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Behaviorally mediated coexistence of ocelots, bobcats and coyotes using hidden Markov models

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The competitive exclusion principle states that ecologically similar species will be unable to coexist due to competition for resources, however, similar species coexist across a variety of ecosystems. Understanding mechanisms of coexistence is essential for managing a target species. Advances in monitoring technology have provided the ability to obtain reliable, high-frequency data on wildlife. From these data, behavioral states can be approximated by analyzing turning angles and distances between locations. We monitored 8 ocelots *Leopardus pardalis*, 13 bobcats *Lynx rufus* and 5 coyotes *Canis latrans* on the East Foundation's El Sauz Ranch and the Yturria San Francisco Ranch in south Texas, USA, which were fitted with GPS collars that collected locations every 30 min. We characterized behavioral states using hidden Markov models. We assumed low turning angles and longer steps to represent patrolling territory, larger turning angles with shorter steps would represent hunting behavior, and low angles and minimal movement would indicate periods of rest. If differences in timing and space use exist between species, these differences may help facilitate coexistence. We predicted 1) each species exhibits three behavioral states: resting, hunting and territory patrolling; 2) ocelots moved farther (i.e. territory patrolling) in open areas and rested in dense cover; and 3) bobcats and coyotes would remain in more open areas than ocelots. We found ocelots and bobcats remained closer to heavy cover when resting and foraging and used open areas more when patrolling territory while coyotes rested in the open and selected for cover when hunting or patrolling. Further, we found evidence of temporal partitioning of behaviors both within and across species. Our study provides a novel approach to examining coexistence and identifies behaviorally mediated spatial and temporal differences in habitat use that may facilitate coexistence between ocelots, bobcats and coyotes.

Keywords: behavioral states, bobcats, coyotes, hidden Markov models, ocelots, movement path, spatial ecology

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Introduction

Under the competitive exclusion principle, ecologically similar species will have difficulty coexisting due to competition for shared resources (Gause 1934). Species with similar ecological niches may face competition for food, secure habitat and other vital resources (Smith and Remington 1996, Maitz and Dickman 2000). Yet, animals across taxa coexist in various ecosystems around the globe (Whitney et al. 2011, Eurich et al. 2018, Miller et al. 2018, Powell et al. 2021). As coexistence has been extensively documented, certain mechanisms must exist to facilitate this coexistence, allowing animals to share an environment spatially and temporally. Some proposed explanations have included fine-scale partitioning of habitat (Mori et al. 2019), temporal shifts (Hood et al. 2021) and varying dietary preferences (Booth-Binczik et al. 2013), resulting in enough variation in ecological niche to allow for coexistence. In some cases, species are found to coexist despite an apparent overlap in these resources. Another less documented mechanism of coexistence may be through behaviorally mediated partitioning of time and space, wherein spatial and temporal differences in behaviors can allow species to inhabit a shared space (Picardi et al. 2021). Understanding the behavior of a species is an essential component of its ecology and vital for management (Patterson et al. 2009).

Behavior can be influenced by a variety of factors such as time of day, season, competition, predation, habitat type and abiotic conditions (Smith-Hicks et al. 2016, Spitz et al. 2018). It is often difficult to characterize behavior of wildlife, particularly for elusive species (King et al. 2017). Behavior can generally be classified into one of several discrete states (e.g. resting, foraging, exploring; Michelot et al. 2016). Further, these behaviors are closely linked to the movement of an animal (Morales et al. 2004, Leos-Barajas and Michelot 2018). Movement of animals is often highly variable and difficult to model (Kosović and Fertalj 2014) but can typically be classified into various types of walks (Morales et al. 2004). Simple random walks have no bias or direction, correlated random walks have persistence and direction, biased random walks have biased direction and correlated biased walks have bias and persistence (Codling et al. 2008). These movements have an observable sequence Z and an underlying state sequence S that is unobservable (Langrock et al. 2012). Identifying differences in the observable movement path can distinguish between the sequence of behavioral states (Kosović and Fertalj 2014) and in doing so, can provide inference on the behavior of the animal.

Hidden Markov models (hereafter referred to as HMMs) attempt to identify underlying state sequence based on the observed movement data (Langrock et al. 2012). These models use variables such as turning angle and step length between locations to identify a hidden state variable as one of n states depending on the ecology of the species (McClintock and Michelot 2018). Hidden Markov models use a recursive algorithm and likelihood estimation to attribute movement sequences to one of the states of interest (Leos-Barajas and Michelot 2018). States typically correlate to specific behaviors of the species such as a resting/encamped state or a patrolling/exploratory state (Langrock et al. 2012). Further, these models can incorporate covariates of interest that may influence behavioral states and can incorporate animal ID to distinguish between movements of specific individuals (Patterson et al. 2009). As a result, this class of models effectively links spatial patterns and behaviors into a single analysis (Leos-Barajas et al. 2017). This can provide an improvement over other remote sensing techniques such as remote cameras by providing a longer window of monitoring, which can be particularly important for elusive species such as the ocelot *Leopardus pardalis* (Goulart et al. 2009).

Ocelots are a medium sized, nocturnal felid native to North, Central and South America (Di Bitetti et al. 2006, Cruz et al. 2018). Ocelots exhibit a strong preference for dense, woody vegetation (Shindle and Tewes 1998, Harveson et al. 2004). Understanding the behavior of ocelots and other wild felids can often be difficult as felids tend to be elusive and often nocturnal, making observation a challenge (Cheyne and Macdonald 2011). In south Texas, ocelots co-occur with bobcats *Lynx rufus* and coyotes *Canis latrans*, two similar-sized carnivores with similar ecological niches (Neale and Sacks 2001, Booth-Binczik et al. 2013, Lombardi et al. 2020). While ocelots are heavily linked to dense woody cover (Horne et al. 2009), bobcats and coyotes often select for open areas and less dense vegetation, generally using a broader range of cover types (Koehler and Hornocker 1991, Horne et al. 2009, Crimmins et al. 2012). Because these species have similar diets and occur sympatrically, there is the potential for interspecific competition (Horne et al. 2009, Booth-Binczik et al. 2013, Lombardi et al. 2020). Further, extensive overlap in home ranges and occupancy has been documented (Horne et al. 2009, Lombardi et al. 2020), showing overlap even at a fine scale. Despite these similarities, these species are able to coexist, suggesting other mechanisms of coexistence may explain the high degree of overlap. Differences in spatial and temporal patterns associated with differing behaviors may explain the mechanisms of coexistence between these three carnivores. As a federally endangered species, understanding how ocelots share their environment with ecologically similar species is paramount to conservation.

Our objectives were to identify the behavioral states of ocelots, bobcats and coyotes in the field using HMMs and to compare spatial and temporal differences between behaviors within a species and across species. If behavioral differences in timing and space use exist between species, these differences may help facilitate coexistence. We assumed that differences in step length and turning angle can be used to identify differences in behavior of ocelots, bobcats and coyotes. We predicted three behavioral states: resting, hunting and territory patrolling. Further, we predicted that ocelots would select for greater woody cover when resting and hunting than when exploring their territory. We predicted bobcats and coyotes would use dense cover to a lesser extent than ocelots overall but use cover greater when resting compared to hunting and exploring. Finally, we predicted that differences in the timing of behaviors across species may further increase partitioning of the environment. Understanding the behavior of ocelots can improve management strategies by identifying key areas of the landscape needed to accommodate the various aspects of ocelot ecology and ensure that adequate areas are available for resting, foraging and patrolling territory. Further, identifying differences in the behavior of sympatric carnivores can provide new insight into the mechanisms facilitating coexistence between these species and improve our understanding of how to manage areas with multiple ecologically similar species of carnivores.

