovery of ocelots in the United States has been slow and thought to be constrained by available habitat, thereby requiring action to improve connectivity and maximize available space through habitat restoration. We found that interactions between intrinsic and extrinsic factors can influence home range size and that efforts to promote woody vegetation and structural complexity could potentially (1) increase density by providing habitat to minimize female home range size and (2) provide landscape connectivity through restoration of habitat structure that males can utilize to maximize resources. Consequently, understanding the drivers of sex-specific home range size across space and time in the presence of habitat loss, shifting climate patterns, and resource productivity can help provide the necessary management and habitat restoration targets for the conservation of small and declining populations.

Methods

Study area

This study was conducted at two sites within coastal southern Texas, USA: one on private working ranch lands and the other in and around the Laguna Atascosa National Wildlife Refuge (Fig. 5; < 35 km apart). These areas are home to the last two breeding populations of ocelots in the United States and have limited connectivity between them (Lehnen et al. 2021, Veals et al. 2022). Ranchlands included inland dunes, coastal prairie, emergent herbaceous and woody wetlands, and large extensive mixed to dense live oak (*Quercus virginiana*)-thornscrub and mesquite (*Proposis glandulosa*)-thornscrub communities (Lombardi et al. 2021). Laguna Atascosa National Wildlife Refuge (LANWR) and adjacent private lands were characterized by a mosaic of protected and private patches of mixed to dense thornscrub and coastal prairie within a mosaic with row-crop

