Neo-tropical felid activity patterns in relation to potential prey and intra-guild competitors in the Calakmul Biosphere Reserve, Mexico

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Short title: Felid-prey activity in the Calakmul Biosphere Reserve

ABSTRACT

Predator behaviours influence, and are influenced by, prey and competitor behaviours. Jaguars (*Panthera onca*), pumas (*Puma concolor*) and ocelots (*Leopardus pardalis*) coexist throughout their geographic range as the three largest predators in a multi-predator community across diverse environments. This study tested for non-random segregation and overlap in the activity patterns of these felids and their shared prey in the southern buffer zone of the Calakmul Biosphere Reserve, in southern Mexico, using camera traps during February to August 2019. We detected little temporal segregation between the nocturnal activities of jaguars, pumas, and ocelots, although pumas were more active closer to dawn. Jaguars had low activity overlap with species likely to be common prey, whereas ocelots had high overlap with their potential prey. Pumas displayed finer-scale similarities in activity with species likely to be common prey. In an understudied area of conservation importance, this study shows that temporal segregation is an unlikely mechanism of coexistence. Further research should incorporate spatio-temporal avoidance and dietary differences to improve our understanding of the mechanisms that drive coexistence between generalist species in a diverse assemblage of threatened felids.

Key words: activity patterns; community; competition; jaguar; ocelot; puma; predator-prey

Received: ; Revised: ; Accepted: .

1. Introduction

The activity patterns of terrestrial carnivores are influenced by a number of factors, including niche partitioning amongst their competitors (Hayward & Slotow, 2009; Lucherini *et al.*, 2009; Durant *et al.*, 2010; Karanth *et al.*, 2017), but also behavioural overlap with their prey (Linkie & Ridout 2011, Ramesh *et al.* 2012, Foster *et al.* 2013, Azevedo *et al.* 2018, Vilella *et al.* 2020). Many carnivores coexist with other predators that fill similar dietary and habitat niche dimensions, and are subject to intra-guild competition (Fedriani *et al.*, 2000; Durant *et al.*, 2010). Behavioural and morphological adaptations can minimize the potential for negative interactions amongst such competitors (St-Pierre *et al.* 2006, Hunter & Caro 2008, Sánchez-Barradas & Villalobos, 2020), by separating their niches along a behavioural dimension (Hutchinson, 1959). For sympatric carnivores, substantial differences in body mass and the subsequent size of prey selected can facilitate coexistence (Kiltie, 1984; Karanth & Sunquist, 1995; Rosenzweig, 1996; Hayward, 2006), whereas subdominant carnivores may occupy an opportunistic niche that maximises resource use whilst minimising competitive encounters (Ramesh *et al.*, 2012). In this study, we investigate whether the coexistence of three large predators in an understudied, but critical, area for conservation could be simply facilitated by differences in activity patterns that also relates to the activity patterns of known key prey species.

Amongst Neotropical terrestrial predators, jaguars (*Panthera onca*), pumas (*Puma concolor*), and ocelots (*Leopardus pardalis*) are the three largest felids in a more diverse multi-predator community, where jaguars are typically the dominant competitor (Elbroch & Kusler, 2018), and ocelots dominate within the mesopredator community (Oliveira *et al.*, 2010). The mechanisms potentially facilitating coexistence include selection for different prey (Farrell, *et al.*, 2000; Scognamillo *et al.*, 2003; Novack *et al.*, 2005; De Azevedo, 2008; Foster *et al.*, 2010) and spatio-temporal variation in space use (Harmsen *et al.*, 2009; Romero-Muñoz *et al.*, 2010; Herrera *et al.*, 2018). All three felids select for similar habitats and spatial segregation alone is not thought to be a strong coexistence mechanism (Di Bitetti *et al.*, 2010; Boron *et al.*, 2018; Massara *et al.*, 2018). Ocelot occupancy can even increase in areas of high jaguar occupancy (Davis *et al.*, 2011). Some dietary differentiation occurs between species, most notably with ocelots which, at 20% of the body mass of the large felids, select for small prey including rodents, opossums, and reptiles (Emmons, 1987; Villa Meza *et al.*, 2002; Bianchi *et al.*, 2014). In certain contexts, coexistence between the similar sized jaguar and puma can be facilitated by selecting for different prey within a common pool of prey species (Foster *et al* 2010). In Belize, jaguars select armadillo and peccary (white-lipped and collared), while pumas select paca and deer, although both predators will eat all of these species (Foster *et al.* 2010).