Study area

This study was conducted on the East Foundation's El Sauz Ranch and the Yturria San Francisco Ranch located in Willacy and Kenedy counties in the southern tip of Texas, USA (Fig. 1). The El Sauz Ranch (113 km^2) is an operational cattle *Bos taurus indicus* ranch with an emphasis on managing land for cattle, native wildlife and land stewardship. The ranch features a variety of landscape features ranging from coastal estuarine wetlands, prairies, grasslands, sand dunes, man-made water features and areas of woody vegetation cover (Lombardi et al. 2020). The Yturria San Francisco Ranch (25.9 km^2) is a private ranch with an emphasis on ocelot conservation, land stewardship and ungulate hunting opportunities. The ranch features two conservation easements (1.98 km^2) with highly dense woody vegetation owned by the US Fish and Wildlife Service Lower Rio Grande Valley National Wildlife Refuge Complex and considered to be optimal cover for ocelots in south Texas. Surrounding patches of restored native woody vegetation are managed by The Nature Conservancy. Woody vegetation in these areas is comprised of crucifixion thorn *Castela emoryi*, lotebush *Ziziphus obtusifolia*, white brush *Aloysia gratissima*, desert olive *Forestiera angustifolia*, crucita *Chromolaena odorata*, honey mesquite *Neltuma glandulosa*, lime prickly ash *Zanthoxylum fagara*, live oak *Quercus virginiana*, spiny hackberry *Celtis pallida*, snake-eyes *Phaulothamnus spinescens* and huisache *Acacia farnesiana* (Leonard 2016, Lombardi et al. 2020, 2021). The area receives inconsistent rainfall leading to episodic drought, average rainfall is 68 cm (Haines et al. 2006). The climate in the area is subtropical and semi-arid, with temperatures ranging from 10 to 36°C (Norwine and Kuruvilla 2007).

Methods

Animal capture

We captured 12 ocelots, 19 bobcats and 5 coyotes on the El Sauz Ranch and Yturria San Francisco Ranch from January 2017 to May 2021. We captured animals using single-door Tomahawk box-traps (108 × 55 × 40 cm). We baited box traps with a live chicken *Gallus gallus* or pigeon *Columbia livia* contained within a separate compartment inaccessible

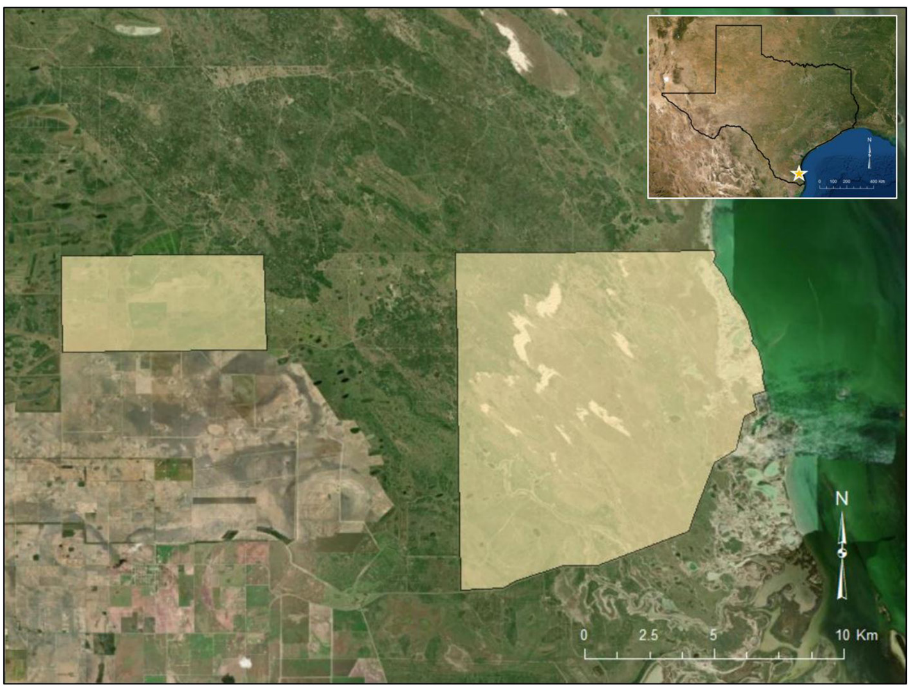

Figure 1. Study area for identifying behavioral states of bobcats *Lynx rufus*, coyotes *Canis latrans* and ocelots *Leopardus pardalis* using hidden Markov models. We captured 8 ocelots, 13 bobcats and 5 coyotes on the Yturria San Francisco Ranch (left) and the East Foundation's El Sauz Ranch (right) in southern Texas, USA from 2017 to 2021 and fitted each individual with a global positioning system (GPS) collar.

from the trap. Captured animals were sedated 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 we used a reversal of 5 mg of atipamezole per 1 mg medetomidine (ZooPharm, Laramie, WY, USA) from 2019 to 2021 (Shindle and Tewes 2000, Lombardi et al. 2021). Each individual was then fitted with a Lotek Minitrack and Litetrack global positioning system (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. All capture and handling of animals were conducted in accordance with United States Fish and Wildlife Service permit (no. PRT-676811), Texas Parks and Wildlife Department permit (no. SP0190-600) and Texas A&M University Kingsville Institutional Animal Care and Use Committee protocols (2012-12-20B-A2, 2019-2-28A-2-28B).

Analysis

After removing poorly functioning GPS collars, we obtained locations from 8 ocelots, 13 bobcats and 5 coyotes. We calculated turning angles and step lengths for the path between each location using the 'moveHMM' package (www.r-project.org, Michelot et al. 2016). We used HMMs to identify behavioral states based on differences in step length and turning angle (Langrock et al. 2012). We evaluated 12 different sets of initial parameters (6 sets of 2-state models and 6 sets of 3-state models) for step lengths to identify the best fitting model, ranging from (0.01–0.15, 0.7–1.0) for 2-state models and (0.01–0.05, 0.25–0.40, 0.7–1.0) for 3-state models. Turning angle parameters were set as (π, 0) for all 2-state models and (π, π, 0) for all 3-state models. We compared different initial parameters using an AIC_c model selection framework (Akaike 1973). We then classified each GPS location as one of three behaviors, based on our top model, using the Viterbi algorithm (Viterbi 1967, van de Kerk et al. 2015).