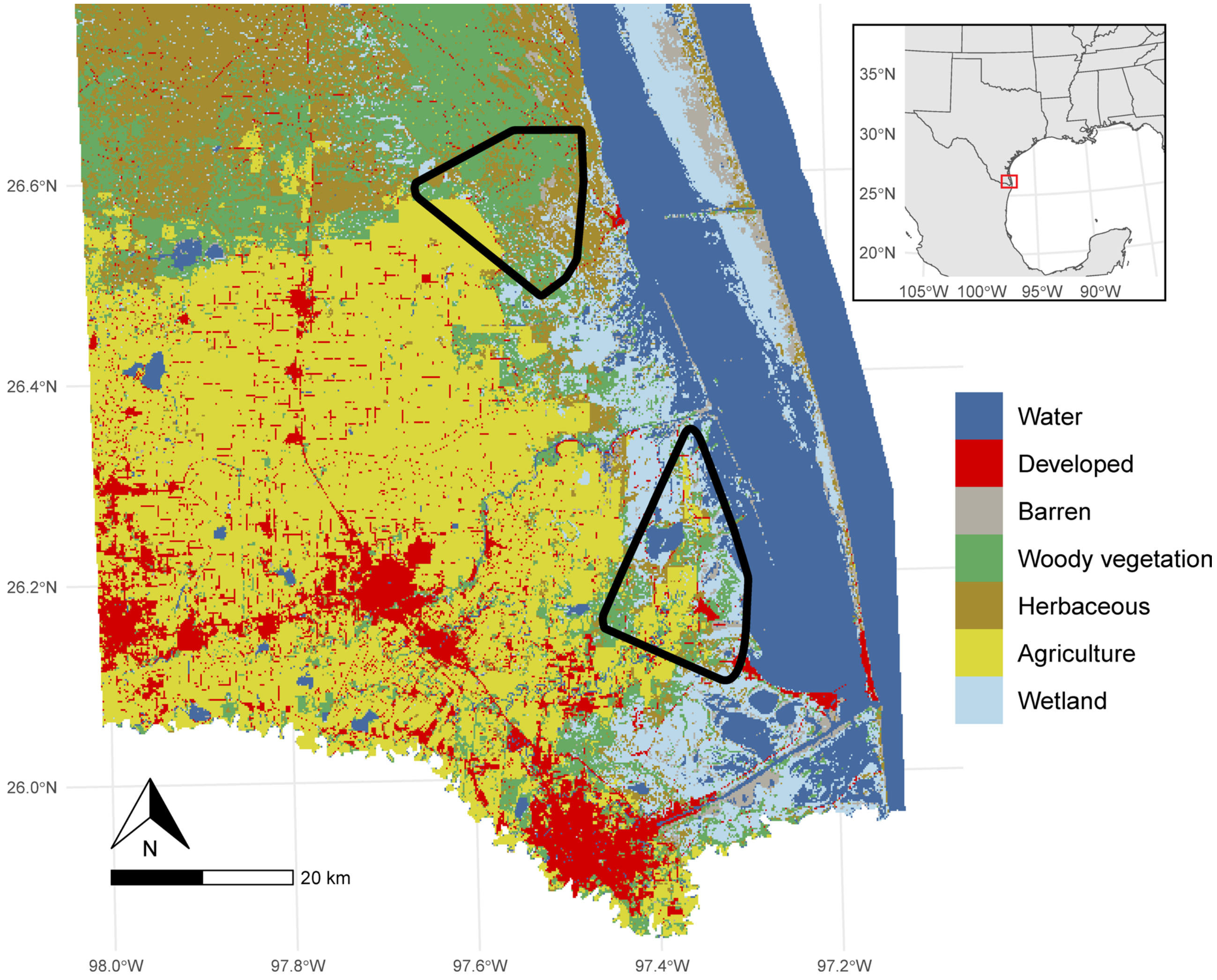

Fig. 5. Study areas of ocelot (*Leopardus pardalis*) GPS collar data in Texas, USA between 2011 and 2024 and land cover from the 2021 National Land Cover Database generated in R (v4.4.3; R Core Team 2024; https://www.R-project.org/). Black polygons represent the general area of ocelot distribution in the region including private working ranch lands in the north and the other in the south around the Laguna Atascosa National Wildlife Refuge.

agriculture, urbanization and extensive road networks[62,63]. The regional climate was semi-arid subtropical with annual temperatures ranging from 10 to 36 °C, with summer peaks of > 40 °C during the summer. Annual precipitation was highly variable (313–529 mm) with more during summer[62]. Episodic moderate and severe droughts were common[62]. Generally, these precipitation patterns lead to a growing season from April to through September and a dry winter season from October through March.

GPS collar data

We collected GPS collar data from 34 individuals (22 M, 12 F) over 12 years across both study sites (17 individuals per site). Ocelots were captured using Tomahawk box-traps (10 × 51 × 38 cm; Tomahawk Trap, Hazelhurst, WI, USA) from January and May from 2011 to 2017 and November and April from 2019 to 2024. We immobilized ocelots using intramuscular injection of a ketamine-medetomidine mixture and medetomidine was reversed with atipamezole. We fit captured ocelots with GPS collars (G5-PC, Advanced Telemetry Systems, Isanti, MN, USA or TGW-4177-4, Telonics, Mesa, AZ, USA) and programmed collars to attempt a fix every 1 h and automatically release after 6 ($N = 7$) or 12 months ($N = 5$). In addition, we incorporated GPS collar data from previously captured ocelots ($N = 22$; 2012 to 2021) that included location fix rates from every 30 min to 5 per day, and were programmed to automatically release after 4–12 months[31,47,64,65]. We filtered data for outliers and erroneous locations by removing points with high dilution of precision (DOP; 3D fixes > 10 or 2D fixes > 5) and improbable velocities (≥ 5 km/h) between successive fixes (Bjørneraas et al., 2009). All experimental protocols were approved by the United States Fish and Wildlife Service, Texas Parks and Wildlife Department, and Texas A&M University - Kingsville's Institute for Animal Care and Use Committee (USFWS: ES822908; TPWD:

Covariate	Representation	Data source	Temporal resolution	Supporting literature
Drought index	Physiological constraint and prey abundance	gridMET (4 km)	Monthly	Haines et al. 2005; West et al. 2024
Mean temperature	Physiological constraint	gridMET (4 km)	Monthly	Sergeyev et al. 2023a
Proportion of woody cover	Horizontal habitat structure	NLCD (30 m)	Annual	Sergeyev et al., 2023b; Wang et al. 2019
Connectivity of woody cover	Horizontal habitat structure	NLCD (30 m)	Annual	Lombardi et al. 2021; Veals et al. 2023
Proportion of canopy cover	Vertical habitat structure	GEDI (25 m)	Annual	Cruz et al. 2019; Sergeyev et al., 2023c
Vegetation productivity	Prey abundance	MODIS (250 m)	Monthly	Chidodo et al., 2019; Kaursrud et al., 2007; Pettorelli et al., 2011
Vegetation heterogeneity	Prey diversity	MODIS (250 m)	Monthly	Tews et al., 2004

Table 2. Summary of covariates used to explain the monthly home range size of ocelots (*Leopardus pardalis*) in texas, USA between 2011 and 2024. The Spatial resolution of the data source appears in parentheses.

SPR-1123-136; TAMUK: 2023-10-20). We carried out all methods in accordance with relevant guidelines and regulations including ARRIVE guidelines for reporting animal research[66].

Home range Estimation

We fit continuous-time movement models to individual ocelot GPS relocations at monthly, seasonal (3-month period), and half-year (6-month period) timeframes using the R (R Core Team 2024) package *ctmm*[67,68]. Our temporal periods reflected differences between the summer growing season and dry winter season. We visually assessed variograms of time-series movement patterns to identify individuals that did show range-residency (i.e., no clear asymptote) and subsequently removed them from further analyses ($n = 4$). We calculated autocorrelated kernel density estimators (aKDE), which account for autocorrelation, small effective sample sizes, and irregular sampling in time[69–71]. We calculated a home range as the minimum area in which an animal has some probability of being located[72]. We considered the 95% home range as an area of active use and the 50% area as an area of core use, hereafter core (50%) and full (95%) home range[67]. We compared the 50% and 95% aKDE isopleth to identify differences in spatial scale.