Temporal segregation has been recorded between jaguars and pumas in some regions (Monroy-Vilchis *et al.*, 2009; Romero-Muñoz *et al.*, 2010), and is considered to be a mechanism for reducing interactions and competition between morphologically similar species (Di Bitetti *et al.*, 2010). Alternatively, when activity patterns are similar, differences in prey species consumed may drive coexistence (Foster *et al.*, 2010; Harmsen *et al.*, 2011). Activity patterns of ocelots may reflect adaptations both for efficient predation and avoidance of larger competitors (Emmons, 1987), although it is difficult to un-confound these two factors. However, ocelots have been shown to increase nocturnal behaviour in response to higher puma densities which suggests avoidance behaviour (Massara *et al.*, 2012).

Activity patterns of predators can show high overlap with activity of the prey species they select for in a local area (Emmons *et al.*, 1989; Di Bitetti *et al.*, 2006; Harmsen *et al.*, 2011; Foster *et al*,. 2013; Pratas-Santiago *et al.*, 2016; Herrera *et al*., 2018). For example, jaguars shift activity patterns from nocturnal to diurnal when switching from wild to domestic prey (Rabinowitz & Nottingham, 1986). The activity patterns of jaguars and pumas vary considerably within and amongst study areas. Both species have shown predominantly nocturnal activity in Central and Western Mexico (Monroy-Vilchis *et al.*, 2009; Núñez *et al.*, 2002), in Cockscomb Basin Belize (Harmsen *et al.*, 2009; Harmsen *et al.*, 2011) and in the Venezuelan llanos (Scognamillo *et al.*, 2003) and Corcovado and Santa Rosa National Parks in Costa Rica (Herrera *et al*., 2018). They are reported as crepuscular in four biomes of Brazil (Foster *et al.*, 2013) and in the Gran Chaco, Bolivia (Maffei *et al.*, 2004); as diurnal in Pantanal, Brazil (Crawshaw & Quigley, 1991) and in Blue Creek in Belize (Dobbins *et al.*, 2018); and as active all day and night in Pantanal, Brazil (Schaller & Crawshaw, 1980). These differences are likely influenced by differences in prey community compositions, seasonal availability of prey, and human disturbance. In contrast, ocelots and their small-bodied prey (i.e., rodents and opossums) are typically nocturnal across their range (Emmons *et al.*, 1989; Di Bitetti *et al.*, 2006; Pratas-Santiago *et al.*, 2016).

The Calakmul Biosphere Reserve (CBR) in the Yucatan Peninsula, contains the largest expanse of tropical forest in Mexico, connecting to south to the forests of Central America. Although there are no recent studies of the ecology of felids in CBR, evidence suggests that it holds stable populations of large felids (Ceballos et al, 2002; Chavez, 2010; Rodriguez-Soto et al, 2011). The area presents an opportunity to study felid ecology in a vast and relatively undisturbed ecosystem that is understudied relative to its conservation importance. Recent encroachment by humans, however, raises the urgency of setting a knowledge baseline for felid ecology and coexistence mechanisms in this region, for monitoring future ecological disturbances if the reserve becomes further encroached by humans. Here, we analysed the activity patterns of jaguars, pumas, and ocelots in the CBR, and we specifically tested for evidence of temporal segregation between felids, and temporal overlap with other co-occurring species that are potential prey. This is the first study of circadian activity patterns of the three felids and their prey in the CBR.

2. METHODS

1. Study Site

The study was conducted in the southern buffer zone of the CBR, in southern Campeche (18^{o}08'-18^{o}38'N, 89^{o}31'-89^{o}44'W) on the Yucatan Peninsula, Mexico (Fig. 1). The study site is situated within tropical semi-deciduous forest which is the primary forest type across the CBR (Martínez & Galindo-Leal, 2002). The wider CBR, comprises 723,185 ha, lies within a larger network of protected forests that covers 10.6 million ha of connected forest within Mexico, Belize and Guatemala (Vester *et al*., 2007). Water availability is highly variable between and within years, and is typically limited to temporary ponds, known as aguadas, during the dry season, which extends from April to November (Reyna-Hurtado *et al*., 2010; Reyna-Hurtado *et al*., 2019).