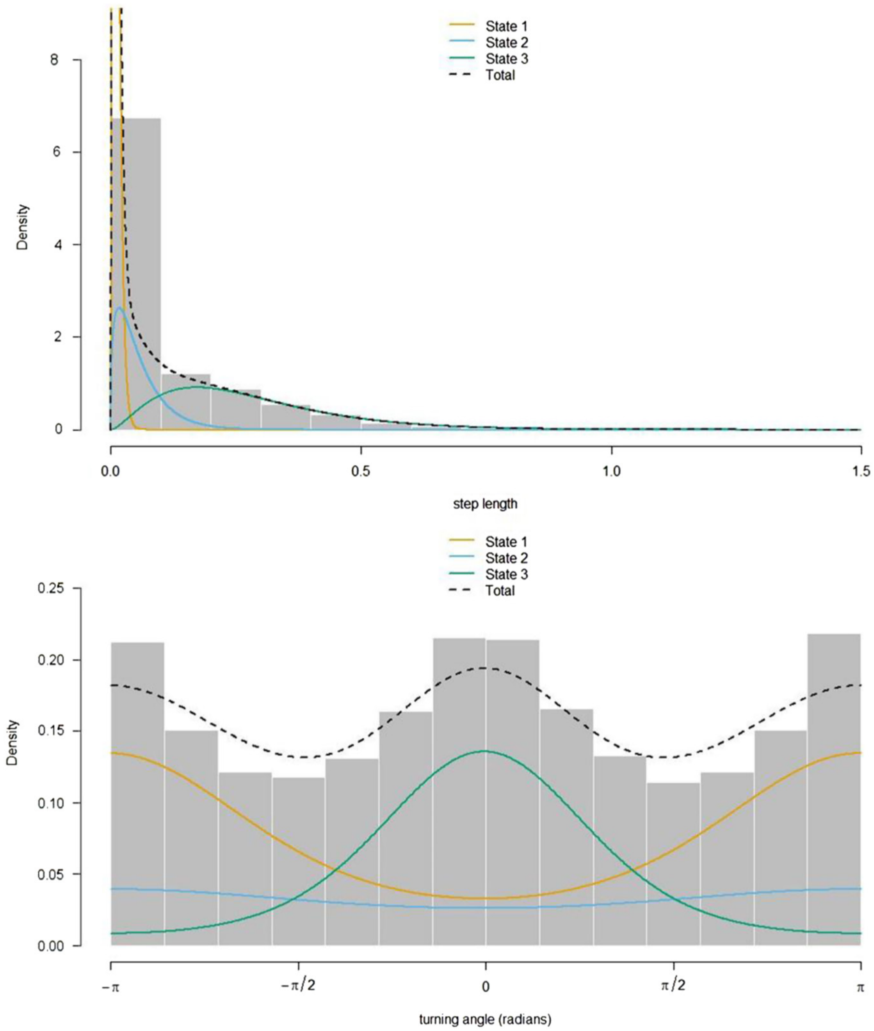

Figure 2. Fitted state-dependent distributions of step length (top) and turning angle (bottom) from a 3-state hidden Markov model of GPS locations from ocelots *Leopardus pardalis* in south Texas, USA from 2017 to 2021. Three behaviors were considered: resting (state 1), hunting (state 2) and territory patrolling/exploring (state 3) based on step length and turning angle between successive locations.

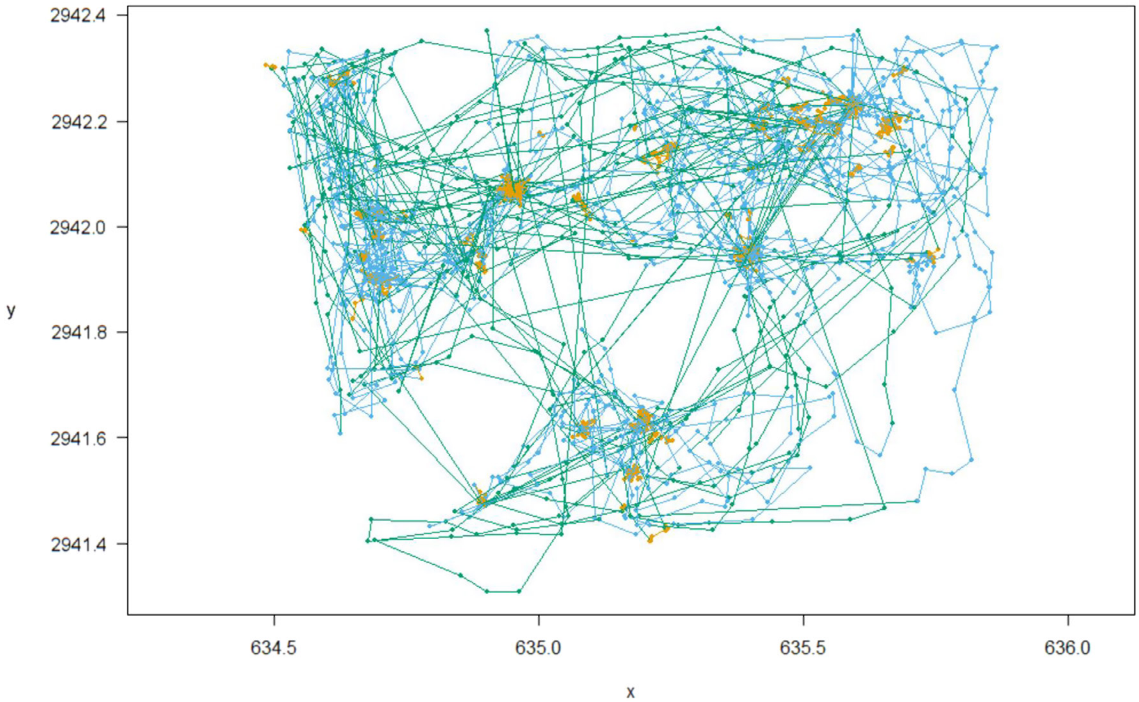

Figure 3. Example of a movement path of an individual ocelot *Leopardus pardalis* in south Texas, USA from 2017 to 2021. Movement between successive locations is classified into one of three behavioral states (yellow = resting, green = intermediate (hunting) and blue = exploratory) based on step length and turning angle using hidden Markov models.

We evaluated differences in habitat selection based on behavioral state using a resource selection function (Picardi et al. 2021). We created 95% minimum convex polygons (MCP) for each captured individual to characterize availability. Within each MCP, we created five random locations for each true location to examine selection for landscape characteristics. We calculated percent canopy cover using LP360 software from GeoCue using light detection and ranging (LiDAR) data flown by the United States Geological Survey (USGS 2018), downloaded from Texas Natural Resources Information Systems (TNRIS). We considered > 75% as heavy woody cover and considered < 25% as low cover/open areas and calculated distance to heavy cover and low cover/open areas using ArcMap 10.8 (ESRI). We used the LiDAR data to calculate point density of vegetation and considered 3 height strata: 0–1, 1–3 and > 3 m as a measure of horizontal

Table 1. Output from logistic regression model of habitat selection of ocelots *Leopardus pardalis* in south Texas, USA, from 2017 to 2021. Habitat selection was modeled as a function of 0–1 m vegetation density, percent canopy cover, distance to heavy cover (> 75% canopy) and distance to open areas (< 25% canopy). We used an interaction term between each variable and behavioral state to identify differences in habitat use between behaviors. Dens1m = density of 0–1 m vegetation, CanopyCover = percent canopy cover, State = behavioral state, DistHeavy = distance to heavy cover (> 75% canopy), DistLow = distance to low cover/open areas (< 25% canopy).

	Estimate	SE	p-value
Intercept	−2.6966	0.1024	< 0.0001
Density 1m	1.0663	0.0118	< 0.0001
State 2	0.2393	0.0333	< 0.0001
State 3	0.1987	0.0345	< 0.0001
DistHeavy	−0.1648	0.0688	0.0166
Canopy Cover	1.8696	0.0354	< 0.0001
DistLow	0.2255	0.0120	< 0.0001
Dens1m ×State 2	−0.6366	0.0171	< 0.0001
Dens1m ×State 3	−0.9801	0.0199	< 0.0001
DistHeavy ×State 2	0.0486	0.0864	0.5738
DistHeavy × State 3	−0.9847	0.1022	< 0.0001
Canopy Cover ×State 2	−0.6401	0.0485	< 0.0001
Canopy Cover ×State 3	−1.3686	0.0496	< 0.0001
DistLow × State 2	0.0014	0.0164	0.9336
DistLow × State 3	−0.3198	0.0203	< 0.0001

vegetation cover. All vegetation metrics were calculated at a 10 m spatial resolution. All variables in the model were standardized. We used mixed-effect binomial regression models to evaluate habitat selection of landscape variables. We used an interaction term between behavioral state and landscape metrics to assess how selection changed between behaviors. We compare the same model separately for each of the three species (ocelots, bobcats, coyotes). Our final model included density of 0–1 m vegetation, distance to heavy cover, distance to low cover/open areas and percent canopy cover, with an interaction between each of these landscape variables and behavioral state and a random effect of animal ID.