We used a cosinor model to examine how monthly home range size changes within the year (*sensu*[24]. We had an average of 4.25 (range: 1–10) and 9.7 (range: 1–19) observations per month for females and males, respectively. This model fits a cosine curve to periodic data within a regression model and can be used to identify seasonal patterns. We implemented a single component cosinor analysis using the R (R Core Team 2024) package *GLMMcosinor*[68,73]. The cosinor model was fit with a Gamma distribution with a log link and included sex as a fixed effect and a single cosinor component grouped by sex over 12 months. We assessed the effect of an annual cycle on home range size by comparing our cosinor model with an intercept-only model without temporal change within the year using Akaike information criterion (AIC_c).

Home range size analysis

We identified a set of landscape variables a priori that could influence the size of an ocelot home range by impacting foraging, competitive interactions, and physiological constraints (Table 2). Across their geographic range, ocelots select for a high proportion of woody cover and closed canopy that provides foraging opportunities, denning locations, and protection from competitors[45,49,74]. We characterized horizontal habitat structure through composition and configuration of woody vegetation. We created a woody cover land cover category by combining National Land Cover Dataset (NLCD) cover classes (forest, shrubland, and woody wetlands; Fig. 5[75];. We then calculated the proportion and connectivity (i.e., the average distance an organism can move within a patch) of woody cover within each home range using the R (R Core Team 2024) package *landscapemetrics*[68,76]. To estimate land cover metrics, we matched the time of the individual home ranges to the closest available NLCD year (2011, 2013, 2016, 2019, 2021). We represented vertical habitat structure by estimating the percentage of canopy cover across our study area using a GEDI-fusion approach (e.g[74].,. We acquired canopy cover estimates from GEDI level 2b product footprints[77] and filtered footprints by degrade flag (0), quality flag (1), and beam sensitivity (≥ 0.95) through Google Earth Engine. To predict continuously across our study area, we fitted a random forest regression model of canopy cover to continuous remote sensing products, including Landsat, synthetic aperture radar, and spectral indices (see Supplementary Information for additional details; Table S2; Fig. S1). We calculated the average proportion of canopy cover within individual home ranges from annual rasterized maps.

In addition, as a proxy for prey abundance, we estimated vegetation productivity using MODIS vegetation index products[78,79]. We calculated the average monthly normalized difference vegetation index (NDVI) from both Terra and Aqua satellite datasets to represent vegetation productivity. NDVI has been associated with changes in small mammal abundance in many systems[80–82] and has a broader spatial and temporal coverage than many field studies, making it an important proxy to describe prey abundance[83]. As a proxy for prey diversity, we calculated a metric of vegetation heterogeneity (i.e., 2nd order entropy) within individual home ranges from a gray-level co-occurrence matrix (GLCM) derived from composite MODIS images of vegetation productivity (i.e., NDVI[84,85];. Vegetation heterogeneity is often associated with greater species richness and diversity[86].

We selected climate variables of temperature and drought as they could influence the availability of prey and impose physiological constraints on ocelot movement and space use[61,87]. We calculated average monthly temperature and drought from gridMET datasets[88]. Drought was estimated using the standardized precipitationevaporation index (SPEI) that accounts for atmospheric evaporative demand and precipitation at a scale of three months[89]. SPEI values indicate the number of standard deviations by which the observed water balance deviates from the long-term mean. A SPEI time scale of threemonths is a measure of short-term drought that has been associated with changes in vegetation productivity in arid systems[90]. For all extrinsic variables, we accounted for temporal variation throughout by estimating landscape and climate variables for the specific month or year for which each individual's home range was estimated.

We used Bayesian generalized linear mixed models to test the effect of sex, landscape, and climate variables on home range size. We fit a Gamma distribution with a log link because of non-negative and right-skewed home range sizes in separate models for each sex and aKDE isopleth (50% and 95%) with individual identification as a random effect. Models were implemented in the R (R Core Team 2024) packages *brms*[91] with four chains of 4,000 iterations and 2,000 iterations as burn-in. To evaluate model convergence, we required *R-hat* values < 1.01 and visually inspected traceplots[92]. We assessed model fit through posterior predictive checks (Fig. S2)[93]. All variables were scaled and centered prior to model fitting and had Pearson's correlation coefficients |<0.7|. To describe the posterior effects of parameter estimates, we calculated the 95% credible intervals and probability of direction using the R (R Core Team 2024) package *bayestestR*[68,94]. The probability of direction (pd) is the percentage of the posterior distribution of the parameter that is greater than or less than zero.

Data availability

The data and code that support the findings of this study are available on Dryad at https://doi.org/10.5061/dryad.1ns1rn95b

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Author contributions

MMS, AMVD, and LSP conceived the ideas and designed methodology with support from JVL; AMVD, JVL, ABB, AMR, DGS, MS, ZMW, MET, and LSP collected the data; MMS analysed the data with support from AMVD; MMS and LSP led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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