2. Data collection

A total of 36 passive infrared digital cameras activated by a heat-motion sensors (Bushnell Trophy HD, Cuddeback C1, and Browning Strike Force Extreme) were positioned on and off trails, individually or in pairs, with a total of 27 camera-trap stations in 2019. The camera-trap grid followed the standardised design of the 'National Census of the Jaguar and its Prey' (CENJAGUAR; Chávez *et al.,* 2007), whereby nine contiguous 3×3-km cells, totalling an area of 81 km^2, within our study site were each assigned three camera stations, with one positioned next to an aguada if present, and all stations separated by a minimum of 1 km (Fig 1).

Cameras were positioned on trees ~50cm off the ground and set to take a burst of three photos whenever activated across the 24-hour period. Data were collected continuously from February to August 2019, avoiding the peak rainy season after August to prevent camera damage from flooding. The cameras were checked once each month to verify their functioning and change the SD card and/or batteries as necessary. Cameras were active 183 days, making a total sampling effort of 4,941 camera-trap days. Animals in photos were identified to species with reference to field guides (Reid, 2006) and species identification and other metadata (e.g., time and date) encoded for using Timelapse software (Version 2; Greenberg, 2018).

To avoid pseudoreplication, each photographic record of a species was treated as an independent event if separated by at least 30 minutes from a capture of the same species at the same camera-trap station (Sollmann, 2018). Where possible, we identified jaguars and ocelots by cataloguing the spot pattern shown on both flanks in photographs a pair of cameras. This allowed to understand the minimum number of individuals that the activity patterns were based upon for these two species.

3. Potential prey species

Based on previous dietary studies and observed predation events in the CBR and the Yucatan Peninsula (Aranda & Sánchez-Cordero, 1996; Ávila-Najera *et al*,, 2018; Piña-Covarrubias, 2019; Pérez-Flores *et al.*, 2020), we considered 10 species that are potential prey for at least one of jaguars, pumas, or ocelots in the CBR for which we had sufficient sample sizes for analysis (see Table S1 for full details): Baird’s tapir (*Tapirus bairdii*), collared peccary (*Pecari tajacu*), brocket deer (*Mazama* sp.), white-tailed deer (*Odocoileus virginianus*), ocellated turkey (*Meleagris ocellata*), great curassow (*Crax rubra*), white-nosed coati (*Nasua narica*), paca (*Cuniculus paca*), agouti (*Dasyprocta punctata*), and common opossum (*Didelphis* *virginiana*). Low sample sizes (*n* < 20 independent capture event) for nine-banded armadillo (*Dasypus novemcinctus*) and white-lipped peccary (*Tayassu pecari*) precluded their inclusion. Common prey species for jaguars and pumas in the Yucatan Peninsula are frequently document as being medium-large prey, which are primarily ungulates. There have been no published diet studies of ocelots from the Yucatan Peninsula, so we use studies from outside of this area (Villa-Meza et al., 2002; Moreno et al., 2006; Aliaga-Rossel et al., 2006). While we accept this reduces the robustness of our inferences of ocelot prey within the Yucatan Peninsula, we use this information to infer potentially common prey species where smaller prey, including agoutis, pacas, and common opossums, are typically the most common prey of ocelots.

4. Statistical analysis

Activity patterns for each species were classified by the proportion of activity records detected at different periods of the day, as in Foster *et al.* (2013). Species were classified as: diurnal if activity records predominantly occurred between an hour after dawn (06:30 h) and an hour before dusk (19:00 h); nocturnal if activity records predominantly occurred between an hour after dusk and an hour before dawn; crepuscular if activity records predominantly occurred an hour either side of dawn and dusk; and cathemeral if evenly distributed across the 24-hour cycle.

Species specific activity patterns were estimated with non-parametric kernel densities, using the ‘*densityPlot*’ function in the ‘*Overlap*’ package (Meredith *et al*., 2018). Overlap in activity patterns amongst felids and between felids and their prey was estimated using the ‘*overlapEst*’ function to calculate an overlap coefficient (Δ) that ranged from 0 (no overlap) to 1 (complete overlap). Alternative versions of this coefficient were used, depending on sample sizes: Δ_1 for < 50 activity records, and Δ_4 for ≥ 50 activity records, as recommended by Meredith *et al*. (2018). A confidence interval (CI) was calculated for each pairwise activity overlap by bootstrapping the original sample 1,000 times. Finally, a Mardia-Watson-Wheeler (MWW) test was applied to each pair-wise comparison amongst felid species, and felid with prey species, to identify whether the pair shared a similar temporal distribution of activity.

All analyses were run in R version 4.0.3 (R Core Team, 2017). Data and codes used for statistical analyses and production of figures are available on GitHub.