In addition to spatial differences between behaviors, we examined temporal partitioning of behaviors within and across species to identify if a species exhibited behaviors at distinct periods of the diel cycle and if there were differences between species. We compared the timing of each behavior (in radians) using the 'circular' package in R (Agostinelli and Lund 2022) . We used a Watson's U test for pairwise comparisons of behaviors of a single species and behaviors across species. We also calculated the coefficient of overlap between activity patterns using the 'overlap' package in R (Rideout and Linkie 2009) and again compared within and across species.

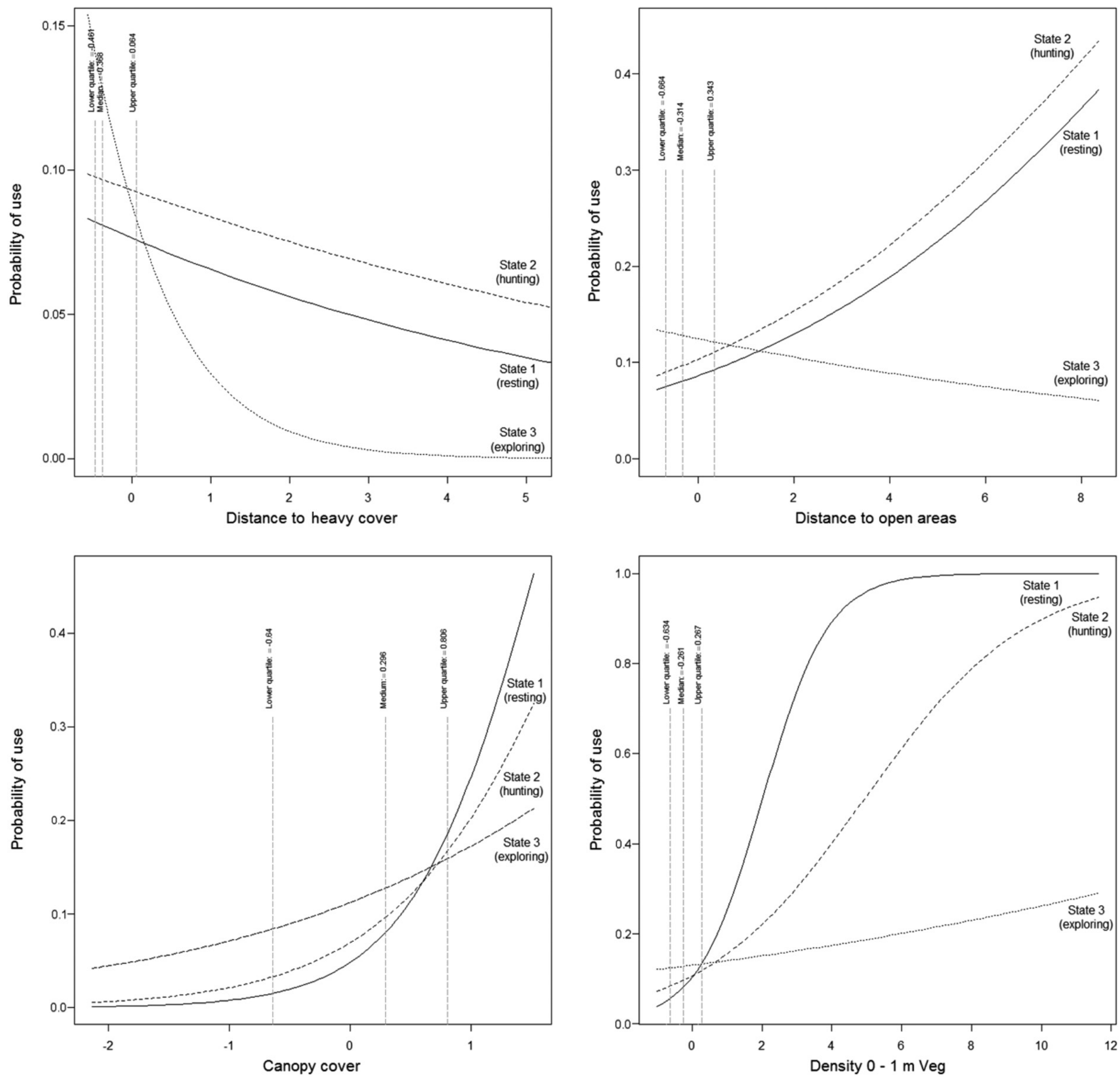

Figure 4. Predictive plots of use of canopy cover (top), 0–1 m vegetation (middle) and distance to heavy cover (> 75% canopy), and distance to open areas (< 25% canopy) by ocelots *Leopardus pardalis* across three behavioral states in south Texas, USA from 2017 to 2021. Behavioral states were classified using hidden Markov movement models. From left to right, the vertical lines represent the lower quartile, the median and the upper quartile for the given variable. All variables were scaled in the model and are plotted as such.

Results

We found support for a 3-state model over a 2-state model ($\Delta AIC_c > 2.0$) for all 3 species. We considered low movement and high turning as an encamped or resting state (Fig. 2). Long distances with low turning angles represented an exploratory state (patrolling territory). An intermediate state with high turning and moderate distances traveled was identified, which we considered as a foraging or hunting state. For each species, the top three models according to AIC_c all converged to the same parameters for step length and turning angle and had identical AIC_c values. These 3-state models were selected for each species. Model fit was supported by a pseudoresidual plot (Supporting information). Locations of each species were classified as one of three behavioral states using the Viterbi algorithm based on the top model (Fig. 3).

Ocelots selected for greater canopy cover and greater vegetation density across each behavior, however, we found that selection of canopy cover and dense vegetation was greatest when resting and least when exploring (Table 1, Fig. 4). Areas of high canopy cover had ~45% probability of being used in a resting state, compared to ~35% in a hunting state and only 20% in an exploratory state. A similar relationship was observed with density of 0–1 m vegetation such that there was > 80% probability of use of highly dense vegetation when in a resting state or hunting state compared to ~20% during exploratory state. Ocelots remained further from open areas when resting and hunting (~30–40% probability of state 1 or 2 at greater distances from open areas, compared to ~10% for state 3). Areas near woody cover were preferred across behaviors but at the greatest extent when exploring, such that probability of use fell nearly to 0% at greater distances from heavy cover. Bobcats selected for areas near both heavy cover and open areas across all behavioral states (Table 2, Fig. 5). Preference for open areas did not differ across states; preference for heavy cover differed across behaviors and was strongest for resting and hunting states. Use of canopy cover differed across behaviors, such that probability of use of heavy canopy cover was approximately double during resting and hunting versus exploring (~30 to ~15%). Bobcats selected areas of greater cover at the highest rate when resting, then hunting and the least when exploring and showed a similar relationship for 0–1 m vegetation (70% probability of use compared to 50% at high densities). Similar to bobcats, coyotes selected for both open areas and closer to heavy cover across all behaviors (Table 3, Fig. 6). Selection for areas near heavy cover differed across behaviors and was strongest when hunting and least when resting. Similarly, coyotes were more likely to use open areas when resting (~30%) compared to hunting and exploring (~12 and ~20% respectively), with probability of use sharply decreasing during the resting state as distance to open areas increased (~0%). Selection for canopy cover differed across states and was positive when resting and hunting but reversed direction when in an exploratory state. Probability of use of low canopy areas fell from ~22% when resting or exploring to ~ 8% when hunting and from ~25 to ~12% in high canopy when comparing resting to hunting. Probability of use increased greatly with increasing 0–1 m vegetation when resting but was consistent or decreased when hunting or exploring.

