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Spatial and temporal coexistence of medium-sized felines and their potential preys in Sierra Madre del Sur of Guerrero, México

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Two species of similar size and trophic niche could not coexist in the same space and time unless the resources are diverse, abundant, and can be shared. In the Sierra Madre del Sur, Guerrero, Mexico, three felines of similar size coexist, *Herpailurus yagouaroundi*, *Leopardus pardalis,* and *Leopardus wiedii*. The objective of this research was to identify the spatiotemporal patterns that allow the coexistence of three felines and their potential preys, as well as to evaluate how the presence of humans and livestock influence their use of space and time. We hypothesized that the three felines coexist due to a differential use of time and space. Therefore, low or moderate overlap is expected, as well as a positive relationship with prey richness but negative regarding the presence of humans and livestock. Between 2009 and 2019, information was obtained on how the three feline species and their potential prey use time and space in eight landscapes with wide environmental variation using camera trapping. With a total sampling effort of 27,014 days/trap in 1,170 km^2, 362 independent records of felids and 2,287 of 12 potential preys were obtained. Overlap in daily activity patterns (Δ) was estimated, and spatial co-occurrence was calculated using epsilon ($\mathcal{E}$) values. Our results show that jaguarundi displayed a diurnal activity pattern and had an overlap of $\Delta = 0.22$ with ocelot and $\Delta = 0.26$ with margay; ocelot and margay were nocturnal with an activity overlap of $\Delta = 0.87$. The spatial co-occurrence between the three felid species was positive: $\mathcal{E} = 2.61$ between ocelot and margay, $\mathcal{E} = 3.22$ between ocelot and jaguarundi; and $\mathcal{E} = 6$ between jaguarundi and margay. The temporal overlap and spatial co-occurrence among felines showed a similar use of resources, and their distribution coincide with the one of some of their potential preys, may be related to predation strategies. Temporal overlap and spatial co-occurrence alone do not limit the coexistence of species; but the environmental differences of the landscapes do influence the variation and temporal dynamics of the felines studied in the Sierra Madre del Sur de Guerrero.

Dos especies de tamaño y nicho trófico similar no podrían coexistir en un mismo espacio y tiempo, a menos que los recursos sean diversos, abundantes y puedan ser repartidos. En la Sierra Madre del Sur (SMS) del estado de Guerrero, México, cohabitan tres felinos de talla similar: *Herpailurus yagouaroundi*, *Leopardus pardalis* y *Leopardus wiedii*. Por lo que, el objetivo de esta investigación fue identificar los patrones espacio-temporales que permiten la coexistencia de los tres felinos y sus presas potenciales, así como evaluar el efecto de la presencia humana y de ganado sobre el uso que las especies hacen del tiempo y el espacio. Se planteó la hipótesis de que los tres felinos coexisten debido a un uso diferente del tiempo y del espacio; por lo que se esperan traslapes bajos o moderados, así como una relación positiva con la riqueza de presas, pero negativa respecto a la presencia de humanos y de ganado. Entre los años 2009 y 2019, en ocho paisajes con una amplia variabilidad ambiental y mediante fototrampeo, se obtuvo información sobre como las tres especies de felinos y sus presas potenciales usan el tiempo y el espacio. Con un esfuerzo total de muestreo de 27,014 días/trampa en 1,170 km^2, se obtuvieron 362 registros independientes de los felinos y 2,287 de 12 presas potenciales. Se estimó el traslape en los patrones de actividad diaria (Δ), y se calculó la co-ocurrencia espacial mediante el valor de épsilon ($\mathcal{E}$). Nuestros resultados muestran que, el patrón de actividad diaria del jaguarundi fue diurno y tuvo un traslape de $\Delta = 0.22$ con el ocelote y $\Delta = 0.26$ con el margay, el ocelote y el margay fueron nocturnos y presentaron un traslape de actividad de $\Delta = 0.87$. La co-ocurrencia espacial entre las tres especies de felinos fue positiva: entre el ocelote y margay de $\mathcal{E} = 2.61$, entre el ocelote y jaguarundi de $\mathcal{E} = 3.22$; y entre el jaguarundi y el margay fue de $\mathcal{E} = 6$. El traslape temporal y la co-ocurrencia espacial, entre estos felinos mostró un uso similar de los recursos, que también coinciden con algunas de sus presas potenciales, lo que podría estar relacionado con las estrategias de depredación. El traslape temporal y la co-ocurrencia espacial por sí solas no limitan la coexistencia de las especies; pero las diferencias ambientales de los paisajes si influyen en la variación temporal de los felinos en la Sierra Madre del Sur de Guerrero.

Keywords: Activity pattern; *Herpailurus yagouaroundi; Leopardus pardalis*; *Leopardus wiedii*; potential prey; spatial co-occurrence; time.

Introduction

Understanding species coexistence and biodiversity maintenance has long been a central subject for ecologists, so the theory of community assembling based on the ecological niche concept has dominated community ecology for almost a century. However, understanding the mechanisms of species coexistence remains hard to elucidate (Niu *et al.* 2009). One of the most widely cited principles is competitive exclusion (two or more species cannot have exactly the same niche in a habitat and achieve long-term coexistence), which shapes community dynamics (Gause 1934; Albrecht and Gotelli 2001; Valeix *et al.* 2007). Therefore, if the resources available for species (food, space, shelter, and others) in a given ecosystem are limited, one species is ultimately displaced from the community, or this triggers changes in its morphology and behavior, thereby modifying its essential resource requirements (Hutchinson 1959; MacArthur and Levins 1967; Di Bitetti *et al.* 2010). When resources and habitat availability are limited, potentially competing species can coexist through niche differentiation (Schoener 1974; Gordon 2000; Nunez 2011), body sizes, or traits (Rosenzweig 1966; Hunter and Caro 2008). For example, they can change the time of daily activity, select a different area, modify their morphology to use different strata of the habitat, or feed on different prey species, thereby decreasing competition intensity. This has been explained for several groups of carnivores, such as mustelids (Rosenzweig 1966), canids, mephitids, procyonids, and ursids (Hunter and Caro 2008), as well as felids (Di Bitetti *et al.* 2010; Romero-Muñoz *et al.* 2010; Hernández-Saintmartín *et al.* 2013; Ávila-Nájera *et al.* 2016; Porfirio *et al.* 2017; Santos *et al.* 2019).