RESULTS

The study period yielded a total of 2,616 independent camera-trap records of predator and prey species. The dataset included 95 jaguar, 85 puma, and 117 ocelot records. Sample sizes were generally higher and more variable for prey species, with 94 tapir, 136 collared peccary, 101 brocket deer, 478 white-tailed deer, 260 agouti, 239 coati, 23 paca, 37 common opossum, 578 great curassow, and 373 ocellated turkey records. We identified 12 jaguars, including two females, seven males, and three individuals that we could not identify their sex, and 17 ocelots, including five females, 11 males, and one individual that we could not identify their sex.

1. Species activity patterns

Jaguars, pumas, and ocelots displayed nocturnal behaviours with some crepuscular tendencies (Table 1; Fig. S1). Jaguars and ocelots had activity peaks in the middle of the night, whereas pumas had the greatest activity peak closer to dawn. Amongst prey species tapir, opossums, and paca had nocturnal behaviours with peaks in the middle of the night, whereas brocket deer showed a cathemeral behaviour Table 1; Fig. S1). All other prey species showed diurnal behaviours with peaks in activity closer to dawn and/or dusk, other than coatis which displayed an activity peak at midday.

2. Species activity overlap

All three felids showed high overlap in their nocturnal activity patterns (Figs 2 and 3; jaguars and ocelots: $\Delta_4 = 0.87$ CI: 0.77-0.93; jaguars and pumas: $\Delta_4 = 0.75$, CI: 0.62-0.85 pumas and ocelots: $\Delta_4 = 0.77$, CI: 0.63-0.86). Activity patterns of jaguar and ocelot were indistinguishable with near identical peaks in activity (MWW test: $W = 0.15$, $p = 0.93$; $\Delta_4 = 0.87$), although both differed detectably from puma (jaguar and puma: $W = 11.8$, $p = 0.002$; ocelot and puma: $W = 8.9$, $p = 0.02$).

The proportion of activity overlap between jaguars and potential prey was high only for nocturnal species (Figs 3 and 4), including tapir ($\Delta_4 = 0.81$, CI: 0.69-0.89) and common opossums ($\Delta_4 = 0.75$, CI: 0.62-0.85), which were likely only incidental prey for jaguars (Table S1). These nocturnal mammals had indistinguishable activity patterns from jaguar (tapir: $W = 4.97$; $p = 0.08$; opossum: $W = 4.8$; $p = 0.09$). Activity overlap with jaguar was relatively high for brocket deer ($\Delta_4 = 0.69$, CI: 0.56-0.79) and paca ($\Delta_4 = 0.61$, CI: 0.47-0.74), and relatively low for collared peccary ($\Delta_4 = 0.48$, CI: 0.39-0.58) as well as for diurnal species, which were likely more common prey for jaguar.

Compared to jaguars, pumas had higher activity overlap with potential prey that had more diurnal tendencies and were likely to be common prey (Figs 3 and 4; Table S1). Puma activity overlapped most with brocket deer ($\Delta_4 = 0.83$, CI: 0.56-0.79) and was indistinguishable from their activity patterns ($W = 1.99$, $p = 0.36$). Activity overlap with puma was also relatively high for paca ($\Delta_4 = 0.65$, CI: 0.52-0.76), opossum ($\Delta_4 = 0.67$, CI: 0.55-0.78), white-tailed deer ($\Delta_4 = 0.64$, CI: 0.54-0.73), and tapir ($\Delta_4 = 0.71$, CI: 0.69-0.89).

The proportion of activity overlap between ocelots and potential prey involved high overlap with nocturnal species (Figs 3 and 4), including common opossums ($\Delta_4 = 0.78$, CI: 0.65-0.87) and relatively high for paca ($\Delta_4 = 0.65$, CI: 0.51-0.76), both of which were likely common prey (Table S1). For both paca and common opossums, activity patterns were indistinguishable from those of ocelots (paca: $W = 6.00$, $p = 0.05$; common opossum: $W = 6.1$, $p = 0.05$).