We observed temporal differences in behavior within and across species. Ocelots rested during the day (~ 10:00–22:00), explored from ~ 0:00 to 10:00, and exhibited hunting behavior from evening to until the morning (~18:00–07:00; Fig. 7). Bobcats rested during the day (~ 08:00–20:00), hunted throughout the day with greater activity during the night, and explored throughout the night (~18:00–07:00). Coyotes hunted and explored throughout the day (~ 07:00–21:00) and rested at night (~21:00–07:00). Ocelots showed less overlap between behaviors than bobcats and coyotes, both of whom showed a high degree of overlap (Table 4).

Table 2. Output from logistic regression model of habitat selection of bobcats *Lynx rufus* in south Texas, USA, from 2017 to 2021. Habitat selection was modeled as a function of 0–1 m vegetation density, percent canopy cover, distance to heavy cover (> 75% canopy) and distance to open areas (< 25% canopy). We used an interaction term between each variable and behavioral state to identify differences in habitat use between behaviors. Dens1m = density of 0–1 m vegetation, CanopyCover = percent canopy cover, State = behavioral state, DistHeavy = distance to heavy cover (> 75% canopy), DistLow = distance to low cover/open areas (< 25% canopy).

	Estimate	SE	p value
Intercept	−1.6028	0.0735	< 0.0001
Density 1m	0.1940	0.0080	< 0.0001
State 2	0.2558	0.0119	< 0.0001
State 3	−0.2848	0.0132	< 0.0001
DistHeavy	−0.1211	0.0150	< 0.0001
Canopy Cover	0.4638	0.0134	< 0.0001
DistLow	−0.1404	0.0117	< 0.0001
Dens1m × State 2	−0.0334	0.0110	0.0023
Dens1m ×State 3	−0.0536	0.0123	< 0.0001
DistHeavy × State 2	−0.0526	0.0194	0.0068
DistHeavy × State 3	−0.0319	0.0205	0.1202
Canopy Cover × State 2	−0.1919	0.0186	< 0.0001
Canopy Cover × State 3	−0.3018	0.0208	< 0.0001
DistLow × State 2	0.0144	0.0159	0.3670
DistLow × State 3	0.0287	0.0184	0.1181

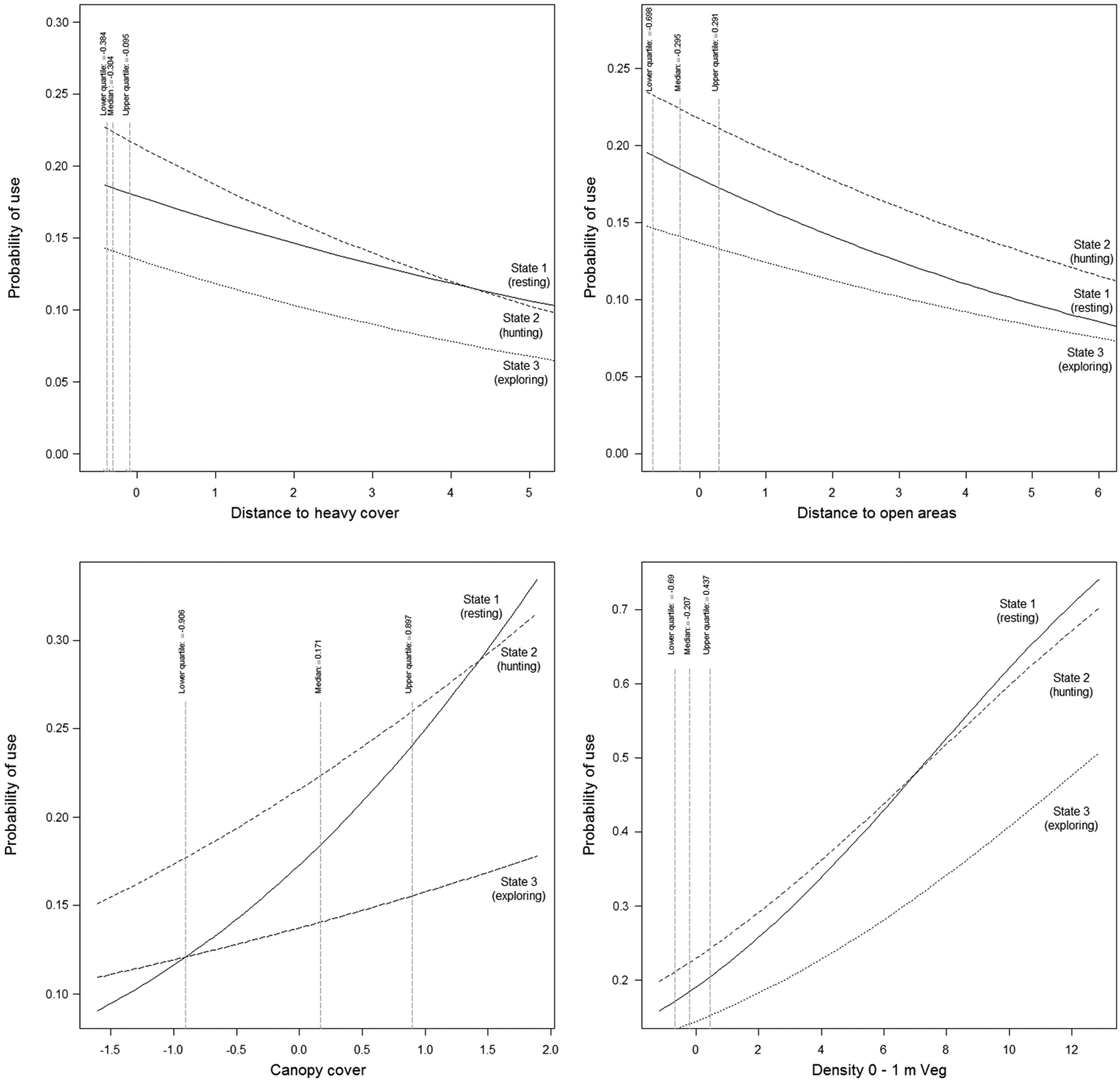

Figure 5. Predictive plots of use of canopy cover (top), 0–1 m vegetation (middle) and distance to heavy cover (> 75% canopy), and distance to open areas (< 25% canopy) by bobcats *Lynx rufus* across three behavioral states in south Texas, USA from 2017 to 2021. Behavioral states were classified using hidden Markov movement models. From left to right, the vertical lines represent the lower quartile, the median and the upper quartile for the given variable. All variables were scaled in the model and are plotted as such.

Between species, coefficients of overlap were highest for states one and two and lowest for state three. Each pairwise comparison, within and across species, was signficant at $\alpha = 0.001$ (Table 4, Fig. 8).

Discussion

As a species of conservation concern, understanding how ocelots coexist with potential competitor species is essential to management. Our objectives were to examine spatial and temporal coexistence between ocelots, bobcats and coyotes through the lens of behavior. We observed differences in habitat use of all three species across behaviors. Overall, we found a strong preference for dense woody vegetation by ocelots and to a lesser extent bobcats, consistent with documented patterns of the species (Harveson et al. 2004, Horne et al. 2009). Use of woody vegetation by both felids was greatest when resting and hunting and lowest when exploring. While HMMs models were unavailable for a direct comparison of ocelots or bobcats, research on other felids offered comparable results. Florida panthers exhibited resting behavior throughout the day and switched from intermediate state to exploring state when traveling between patches in more open

Table 3. Output from logistic regression modelof habitat selection of coyotes *Canis latrans* in south Texas, USA, from 2017 to 2021. Habitat selection was modeled as a function of 0–1 m vegetation density, percent canopy cover, distance to heavy cover (> 75% canopy) and distance to open areas (< 25% canopy). We used an interaction term between each variable and behavioral state to identify differences in habitat use between behaviors. Dens1m = density of 0–1 m vegetation, CanopyCover = percent canopy cover, State = behavioral state, DistHeavy = distance to heavy cover (> 75% canopy), DistLow = distance to low cover/open areas (< 25% canopy).