The temporal and spatial axes of the fundamental niche, which include the abiotic and biotic elements used by a species that does not face competition, have been used to explain the coexistence of species through their differential use of these elements as a segregation strategy to evade competitors or predators. This strategy can strongly influence the structure of feline populations, affecting their distribution, relative abundance, and activity patterns (Carothers and Jaksic 1984; Di Bitetti *et al.* 2010). Similar-sized sympatric felines sharing similar ecological requirements and life histories frequently exploit the same resources (Foster *et al.* 2013), which should lead to competitive exclusion if it were not for the spatial or temporal partition of the ecological niche (Valeix *et al.* 2007). Therefore, interspecific competition can induce niche segregation to avoid interference and improve hunting efficiency through optimal foraging (Cozzi *et al.* 2012).

Human disturbance of natural areas decreases biodiversity and generates indirect and cascading negative effects, such as the alteration of species behavior and interspecific interactions. These can limit the use of space and time, thus affecting the activity patterns of species, niche partitioning, and community structure (Frey *et al.* 2017). Information on these aspects can only be obtained by using non-invasive monitoring technologies and techniques such as camera traps and photo trapping, whose implementation in large areas in the mid and long term is essential in generating this important knowledge.

Three species of medium-sized felines are distributed in the Sierra Madre del Sur (SMS) of Guerrero: jaguarundi (*H. yagouaroundi*), ocelot (*L. pardalis*), and margay or tigrillo (*L. wiedii;* Ruiz-Gutiérrez *et al.* 2020). Many aspects of the natural history of these felids and the factors allowing their coexistence in this area are unknown. Therefore, the present work analyzes information gathered over 10 years in the SMS of Guerrero to establish the temporal and spatial use patterns of these three species as a coexistence mechanism.

Our initial hypothesis was that if the three medium-sized felines coexist through the differentiated use of time and space in the SMS of Guerrero, a low or moderate overlap would be expected in these two ecological niche axes. In addition, we also expected a coincidence between the use of time and space concerning the presence of potential prey and a discrepancy relative to the presence of humans and livestock. Finally, activity patterns were expected to be consistent for all three species across the study area.

Therefore, this work aimed to identify the spatio-temporal patterns of the three felines and their potential prey and the influence of the presence of humans and livestock on the use of collection stations during sampling through information recorded with camera traps.

Materials and methods

Study Area. The study consisted of nine systematic sampling campaigns using camera traps in eight landscapes of the Sierra Madre del Sur (SMS) ecoregion of the state of Guerrero (INEGI-CONABIO-INE 2008). The landscapes considered cover an area of 1,170 km^2 and are located within ejidos and rural communities in the SMS foothills and highlands. They display wide environmental heterogeneity, which includes eight vegetation types: Tropical Deciduous Forest (TDF), Tropical Subdeciduous Forest (TSF), Pine Forests (PF), Oak Forest (OF), Pine-Oak Forest (POF), Oak-Pine Forest (OPF), Mountain Cloud Forest (MCF), Savanna (SAV), in addition to areas with secondary vegetation, grasslands, and crops (Ruiz-Gutiérrez *et al.* 2020). These landscapes stretch across an altitudinal range from 350 masl to more than 2,800 masl (Table 1). They are located in the municipalities of Ajuchitlán del Progreso, Chilpancingo de los Bravo, Coyuca de Benítez, Petatlán, Técpan de Galeana, Tecoanapa, Tlacoachistlahuaca, and Xochistlahuaca (Figure 1).

Field Work. Sampling took place from April 2009 to June 2019 in the eight landscapes. In each, sampling was carried out with a duration between two and six months, covering areas of different sizes (between 81 km^2 and 270 km^2); these comprised 9 to 21 quadrants measuring 9 km^2 each (Table 1). This work was part of the National Census of the jaguar and its preys (Chavez *et al.* 2007).

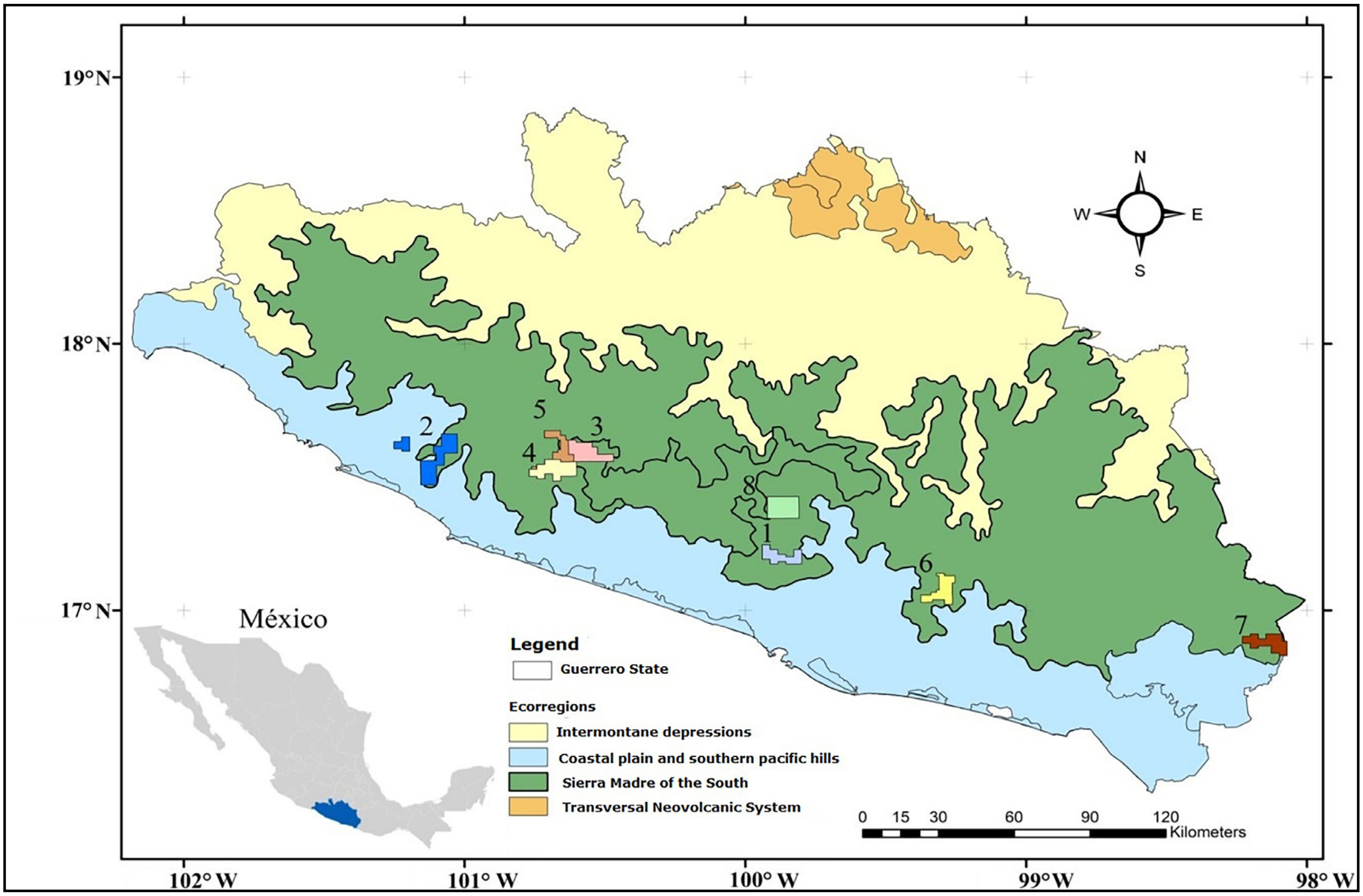

Figure 1. Location of the study area. The figure shows the eight landscapes where sampling was conducted and the ecoregions in the state of Guerrero, Mexico.