DISCUSSION

Ecological niche segregation between felids typically occurs in spatial, temporal, or dietary dimensions, or some combination of these (Crashaw & Quigley, 1991). In our study, we found that temporal segregation was not a clear driver of coexistence and that, for jaguars at least, activity patterns did not coincide with species that are likely to be key prey. In highly disturbed protected areas of the Northern Yucatan Peninsula, Piña-Covarrubias (2022) likewise found no temporal segregation between the nocturnal jaguar and puma and no major overlap with the activity patterns of their main prey. In contrast, Ávila-Najera *et al* (2016) in the Selva Maya, and Harmsen *et al*. (2011) in Belize, detected activity overlap of nocturnal jaguars and pumas with their prey. Similarly, in Northern Mexico, jaguars and pumas were mainly nocturnal, and their activity patterns overlapped with those of deer and domestic cow calves (Gutiérrez-González & López-González, 2017).

We did not detect a trend of temporal segregation between these three nocturnal predators which contrasts to some studies across their range where temporal segregation is strong, including in southern Bolivia (Romero-Munoz *et al*., 2010) and in the Paraguayan Chaco (Taber *et al.*, 1997). However, fine-scale differences in activity patterns were detected, particularly between morphologically similar jaguar and puma. Although pumas and jaguar were both nocturnal, pumas presented a higher activity peak closer to dawn, which reduced activity overlap with jaguars. This difference in activity patterns caused pumas to have a higher overlap with potential prey species than did jaguars, particularly with peccary, that were previously reported as main prey of jaguars. Such fine-scales differences in activity patterns could play a key role in facilitating the coexistance of predators in the CBR (Di Bitetti *et al*., 2010; Herrera *et al.*, 2018), but further research is required. Such trends were also found in Costa Rica (Herrera *et al*., 2018) and in Belize (Davis et al., 2011) with almost identical activity patterns between the jaguars and ocelots, but with differences in activity patterns being greater between these two felids and pumas as the intermediate sized felid.

The near identical activity peaks of jaguars and ocelots suggests that trophic segregation determines their coexistence, which could be assumed based on large morphological differences driving distinct prey preferences (Emmons 1987, Farrell *et al*., 2000, Herrera *et al.*, 2018). Ocelot activity overlapped highly with common opossums, a nocturnal species that has the potential to be a main prey species. However, jaguars did not strongly overlap their activity patterns with their reported preferred prey of collared peccary. They did overlap with the activity of tapirs, which jaguars have been observed hunting in the CBR (Pérez-Flores *et al*., 2020), 2020), and to a lesser extent brocket deer. This could suggest differences in preferred prey in the CBR to what was previously observed (Aranda & Sánchez-Cordero, 1996), but it could also indicate that jaguars were not necessarily detected during periods of active hunting because tapir and opossums are unlikely to be common prey. The near identical activity patterns of jaguars and ocelots could potentially increase mortality risk for ocelots, although evidence remains scarce (ocelot remains in jaguar scats: Gonzalez-Maya *et al*., 2010; hunting of an ocelot by a jaguar observed directly: Perera-Romero *et al.*, 2021). Further research into spatio-temporal avoidance of jaguars by ocelots could reveal further mechanisms that facilitate their co-existence in the CBR.

Our results contribute to this growing body of evidence that mechanisms of coexistence vary considerably throughout the geographic range of these felids but also that behaviour of felids can be similar within vast stretches of habitat compared to smaller reserves (Piña-Covarrubias *et al.,* 2019). We conclude that temporal and trophic segregation, the latter implied through differences in overlap with shared prey, were not strong mechanisms determining coexistence of felids in the CBR. Further research on this community of predators and their prey should add the spatial to the temporal dimension, which in combination are suggested mechanisms of coexistence elsewhere (Foster *et al*., 2013; Porfirio *et al*., 2016; Gutierrez-González & Lopez-González, 2017). In the meantime, we rule out temporal segregation as a means of coexistence between predators, which informs understanding and conservation of these species within the CBR, a key area of conservation in Central America.

TABLE 1. *Sample size (n) of independent records for each species, with the proportion of diurnal, nocturnal, and crepuscular records. Activity schedule is based on the proportion of activity records (diurnal >50% records during the day; nocturnal >50% of records during the night; cathemeral <50% records falling within any day, night, dusk, and dawn period).*

Species	*n*	*Diurnal*	*Nocturnal*	*Dusk/Dawn*	*Activity schedule*
Felids					
Jaguar	95	0.19	0.63	0.18	Nocturnal
Puma	85	0.25	0.52	0.24	Nocturnal
Ocelot	117	0.12	0.64	0.24	Nocturnal
Large mammal prey (>15kg)					
Tapir	94	0.03	0.82	0.15	Nocturnal
Collared peccary	136	0.59	0.15	0.26	Diurnal
Brocket deer (sp.)	101	0.33	0.44	0.24	Cathemeral
White-tailed deer	478	0.61	0.16	0.23	Diurnal
Small mammal prey (<15kg)					
Agouti	260	0.61	0.03	0.37	Diurnal
Coati	239	0.84	0.03	0.13	Diurnal
Paca	23	0	0.91	0.09	Nocturnal
Common opossum	37	0	0.92	0.08	Nocturnal
Terrestrial birds					
Great curassow	578	0.62	0.01	0.38	Diurnal
Ocellated turkey	373	0.69	0.03	0.28	Diurnal