	Estimate	SE	p value
Intercept	−1.4549	0.0340	< 0.0001
Density 1m	0.1985	0.0128	< 0.0001
State 2	−0.8945	0.0243	< 0.0001
State 3	−0.0559	0.0197	0.0044
DistHeavy	−0.1413	0.0185	< 0.0001
Canopy Cover	0.0648	0.0224	0.0038
DistLow	−0.7924	0.0310	< 0.0001
Dens1m × State 2	−0.1869	0.0236	< 0.0001
Dens1m × State 3	−0.2448	0.0198	< 0.0001
DistHeavy × State 2	−0.0860	0.0434	0.0476
DistHeavy × State 3	−0.0598	0.0290	0.0394
Canopy Cover × State 2	0.1125	0.0384	0.0034
Canopy Cover × State 3	−0.1510	0.0308	< 0.0001
DistLow × State 2	0.4914	0.0436	< 0.0001
DistLow × State 3	0.6706	0.0366	< 0.0001

areas (van de Kerk et al. 2015), consistent with ocelots and suggesting both species selected for a faster, more directional movement in open areas and an intermediate (foraging) state within cover. Habitat use of coyotes was similar to bobcats, showing a preference for heterogeneous landscapes and edges. Overall, coyotes selected for areas closer to dense woody cover and closer to low cover/open areas, similar to bobcats and supporting past evidence that coyotes use a variety of cover types (Crimmins et al. 2012, Lesmeister et al. 2015, Flores-Morales et al. 2019). However, when we compared differences in behaviors, coyotes showed a pattern opposite the two felids, wherein they rested in open areas and used vegetation at a greater extent when hunting and exploring. Distance to low cover–open areas increased when foraging or exploring, suggesting coyotes may be selecting for more secure areas when moving across the landscape, although use of canopy cover decreased when exploring, suggesting coyotes may be using areas of moderate cover. Ellington (2020) found a preference for heterogeneous landscapes when traveling, consistent with our study differences. Further, they observed differences in use of open areas when foraging or traveling based on diurnal or seasonal patterns. Other hidden Markov analyses on coyotes focused on use of urban landscapes and offer little in direct comparison but provide further evidence that behavior of coyotes can be described with this methodology and that habitat use differs across behaviors (Ellington and Gehrt 2019). Hidden Markov models applied to another canid, the wolf *Canis lupus*, showed a high predictive ability in classifying behaviors, however, they did not evaluate differences in habitat selection across behaviors (Kosović and Fertalj 2014). As such, we observed differences between species that suggest that ocelots and bobcats heavily select for dense cover when in low-movement states while coyotes show an opposite pattern wherein they rest in open areas.

We observed differences in the timing of behaviors suggesting temporal partitioning between species. Ocelots and bobcats rested in the afternoon (~ 12:00–17:00) while coyotes rested at night; we observed the least overlap between ocelots and coyotes. Hunting behavior of ocelots showed a peak around 01:00 while bobcats exhibited this intermediate state more consistently throughout the day suggesting greater diurnal and crepuscular activity, consistent with prior studies (Neale and Sacks 2001, Lesmeister et al. 2015, George and Crooks 2016, Flores-Morales et al. 2019). In contrast, coyotes hunted during the day. Exploratory behavior generally occurred in the middle of the night until early morning for ocelots and was similar for bobcats but began and ended earlier in the night, consistent with Persian leopards and black bears that exhibited exploratory behavior at night (Karelus et al. 2019, Farhadinia et al. 2020), likely patrolling territory at the darkest point of night (Farhadinia et al. 2020). Coyotes again showed opposite patterns to the two felids with exploratory behavior occurring primarily during the day. Behavior of coyotes shows a strong diurnal pattern in our study area, in contrast to prior literature in which coyotes were described as nocturnal (Way et al. 2004, Cooper et al. 2015, Melville et al. 2020). Within a species, overlap among behaviors was low for ocelots suggesting behaviors were more distinctly partitioned across the diel period, while bobcats and coyotes showed high overlap across behaviors. Across species, overlap was higher when resting or hunting but showed little overlap in exploratory behavior for all species pairs, suggesting that when moving longer distances in more open areas, these species highly partitioned their temporal environment to minimize interactions.

The competitive exclusion principle suggests that species with similar ecological niches would face difficulty coexisting due to overlapping use of resources (Gause 1934). As similar-sized carnivores with similar diets, ocelots, bobcats and coyotes likely exhibit considerable overlap in resource use, however, these species do spatially co-occur, and the mechanisms of coexistence have been previously examined.