In each quadrant, we installed two to three photo trapping stations, each including one and sometimes two camera traps (double stations) separated by 1 to 3 linear kilometers between them. To capture the photographs, we used mainly Cuddeback Digital® camera traps (Xpert, Attack, F2 IR, C1 X-Change Color, and E3 IR), supplemented with Scoutguard® (Sg560) and LTL Acorn® 6210MC. The number of camera traps used for landscape sampling varied between 20 and 80, using a total of 382 cameras in 363 sampling stations; the sampling period fluctuated between 30 and 165 consecutive days. The photo trapping stations were installed on footpaths, roads, nature trails, and water bodies, considering sites with traces (Chavez *et al.* 2013). Cameras were affixed to tree trunks at a height between 30 cm and 50 cm above the ground, at an angle that allowed capturing the flanks of the individuals; these cameras were set with the date and time, to capture one event per minute over 24 hours (Chavez *et al.* 2013; Ruiz-Gutiérrez *et al.* 2020).

Daily Activity Patterns and Overlap Coefficient. The factors analyzed to understand the coexistence of species included daily activity patterns, their overlap, spatial co-occurrence of felines, and the influence exerted by the presence of potential prey, humans, and livestock in the use of the habitat by felines.

Daily activity patterns were analyzed using independent records for each feline species and their potential prey. Only those species with at least 11 independent records were considered (Monroy-Vilchis *et al.* 2011). Photographic records were considered independent when they met any of the following characteristics: 1) consecutive photographs of different individuals of the same species, 2) photographs of the same species with a separation of one hour when the identification of each individual was impossible, and 3) each individual in a photographed group (Ávila-Nájera *et al.* 2016; Contreras-Díaz *et al.* 2021).

The analysis considered independent records of jaguarundi, ocelot, and margay, while potential prey included 12 recorded species that can be potentially preyed on by these felines due to their size and habits. These species are American hog-nosed skunk (*Conepatus leuconotus*), nine-banded armadillo (*Dasypus novemcinctus*), opossum (*Didelphis virginiana*), weasel (*Mustela frenata*), coati (*Nasua narica*), raccoon (*Procyon lotor*), gray squirrel (*Sciurus aureogaster*), porcupine (*Coendou mexicanus*), rabbit (*Sylvilagus cunicularius*), gray fox (*Urocyon cinereoargenteus*), long-tailed wood partridge (*Dendrortyx macroura*) and crested guan (*Penelope purpurascens*; Silva-Pereira *et al.* 2011; Cinta-Magallón *et al.* 2012; Hidalgo-Mihart *et al.* 2020; Pérez-Arteaga *et al.* 2020). The species of mammals (mid-sized and large) and birds were identified by scientific name based on the Mammal Diversity Data Base (2022) and the Peterson and Chalif field guide (1989) field guide, respectively.

The photographs of each species were grouped according to the time of capture into nighttime (20:01 hrs to 6:00 hrs), twilight (6:01 hrs to 8:00 hrs and 18:01 hrs to 20:00 hrs), daytime (8:01 hrs to 18:00 hours; Ávila-Nájera *et al.* 2019). Subsequently, species were sorted according to the observed activity pattern. Daily activity patterns were plotted with the Clock.24 function of the Plotrix package in R version 3.5.1 (Lemon 2006).

The overlap of daily activity patterns between the three felines and their potential prey was assessed through the overlap coefficient (d o Δ), d = , where , are the two functions of activity density over time that are compared; the coefficient can take values between 0 (no overlap) and 1 (total overlap; Ridout and Linkie 2009). Additionally, 95 % confidence intervals for the overlap coefficient were calculated from 1000 repetitions by resampling (*Bootstrap*; Efron and Tibshirani 1993). The statistical and graphical analyses were performed with the *overlay* scrip (Ridout and Linkie 2009) in R version 3.5.1 (R Core Team 2020). It is assumed that activity data are generated by a circular probability distribution. Therefore, activity patterns are contrasted against Δ values. In this sense, Δ values lower than or equal to the 50 percentile of our sample were considered "low-overlap values". Activity patterns ≥ percentile 51 and ≤ percentile 75 were considered "moderate-overlap values", and values equal to or larger than percentile 76 were defined as "high-overlap values" (Monterroso *et al.* 2014).

To analyze whether the time of capture of each of the three species changes in each landscape or across the vegetation types of the Guerrero SMS, a contingency table was constructed with the independent collection records. To determine whether daily activity patterns are random (Zar 2010), a homogeneity test was performed in R version 3.5.1. Specifically, we evaluated a) whether the daily time of capture of the three species remains constant across all the sampled landscapes; b) whether the daily time of capture remains constant when contrasted by vegetation types.

To know whether environments with human activities influence the strategies of temporal and spatial use of the habitat by feline species (Frey *et al.* 2017), we evaluated whether the presence of humans and livestock in photo trapping stations affects the activity patterns of the three felines in the study area. To this end, we categorized the registration data (presence-absence of humans and presence-absence of livestock in the photo trapping stations), and then the patterns were evaluated with the *overlap* package. In addition, to calculate whether there are significant differences in the variation of the hours of activity of the felines in the SMS considering the presence of humans and livestock, a non-parametric Mann-Whitney U-test was performed using the program Past V.4.05. (Zar 2010; Hammer and Harper 2006).

To evaluate the co-occurrence of species, two collection points within the same cell in a two-dimensional grid are considered inputs. To this end, it is necessary to locate the objects in space and measure the distance between those objects (Stephens *et al.* 2017). This work considered the number of photo trapping stations in which each species was recorded within each 9 km^2 quadrant and used the equation by Stephens *et al.* (2019) to estimate the degree of spatial co-occurrence, epsilon (ε).