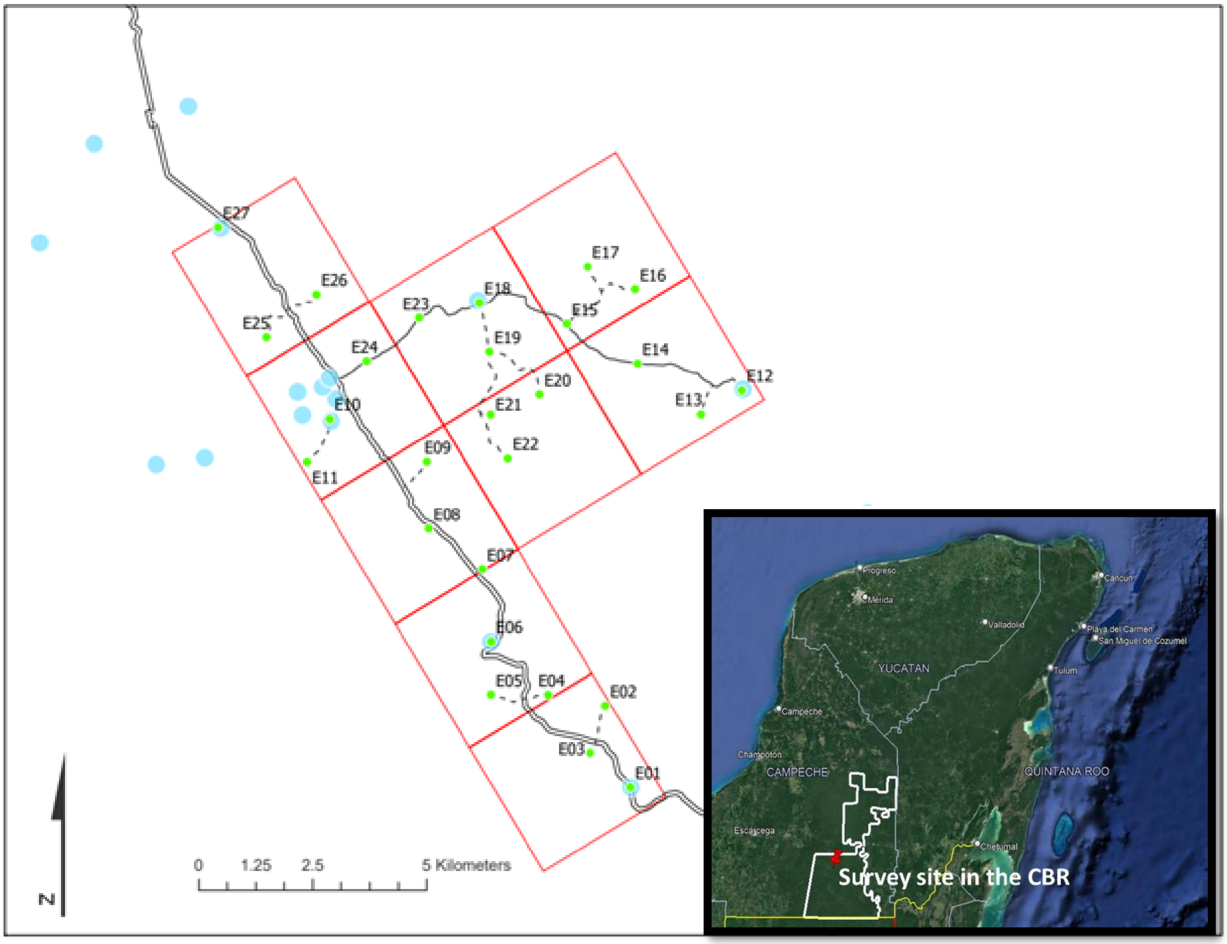

FIGURE 1. *The study area located in the Calakmul Biosphere Reserve, showing the nine 3×3 km cells (red squares) and locations within them of camera-trap stations (small green dots), temporary water bodies (i.e. temporary ponds "aguadas"; large blue dots), roads (double line), access roads (single line) and tracks (dotted line). Stations E1, E4, E6, E8, E10, E11, E13, E15, E17, E18, E20, E22, E25 and E26 were double camera station and the rest were single. Some tracks were made to set the cameras, others were pre-existing. The inset map shows the location of the study site (red pin) within the wider Calakmul Biosphere Reserve (white outline) in the Yucatan Peninsula, Mexico, taken from Google Earth.*