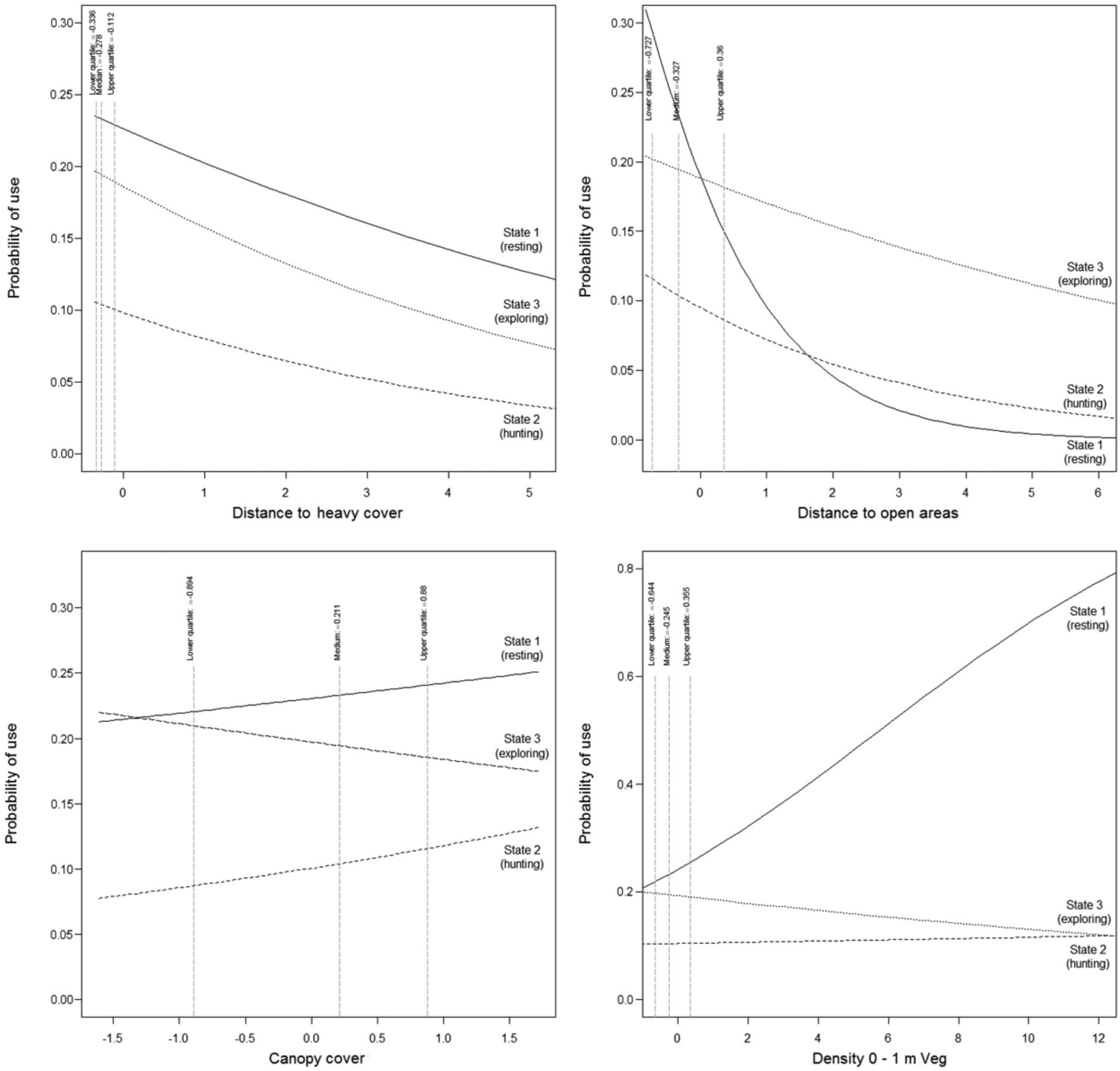

Figure 6. Predictive plot of use of canopy cover (top), 0–1 m vegetation (middle) and distance to heavy cover (> 75% canopy), and distance to open areas (< 25% canopy) by coyotes *Canis latrans* across three behavioral states in south Texas, USA from 2017 to 2021. Behavioral states were classified using hidden Markov movement models. From left to right, the vertical lines represent the lower quartile, the median and the upper quartile for the given variable. All variables were scaled in the model and are plotted as such.

Bobcats and coyotes showed overlap in space use and prey items, however, fine-scale habitat and prey partitioning likely facilitated coexistence (Neale and Sacks 2001, Chamberlain and Leopold 2005, García et al. 2014). Within south Texas, ocelots and bobcats showed differing use of woody vegetation, wherein ocelots preferred > 75% cover and bobcats preferred < 75% cover (Horne et al. 2009). Further, ocelots and bobcats showed extensive overlap of home ranges and use of forested spaces, likely facilitated by fine-scale habitat partitioning (Leonard 2016). Detection and occurrence of coyotes, ocelots and bobcats were greater at sites where one species was detected and occurred, suggesting a high degree of co-occurrence in south Texas (Lombardi et al. 2020). Within this region, the diet of ocelots and bobcats had considerable overlap, however, difference in preference of specific prey species mitigated overlap in resources (Booth-Binczik et al. 2013). Previous studies suggest a high degree of overlap among these three species and suggest differences in fine-scale space use and diet as possible mechanisms of coexistence. Our results suggest that differences in timing and space use associated with different behavioral states may enable coexistence between these three ecologically similar carnivores.

We used hidden Markov models to identify the behavioral states of ocelots, bobcats and coyotes based on step lengths and turning angles of movement path. We found support for a 3-state model over a 2-state model, suggesting

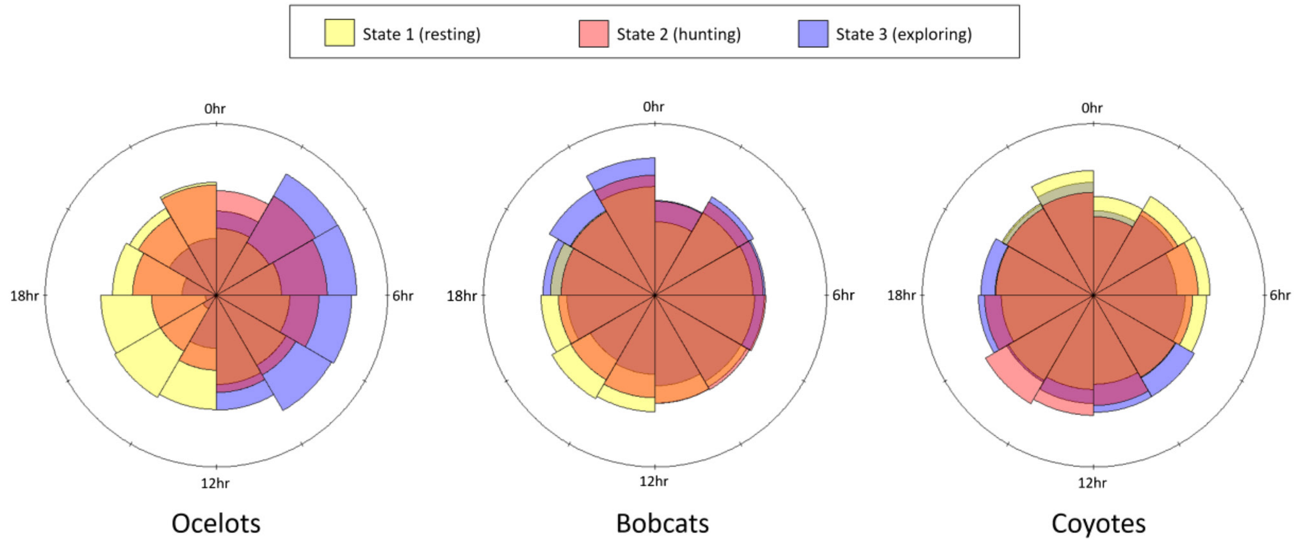

Figure 7. Temporal distribution of behavioral states of bobcats *Lynx rufus*, coyotes *Canis latrans* and ocelots *Leopardus pardalis* in south Texas, USA, from 2017 to 2021. Behavioral states were fitted using hidden Markov movement models and assigned to each GPS location using the Viterbi algorithm. Each plot depicts a 24-h cycle. Behavioral states are denoted by colored sectors (yellow = resting, red = hunting, blue = exploring). Each layer is transparent, such that other colors are the result of overlapping behaviors (i.e. orange representing overlap of resting and hunting behavior, purple representing an overlap of hunting and exploring, and so forth.

three distinct behaviors could be identified (presumed to be resting, hunting, territory patrolling), supporting our first prediction. To our knowledge, this is the first application of HMMs to describe the behavior of ocelots or bobcats. We found two previous studies that applied this methodology to coyotes and similarly used a 3-state model with resting (encamped), foraging and exploring (traveling) states (Ellington and Gehrt 2019, Ellington et al. 2020). Similarly, 3-state models with a resting, intermediate and traveling state have been used to model the behavior of other terrestrial carnivores such as Persian leopard *Panthera pardus saxicolor* (Farhadinia et al. 2020), Florida panther *Puma concolor coryi* (van de Kerk et al. 2015, Li and Bolker 2017), black bears *Ursus americanus* (Karelus et al. 2019) and wolves *Canis lupus* (Kosović and Fertalj 2014). Identifying an intermediate state as a foraging state requires some assumptions, however, this classification has commonly been applied for 3-state models of terrestrial species (Clontz et al. 2011, Kosović and Fertalj 2014, Ellington et al. 2020). While this methodology can be effective in describing behavior, it is not without its limitations and assumptions. First, there is little to no way to confirm that these different behavioral states do relate to the behaviors we consider, although a resting state and a traveling state are less variable than an intermediate state. In addition, an intermediate state can often be difficult to separate from a resting or traveling state, and while we may presume an intermediate state to be foraging based on movement and our understanding of biology, it may relate to other behaviors or encompass several behaviors. Nevertheless, this classification has been used previously and supports our understanding of typical animal movements. Further, past studies have shown a high predictive ability in classifying behaviors using this methodology (Kosović and Fertalj 2014).