Where: X and Y are the species, whose co-occurrence will be evaluated, N is the number of records for each species in a particular site or collection station, and ε corresponds to the degree of spatial co-occurrence between species X and Y.

Epsilon (ε) values of zero indicate no interaction between the species; if $\varepsilon \neq 0$, an interaction is inferred, which can be either positive or negative. If $\varepsilon > 0$, species co-occur more frequently than expected in the absence of interaction; conversely, when $\varepsilon < 0$, these two species co-occur less frequently than expected. ε values lower than -1.96 are interpreted as a repulsive interaction, corresponding to a pair of species that do not co-occur; conversely, positive ε values above 1.96 correspond to a pair of species that do interact, that is, an attractive interaction (Stephens *et al.* 2017).

Table 1. Location information of the landscapes in the municipalities that make up the SMS of Guerrero. It indicates the years and months in which the fieldwork was carried out, the number of stations installed with their respective sampling effort by landscape, the territorial extension sampled, and some landscape characteristics such as altitudinal range and vegetation types. #S, Number of Camera trap stations; SE, sampling effort; BTC, Tropical Deciduous Forest; BTS, Tropical Subdeciduous Forest; BP, Pine Forest; BQ, Oak Forest; BQP, Pine-Oak Forest; BMM, Mountain Cloud Forest; SAB, Savanna.

Landscape number	Municipality name	Sampling year	Sampling months	EF/EM	Altitudinal range (m asl)	Sampling area (km^2)	Vegetation types
1	Coyuca-Chilpancingo	2009	April–May	65/2370	900–1900	117	TDF, POF, PF, OPF
2	Petatlán	2011	April–May	67/3486	408–1479	198	TDF, TSF, OF, OPF, POF, MCF
3	Tecpan, Cordón Grande	2013	January–April	32/2438	1299–2810	108	TSF, OPF, POF, MCF
4	Tecpan, Humedades	2014	March–June	27/1380	514–1417	126	TDF, TSF, OF, PF, POF, MCF
5	Técpan, Regional	2015	November–May	53/6314	648–2317	270	TDF, TSF, OF, PF, POF, MCF
	Tecpan, Regional	2019	March–June	20/2040	648–2317	270	TDF, TSF, OF, PF, POF, MCF
6	Tecoanapa	2016–2017	November–January	38/1700	358–1103	81	TDF, TSF, OF, POF, OPF, SAV
7	Tlacoachistlahuaca–Xochistlahuaca	2017	April–June	25/2618	522–1498	117	TDF, TSF, OF, OPF, POF
8	Chilpancingo, Jaleaca	2017–2018	November–March	36/4668	649–1500	117	TDF, OF, OPF, POF

Results

A total of 413 photographic records of the three feline species were obtained, of which 365 were considered independent; for potential prey, 2,287 independent records were captured (Table 2).

Our results suggest that *H. yagouaroundi* has a daytime activity pattern, with 80 % ($n = 47$) of the total records in this category and a peak of activity occurring between 08:01 hrs and 09:00 hrs. The two *Leopardus* species are considered mainly nocturnal: the ocelot had 79 % ($n = 157$) of its records in nighttime hours, with greater activity between 19: 00 hrs and 23:00 hrs, while the margay had 80 % ($n = 161$) of its records at night (Figure 2).

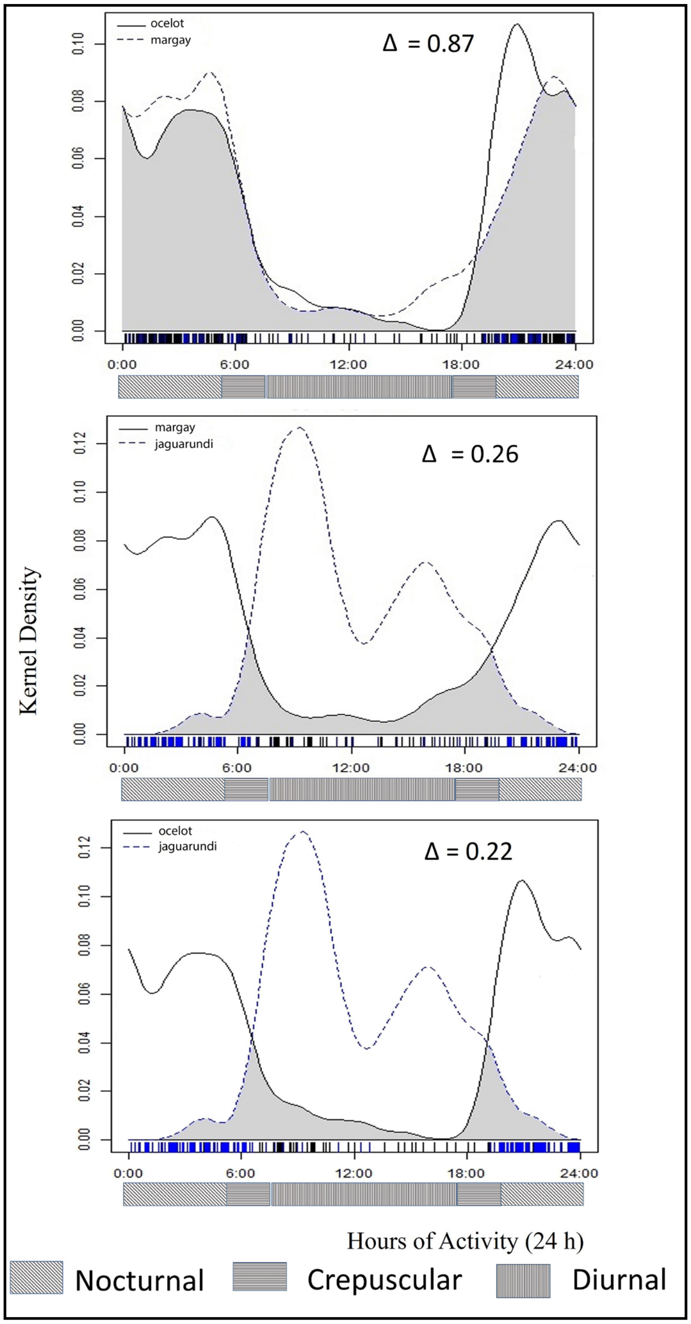

Figure 2. Patterns and overlap of daily activity of medium-sized wild felines in Sierra Madre del Sur of Guerrero, Mexico. The shaded area corresponds to Delta (Δ) values for the overlap between pairs of species.