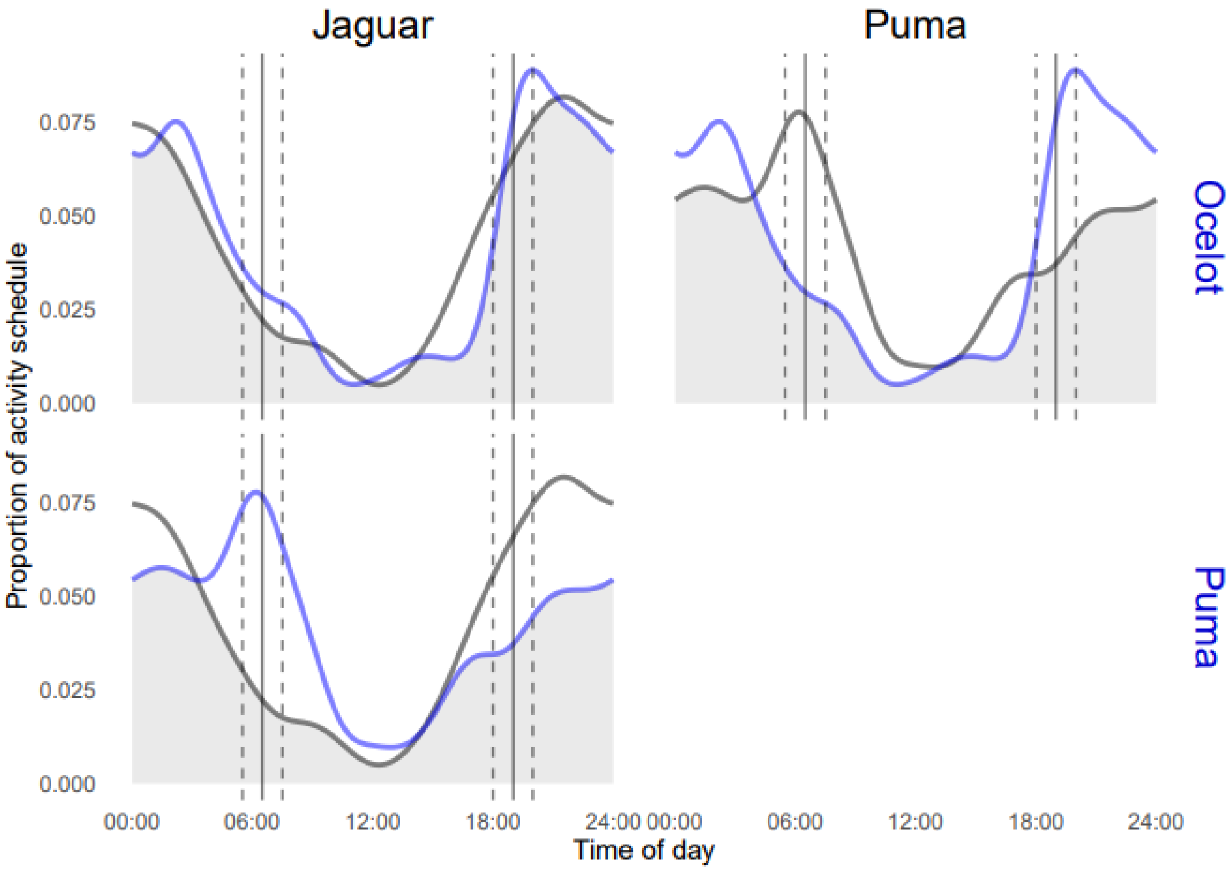

Figure 2. *Activity patterns of predators in the Calakmul Biosphere Reserve. Pairwise comparisons of species activity overlap are shown in each figure with the identity of each activity pattern for each predator indicated by colour, and overlap in grey shading. Dawn and dusk are shown (vertical, solid lines) with 30-minute seasonal variation around these time periods (vertical, dashed lines).*