Our study provides a novel approach to examining coexistence in a carnivore community and the first application of this methodology to describe the movement of the

Table 4. Temporal overlap of behaviors within a species (top) and across species (bottom) for bobcats *Lynx rufus*, coyotes *Canis latrans* and ocelots *Leopardus pardalis* in south Texas, USA from 2017 to 2021. Behaviors were classified using hidden Markov models based on differences in step length and turning angle of successive GPS locations. The first value in each cell provides the coefficient of overlap (estimated using the 'overap' package in R), and the second value provides the test statistic for a Watson's U test (* denotes significance at α = 0.001).

	Resting–hunting	Resting–exploring	Hunting–exploring
Within species			
Ocelot	0.69 | 75.23*	0.41 | 183.66*	0.68 | 44.03*
Bobcat	0.90 | 13.99*	0.80 | 34.25*	0.88 | 12.51*
Coyote	0.85 | 5.95*	0.84 | 10.13*	0.89 | 0.98*
	Resting	**Hunting**	**Exploring**
Across species			
Ocelot–Bobcat	0.86 | 17.94*	0.89 | 10.12*	0.59 | 75.17*
Ocelot–Coyote	0.77 | 39.75*	0.80 | 13.19*	0.54 | 86.38*
Bobcat–Coyote	0.84 | 16.16*	0.90 | 4.11*	0.82 | 17.94*

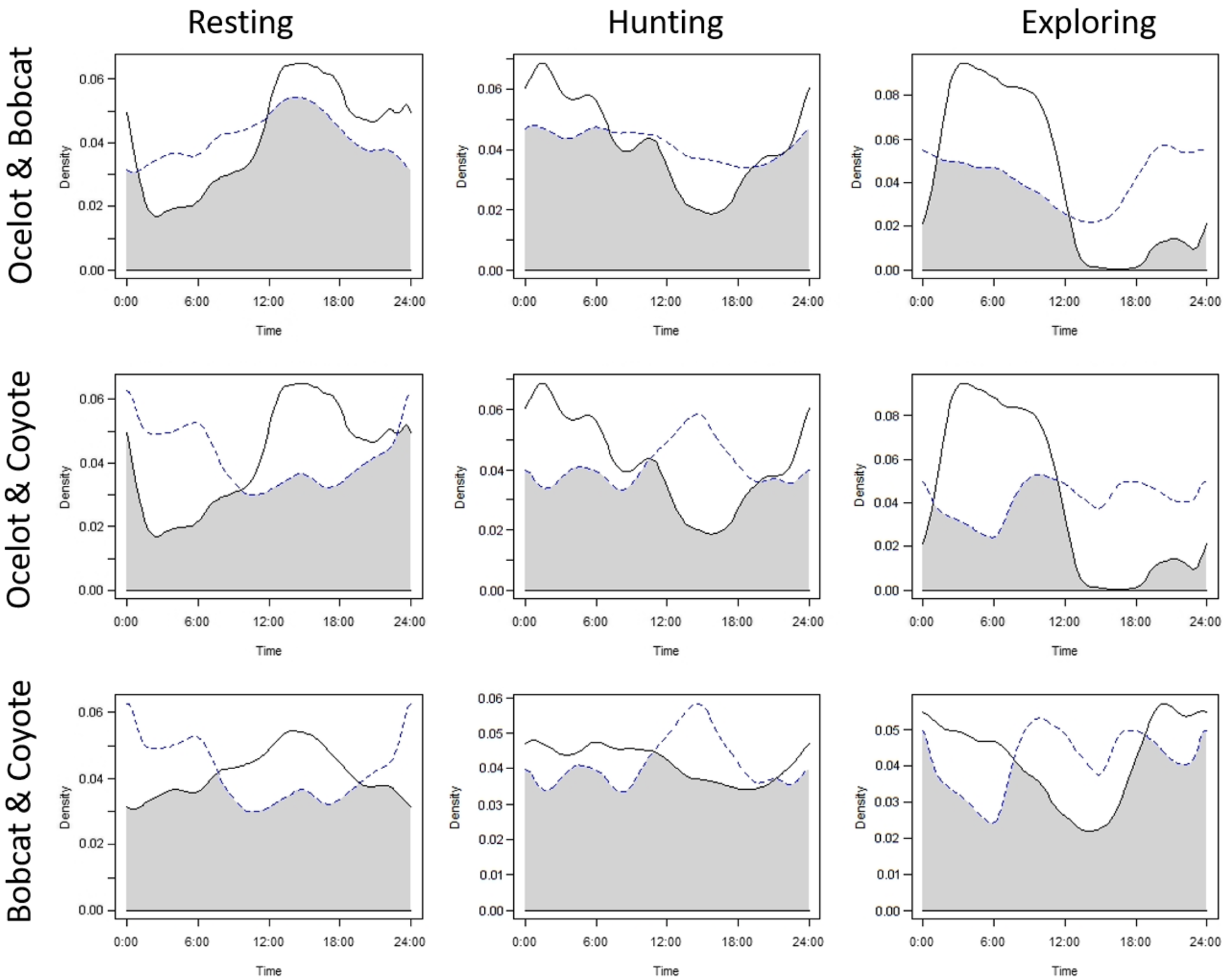

Figure 8. Overlap plots displaying the temporal distribution of behavioral states (resting, hunting and exploring) of bobcats *Lynx rufus*, coyotes *Canis latrans* and ocelots *Leopardus pardalis* in south Texas, USA from 2017 to 2021. Vertical columns display behavior (left = resting, middle = hunting, right = exploratory behavior). Rows compare species overlap (top = ocelots and bobcats, middle = ocelots and coyotes and bottom = bobcats and coyotes). The solid black line represents the first species listed in each row; the dashed line denotes the second species. Areas in gray represent areas of temporal overlap.

endangered ocelot. Results support the idea that these species coexist through fine-scale spatial and temporal partitioning and suggest that these differences may be behaviorally mediated. We show that ocelots and bobcats rest and hunt in dense cover while coyotes rest in the open and prefer moderate cover when hunting or exploring. Timing of each behavior showed strong temporal partitioning between the two felids versus coyotes and showed strong partitioning of exploratory states. While we might assume these species would have antagonistic interactions that may complicate persistence of ocelots, our results suggest these species are able to coexist and that presence of other predators may not pose a significant obstacle to ocelot persistence and reintroduction (Miller et al. 2018). Understanding how ecologically similar species share their environment is vital to understanding the complex mechanics within an ecosystem and improves our ability to manage a landscape to the benefit of multiple species. Particularly for a species of conservation concern such as the ocelot, understanding how they share the landscape with other carnivores and what habitat features they require for the various aspects of their ecology can ensure that habitat is properly protected to sustain native populations. Our study highlights spatial and temporal differences in behaviors as possible explanation for coexistence among ecologically similar species and provides a methodology applicable to other ecological communities.

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Ethics statement – Capture and handling of animals were conducted following United States Fish and Wildlife Service permit (no. PRT-676811), Texas Parks and Wildlife Department permit (no. SP0190-600) and Texas A&M University Kingsville Institutional Animal Care and Use Committee protocol (2012-12-20B-A2).

Author contributions

Maksim Sergeyev: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (equal). **Joseph D. Holbrook**: Conceptualization (equal); Formal analysis (equal); Methodology (equal). **Jason V. Lombardi**: Conceptualization (equal); Data curation (equal); Project administration (equal). **Michael E. Tewes**: Conceptualization (equal); Funding acquisition (lead); Project administration (equal). **Tyler A. Campbell**: Funding acquisition (equal); Project administration (equal).

Data availability statement

Due to the sensitive nature of ocelots as an endangered species, we are unable to make the GPS location data publicly available, however, with proper permitting and approval, data can be provided upon request. R code used in the analysis is available at Github: https://github.com/MaksimSergeyev/HMM_RCode_Oikos. (Sergeyev et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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