Table 2. Results of daily activity patterns and number of records of medium-sized felines and their potential prey in Sierra Madre del Sur of Guerrero, Mexico. Nighttime (20:01 hrs–6:00 hrs); twilight (6:01 hrs–8:00 hrs and 18:01 hrs–20:00 hrs); daytime (8:01 hrs–18:00 hrs); ND, not determined (without the minimum of 11 records).

Order/Family/Species	Number of independent records	Activity patterns
	Mammals	
Carnivora		
Felidae		
Leopardus pardalis	157	Nocturnal
Leopardus wiedii	161	Nocturnal
Herpailurus yagouaroundi	47	Diurnal
Canidae		
Urocyon cinereoargenteus	545	Nocturnal
Procyonidae		
Nasua narica	414	Diurnal
Procyon lotor	40	Nocturnal
Mustelidae		
Mustela frenata	8	ND
Conepatus leuconotus	68	Nocturnal
Didelphimorphia		
Didelphidae		
Didelphis virginiana	495	Nocturnal
Rodentia		
Sciuridae		
Sciurus aureogaster	204	Diurnal
Erethizontidae		
Coendou mexicanus	11	Nocturnal
Cingulata		
Dasypodidae		
Dasypus novemcinctus	187	Nocturnal
Lagomorpha		
Leporidae		
Sylvilagus cunicularius	240	Nocturnal
	Aves	
Galliformes		
Odontophoridae		
Dendrortyx macroura	63	Diurnal
Cracidae		
Penelope purpurascens	12	Diurnal

When human or livestock presence was recorded at the sampling stations, the daily activity patterns of the three feline species showed slight differences according to the Mann-Whitney *U*-test (*e. g.*, $Z = 0.25/0.35$, for jaguarundi); however, these differences are not statistically significant ($P = 0.79$), so the overall activity patterns in the SMS do not vary for this species. The same was observed in the other two species evaluated (Figure 3).

When considering the overlap (Δ) of daily activity patterns in the three species of felines, we observed an overlap of Δ = 0.87 (87 %) between margay and ocelot, with differences in the peaks of activity of each species. The overlap was Δ = 0.26 (26 %) between jaguarundi and margay and Δ= 0.22 (22 %) between jaguarundi and ocelot (Figure 2).

Considering our hypothesis that the activity patterns of the three feline species are constant throughout the study area, our results showed that the frequencies of the time of daily activity of jaguarundi by landscape were constant throughout the study area. By contrast, those of ocelot and margay showed variations in the different landscapes sampled ($P < 0.05$). Considering the vegetation types sampled in the SMS, the period of activity of each of the three species also showed considerable variation, reaching statistical significance ($P < 0.05$).

Regarding potential prey, 2,287 records were captured of 10 species of mid-sized mammals and two bird species, considered here as potential prey for the three feline species. The highest temporal overlap values between predators and their potential prey in this study were as follows. Between ocelot and its potential prey: tlacuache (Δ = 0.83), rabbit (Δ = 0.82), armadillo (Δ = 0.82), porcupine (Δ = 0.80). Between margay and its potential prey: hog-nosed skunk (Δ = 0.90), opossum (Δ = 0.85), gray fox (Δ = 0.84), rabbit (Δ = 0.82), armadillo (Δ = 0.82). And between jaguarundi and its potential prey: long-tailed wood partridge (Δ = 0.79), gray squirrel (Δ = 0.77), coati (Δ = 0.70; Table 3).

Spatial co-occurrence values among the three feline species were significant positive epsilon (ε) values ranging between 2.61 and 6, indicating that these species share the space significantly. With the rest of the mammals (potential

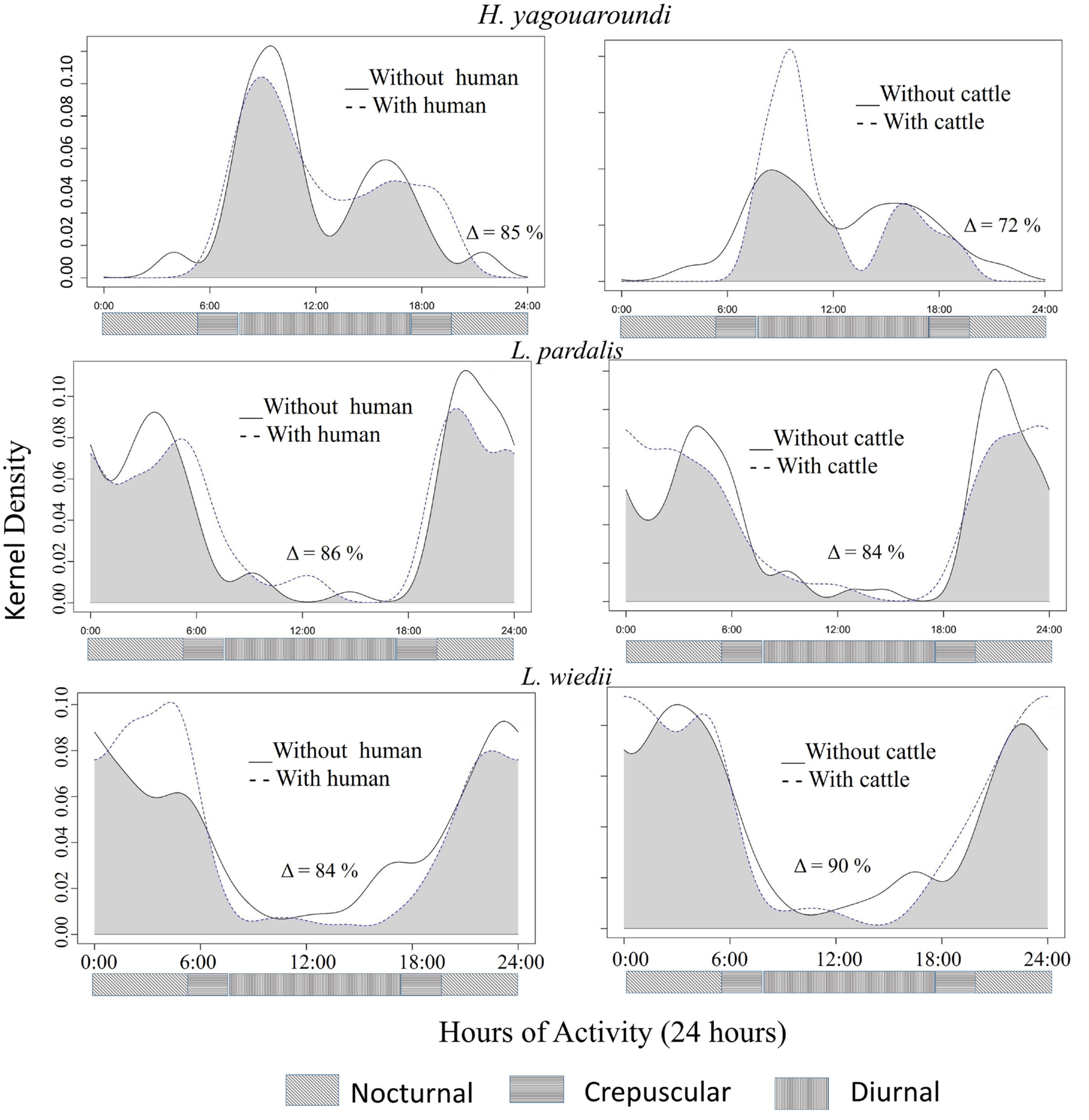

Figure 3. Comparison of daily activity patterns, with emphasis on the overlapping time of activity among the three medium-sized wild feline species, considering the presence of human communities (left) and cattle (right). The shaded area corresponds to Delta (Δ) values for the overlap between pairs of species.

prey), the values are mostly significant and positive, except for some pairs of species with low values (<1.96) and even negative values, such as the case between *H. yagouaroundi* and *P. lotor* or between *L. pardalis* and *Sylvilagus cunicularius*, which showed no spatial co-occurrence (Table 3).

Discussion

The differential use of time (temporal segregation) is one of the factors explaining why species of similar size and feeding patterns can coexist in the same space (Schoener 1974; Kronfeld-Schor and Dayan 2003; Jaksic and Marone 2007). Despite this, the temporal partitioning of the niche is not considered the primary mechanism used by competitors to reduce competition and coexist (Herrera *et al.* 2018), and it is common for animals to be segregated across the trophic or spatial axes of the ecological niche (Schoener 1974). This study documented a diurnal activity pattern of jaguarundi, with a low temporal overlap with ocelot and margay (Giordano 2015). These data support the findings of other studies suggesting that jaguarundi reduces competition by interference with ocelot and margay by selecting opposite periods of activity (Carrera-Trevino *et al.* 2018; Santos *et al.* 2019). We observed that both ocelot and margay are nocturnal and have a wide overlap in their activity patterns. This finding differs slightly from the observations of Santos *et al.* (2019) for Central and South America, who recorded an average overlap of 69 %.

In Sierra Madre del Sur of Guerrero, margay had more records than ocelot, similar to the findings reported elsewhere (*e. g.*, Oliveira *et al.* 2010; Pérez-Irineo and Santos-Moreno 2016). However, for some authors (*e. g.*, Carrera-Treviño *et al.* 2018), ocelot does not appear to negatively influence margay; consequently, there is a wide temporal and spatial overlap between both species. This evidence requires a more in-depth analysis, carrying out specific projects to test whether there are negative spatiotemporal interactions between both species.

The estimated daily activity patterns show that ocelots and margays were active between 17:00 hrs and 06:00 hrs (exclusively at night), similar to other studies (Carrera-Treviño *et al.* 2018; Di Bitetti *et al.* 2010). However, some authors have reported occasional daytime activity (Aliaga-Rossel *et al.* 2006; Di Bitetti *et al.* 2010; Briones *et al.* 2016; Pérez-Irineo and Santos-Moreno 2016; Santos *et al.* 2019). This indicates slight variations in the activity patterns of the species in the different regions it inhabits but that its daily activity is mainly nocturnal. Jaguarundi maintained a consistent daily activity pattern in all landscapes, consistent with our initial hypothesis; however, the pattern changes when vegetation types are considered. Separately, the daily activity patterns of ocelot and margay showed differences considering both factors. As for the records for each of the three species, the presence of livestock generated a difference only in the daily activity pattern of jaguarundi; however, this was not significant.

Table 3. Overlap coefficient (Δ) and co-occurrence values (ℰ) of the three medium-sized felines and their potential prey in Guerrero, Mexico. Epsilon (ℰ) values lower than -1.96 or higher than 1.96 are significant (marked in bold). Negative values (repulsive interaction) correspond to species with which they do not co-occur; positive values above 1.96 correspond to species that co-occur (attractive interaction).

Taxon	***H. yagouaroundi***	***L. pardalis***	***L. wiedii***
	Δ ℰ	**Δ ℰ**	**Δ ℰ**
Mammals			
Carnivora			
Felidae			
Herpailurus yagouaroundi		0.22/ **3.22**	0.26 / **6.00**
Leopardus pardalis			0.88 / **2.61**
Canidae			
Urocyon cinereoargenteus	0.21 / 1.84	0.84 / **3.62**	0.84 / 0.49
Procyonidae			
Nasua narica	0.70 / 0.22	0.44 / 1.53	0.47 / **2.69**
Procyon lotor	0.32 / -0.03	0.78 / 1.42	0.82 / -0.08
Mustelidae			
Mustela frenata	0.13 / **3.51**	0.10 / **3.70**	0.13 / 1.03
Conepatus leuconotus	0.23 / **3.21**	0.86 / **2.09**	0.91 / **4.62**
Didelphimorphia			
Didelphidae			
Didelphis virginiana	0.15 / **2.54**	0.83 / 1.55	0.85 / **4.75**
Rodentia			
Sciuridae			
Sciurus aureogaster	0.77 / **4.65**	0.18/ **2.44**	0.22 / **4.19**
Erethizontidae			
Sphiggurus mexicanus	0.25 / 1.26	0.80 / 0.66	0.81 / 1.89
Cingulata			
Dasypodidae			
Dasypus novemcinctus	0.16 / 1.30	0.82 / 0.53	0.84 / 1.09
Lagomorpha			
Leporidae			
Sylvilagus cunicularius	0.28 / **3.89**	0.82 / -0.72	0.83 / **3.66**
Aves			
Galliformes			
Odontophoridae			
Dendrortyx macroura	0.79 / **6.69**	0.15 / **2.18**	0.19 / **3.45**
Cracidae			
Penelope purpurascens	0.52 / 0.53	0.20 / 0.46	0.23 / 0.78

The presence of potential prey shows a low and moderate overlap of their activity patterns with those of felines (between 25 % and 58 %). Therefore, a broader set of factors likely determines the temporary use of habitat. For example, jaguarundi shared a high temporal overlap (>70 %) with only three of the 12 potential prey (*Dendrortyx macroura, Sciurus aureogaster*, and *Sylvilagus cunicularius*) recorded here; Nonetheless, it is important to consider that this species also feeds on other groups of animals, such as invertebrates, birds, and reptiles (Tófoli *et al.* 2009; Giordano 2015), which are of diurnal habits. Ocelot and margay share a high temporal overlap with seven of their potential prey whose activity is nocturnal. This could influence the daily activity patterns of both species; however, prey abundance may also influence feline patterns, as suggested by Botts *et al.* (2020), An evaluation of the relationship between prey richness, foraging habits, richness of eating habits, and avoidance mechanisms among predators is necessary to identify the factors that influence the daily activity patterns of felines.

Margay showed a high overlap of its daily activity pattern with ocelot, possibly to minimize competition and avoid conflict. This feline uses the arboreal stratum differentially and frequently, preferring sites with low ocelot presence (Di Bitetti *et al.* 2010). This is partially consistent with our data, where margay was the only feline species captured in 63 stations. However, the two species converged in 22 stations, which may indicate that even when the two species were captured at the same time and station, the time elapsed between one record and the next may imply that the two species did not run into one another.

On the other hand, jaguarundi, ocelot, and margay displayed different daily activity patterns, which may allow a high spatial co-occurrence since it substantially decreases the probability of an agonistic encounter between them. However, the latter is hard to demonstrate, although potential intra-guild predation exists (De Oliveira and Pereira 2014).

With respect to prey, eight species co-occurred with felines significantly and more frequently than expected (Table 3). The presence of potential prey species shows a moderate influence on the spatial use of the habitat by felines because only between 41 % and 50 % of these preys coincide with spatial co-occurrence. In contrast, Santos *et al.* (2019) argue that prey availability importantly influences the use of space by these felines, even to a greater degree than environmental variables or interactions between species.

Low ecological niche overlap in some axes indicates coexistence between species (Hardin 1960; Carrera-Treviño *et al.* 2018), as observed along the temporal axis between margay and jaguarundi. However, this work documented that species with high temporal overlap, such as ocelot and margay, can coexist in the same area due to subtle differences in the foraging behavior and daily activity patterns. Therefore, this temporal segregation mechanism may effectively reduce competition between both species (Carothers and Jaksic 1984; Di Bitetti *et al.* 2010). Other mechanisms may also participate in this respect, such as the differentiated use of the habitat and the microhabitat (Hunter and Caro 2008), trophic differentiation, and prey availability, diversity, and abundance (Di Bitetti *et al.* 2010; Botts *et al.* 2020).

The daily activity and habitat use patterns of medium-sized felines result from species adaptation to biotic and abiotic interactions. However, anthropogenic factors such as habitat loss and illegal hunting of these predators and their potential prey may exert an additional influence on them. The results of this study show two coexistence mechanisms. The first implies a marked segregation in the temporal axis of the ecological niche by jaguarundi, whose daily activity pattern is diurnal. In the second, despite a considerable temporal and spatial overlap between ocelot and margay, the coexistence between these species is possible due to the segregation of the ecological niche in one of these two axes.

Our finding of moderate spatial and temporal coincidence with their prey suggests that there are strategies among felines that were not measured in the present study. Therefore, we should evaluate which prey are actually consumed and whether their consumption is different or similar among species (the diet axis of the niche).

Although evaluating the interactions between species with similar biological and ecological traits is an emerging and highly complex topic to analyze in a wide geographic space, as in the present study, it may be the starting point for future studies that address the interactions between pairs of species in further detail. However, future evaluations should cover the three main axes (time, space, and diet) of the ecological niche at different scales and resolutions to improve our understanding of the mechanisms favoring coexistence in these species.

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Literature cited

Albrecht, M., and N. J. Gotelli. 2001. Spatial and temporal niche partitioning in grassland ants. Oecologia 126:134–141.

Aliaga-Rossel, E., *et al*. 2006. Ocelot (*Leopardus pardalis*) predation on Agoutis (*Dasyprocta punctata*). Biotropica 38:691–694.

Ávila-Nájera, D. M., *et al*. 2016. Traslape en patrones de actividad entre grandes felinos y sus principales presas en el Norte de Quintana Roo, México. Therya 7:439–448.

Ávila-Nájera, D. M., *et al*. 2019. Habitat use of jaguar (*Panthera onca*) in a tropical forest in northern Quintana Roo, Mexico. Revista Mexicana de Biodiversidad 90:e902186.

Botts, R. T., *et al*. 2020. Cicardian activity patterns of mammalian predators and prey in Costa Rica. Journal of Mammalogy 101:1313–1331.

Briones-Salas, M., *et al*. 2016. Relative abundance and activity patterns of wild felids in Chimalapas rainforest, Oaxaca, Mexico. Therya 7:123–134.

Carothers, J. H., and F. M. Jaksic. 1984. Times as a niche difference: the role of interference competition. Oikos 42:403–406.

Carrera-Treviño, R., *et al*. 2018. Interacciones temporales y espaciales de mesocarnívoros simpátricos en una Reserva de la Biosfera: ¿Coexistencia o competencia? Biología Tropical 66:996–1008.

Chávez, C., *et al*. 2007. Ecología poblacional del jaguar y sus implicaciones para la conservación en la Península de Yucatán, análisis de viabilidad de poblaciones y hábitat del jaguar en México. Pp. 101–110, *in* Conservación y manejo del Jaguar en México, estudios de caso y perspectivas (Ceballos, G., C. Chávez, R. List, and H. Zarza, eds.). Alianza WWF-Telcel-CONABIO-CONANP-ECOCIENCIAS S. C. Ciudad de México, México.

Chávez, C. *et al*. 2013. Manual de fototrampeo para estudios de fauna silvestre. El jaguar en México como estudio de caso. Alianza WWF-Telcel, Universidad Nacional Autónoma de México. Ciudad de México, México.

Cinta-Magallón, C. C., *et al*. 2012. Dos nuevos registros de margay (*Leopardus wiedii*) en Oaxaca, México, con datos sobre hábitos alimentarios. UNED Research Journal/Cuadernos de Investigación UNED 4:33-40.

Contreras-Díaz, C. A., *et al*. 2021. Temporal and spatial segregation of top predators (Felidae) in a mexican tropical Biosphere Reserve. Zoología 38:1-10.

Cozzi, G., *et al*. 2012. Fear of the dark or dinner by moonlight? reduce temporal partitioning among Africa´s large carnivores. Ecology 93:2590-2599.

De Oliveira, T., and J. Pereira. 2014. Intraguild predation and interspecific killing as structuring forces of carnivoran communities in South America. Journal of Mammalian Evolution 21:427–436.

Di Bitetti, M. S., *et al*. 2010. Niche partitioning and species coexistence in a neotropical felid assemblage. Acta Oecológica. 36:406–412.

Efron, B., and R. Tibshirani. 1993. An introduction to the Bootstrap. Chapman and Hall, New York, U.S.A. https://doi.org/10.1007/978-1-4899-4541-9.

Foster, V. C., *et al*. 2013. Jaguar and puma activity patterns and predatory-prey interactions in four Brazilian biomes. Biotropica 45:373-379.

Frey, S., *et al*. 2017. Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. Remote Sensing in Ecology and Conservation 3:123–132.

Gause, G. F. 1934. Experimental analysis of Vito Volterra´s mathematical theory of the struggle for existence. Science, New Series 79:16–17.

Giordano, A. J. 2015. Ecology and status of the jaguarundi (*Herpailurus yagouaroundi*): a synthesis of existing knowledge. Mammal Review 46:30–43.

Gordon, C. 2000. The coexistence of species. Revista Chilena de Historia Natural 73:175–198.

Hammer, Ø., and D. A. T. Harper. 2006. Paleontological Data Analysis. Blackwell. Malden, U.S.A.

Hardin, G. 1960. The competitive exclusion principle. Science 131:1292–1297.

Hernández-Saintmartín, A. D., *et al*. 2013. Activity patterns of jaguar, puma and their potential prey in San Luis Potosí, Mexico. Acta Zoológica Mexicana (nueva serie) 29:520–533.

Herrera, H., *et al*. 2018. Time partitioning among jaguar *Panthera onca*, *Puma concolor* and ocelot *Leopardus pardalis* (Carnivora: Felidae) in Costa Rica´s dry and rainforest. Revista de Biología Tropical 66:1559-1568.

Hidalgo-Mihart, M., J. A. De la Cruz, and R. Juárez-López. 2020. Ocelot (*Leopardus pardalis*) potential predation on a gray fox (*Urocyon cinereoargenteus*). Therya Notes 1:19-22.

Hunter, J., and T. Caro. 2008. Interspecific competition and predation in American carnivore families. Ethology Ecology & Evolution 20:295-324.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? The American Naturalist 93:145–159.

Instituto Nacional de Estadística Geografía e Informática (INEGI), Comisión Nacional para el Conocimiento y Uso de la Biodiversidad , e Instituto Nacional de Ecología . 2008. Ecorregiones terrestres de México . Escala 1:1,000,000. México. http://geoportal.conabio.gob.mx/metadatos/doc/html/ecort08gw.html.

Jaksic, F. M., and L. Marone (eds.). 2007. Ecología de comunidades. Universidad Católica de Chile. Santiago de Chile, Chile.

Kronfeld-Schor, N., and T. Dayan. 2003. Partitioning of time as an ecological resource. Annual Review of Ecology, Evolution and Systematics 34:153–181.

Lemon, J. 2006. Plotrix: a package in the red light district of R. In R-News. 6:8-12

Macarthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist 101:377–385.

Mammal Diversity Database. 2022. Mammal Diversity Database (1.9). https://doi.org/10.5281/zenodo.6407053. Consulted 17 September 2022.

Monroy-Vilchis, O., *et al*. 2011. Fototrampeo de mamíferos en la Sierra de Nanchititla, México: abundancia relativa y patrón de actividad. Revista Biología Tropical 59:373–383.

Monterroso, P., P. C. Alves, and P. Ferreras. 2014. Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence. Behavioral Ecology and Sociobiology 68:1403–1417.

Niu, K., *et al*. 2009. Community assembly: the relative importance of neutral theory and niche theory. Biodiversity Science 17: 579-593.

Núñez, M. C. 2011. Posible exclusión competitiva entre pumas y jaguares (Carnivora: Felidae) de la Reserva Biológica Alberto Manuel Brenes, San Ramón, Costa Rica. Brenesia 76:115–117.

Oliveira, T., *et al*. 2010. Ocelot ecology and its effect on the small-felid guild in the lowland neotropics. Pp. 559-580, *in* Biology and Conservation of Wild Felids (MacDonald, D., and A. Loveridge, eds). Oxford University Press. New York, U.S.A.

Pérez-Arteaga, A., *et al*. 2020. Photographic confirmation of crested guan (*Penelope purpurascens*) from a relict maple forest in western Mexico. Western North American Naturalist. 3:435-440.

Pérez-Irineo, G., and A. Santos-Moreno. 2016. Abundance and activity patterns of medium-sized felids (Felidae, Carnivora) in southeastern Mexico. The Southwestern Naturalist 61:33–39.

Peterson, R. T., and E. L. Chalif. 1989. Aves de México: Guía de campo, identificación de todas las especies encontradas en México, Guatemala, Belice y El Salvador. Editorial Diana. Distrito Federal, México.

Porfirio, G., *et al*. 2017. Activity patterns of jaguars and pumas and their relationship to those of their potential prey in the Brazillian, Pantanal. Mammalia 81:401–404.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Ridout, M. S., and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural Biological Environmental Statistics 14:322–337.

Romero-Muñoz, A., L. Maffei, E. Cuéllar, and A. J. Noss. 2010. Temporal separation between jaguar and puma in the dry forests of southern Bolivia. Journal of Tropical Ecology 26:303–311.

Rosenzweig, M. L. 1966. Community structure in sympatric carnivora. Journal of Mammalogy 47:602–612.

Ruiz-Gutiérrez, F. *et al*. 2020. Mamíferos medianos y grandes de la Sierra Madre del Sur de Guerrero, México: evaluación integral de la diversidad y su relación con las características ambientales. Revista Mexicana de Biodiversidad 91: e913168.

Santos, F., *et al*. 2019. Prey availability and temporal partitioning modulate felid coexistence in neotropical forests. PlosOne 14: e0213671.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27–39.

Silva-Pereira, J. E., R. Moro-Ríos,D. R. Bilski, and F. C. Passos. 2011. Diets of three sympatric neotropical small cats: food niche overlap and interspecies differences in prey consumption. Mammalian Biology76: 308-312.

Stephens, C. R., V. Sánchez-Cordero, and C. González-Salazar. 2017. Bayesian inference of ecological interactions from spatial data. Entropy 19:547.

Stephens, C. R., *et al*. 2019. Species: a platform for the exploration of ecological data. Ecology and Evolution 9:1638–1653.

Tófoli, C. F., F. Rohe, and E. Z. F. Setz. 2009. Jaguarundi (*Puma yagouaroundi*) (Geoffroy, 1803) (Carnivora, Felidae) food habits in a mosaic of Atlantic rainforest and eucalypt plantations of southeastern Brazil. Journal of Biology. 69: 871-877.

Valeix, M., S. Chamaillé-Jammes, and H. Fritz. 2007. Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. Oecologia 153:739–748.

Zar, J. H. 2010. Bioestatistical Analysis. Pearson Prentice Hall. New Jersey, U.S.A.

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