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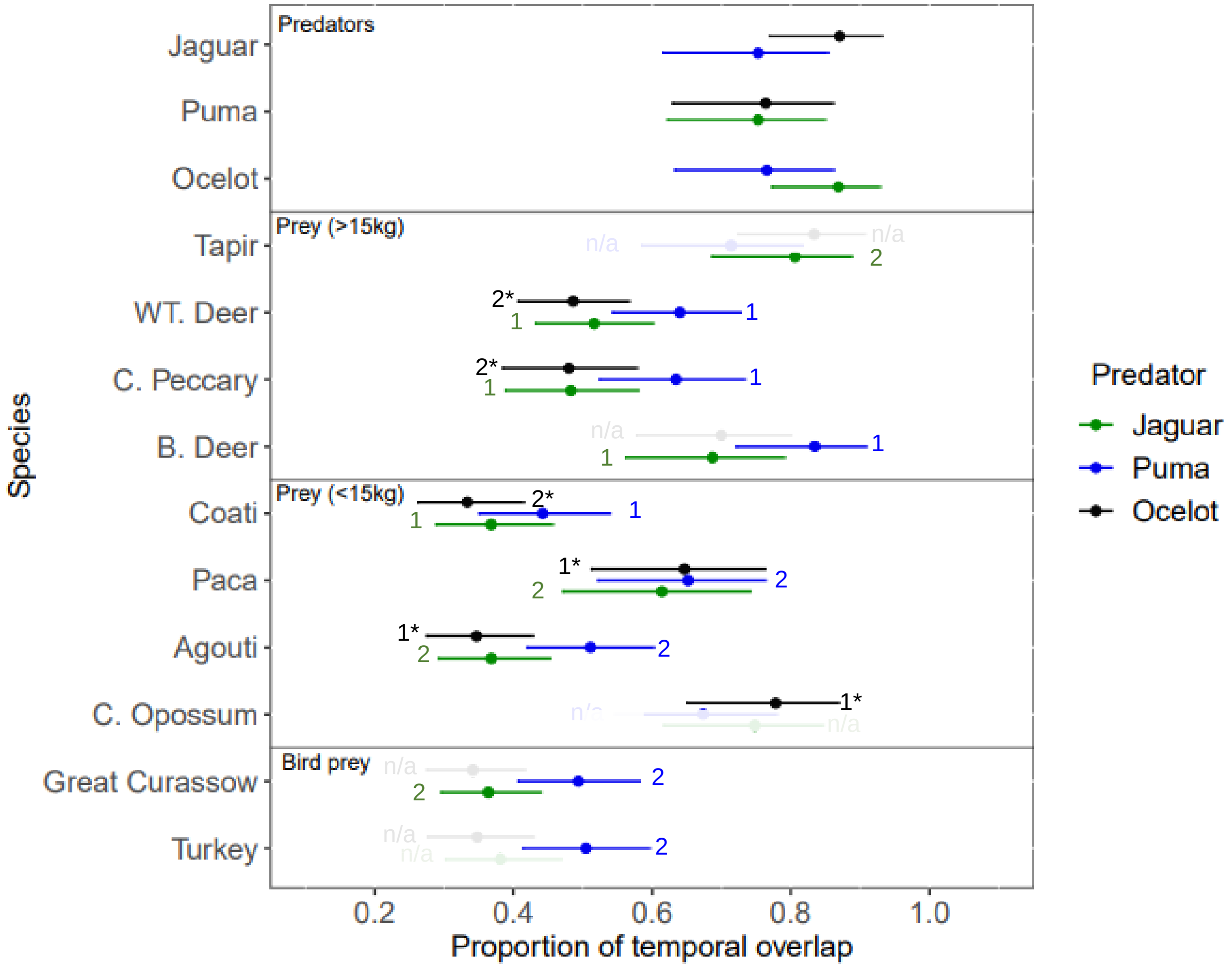

FIGURE 3. *Overlap in activity patterns between y-axis species and jaguar (dark green), puma (blue), and ocelot (black). Bars represent 95% confidence intervals in the estimation of activity overlap after bootstrapping kernel density estimates from activity records 1,000 times. Numbers (and n/a) next to bars indicate potential importance rankings of each prey to each predator, based upon jaguar and diet studies in the Yucatan Peninsula (Aranda & Sánchez-Cordero, 1996; Piña-Covarrubias, 2019;* Ávila–Nájera et al 2018*), whereby 1 = potential common prey; 2 = occasional or at least documented potential prey; n/a = prey not documented.*

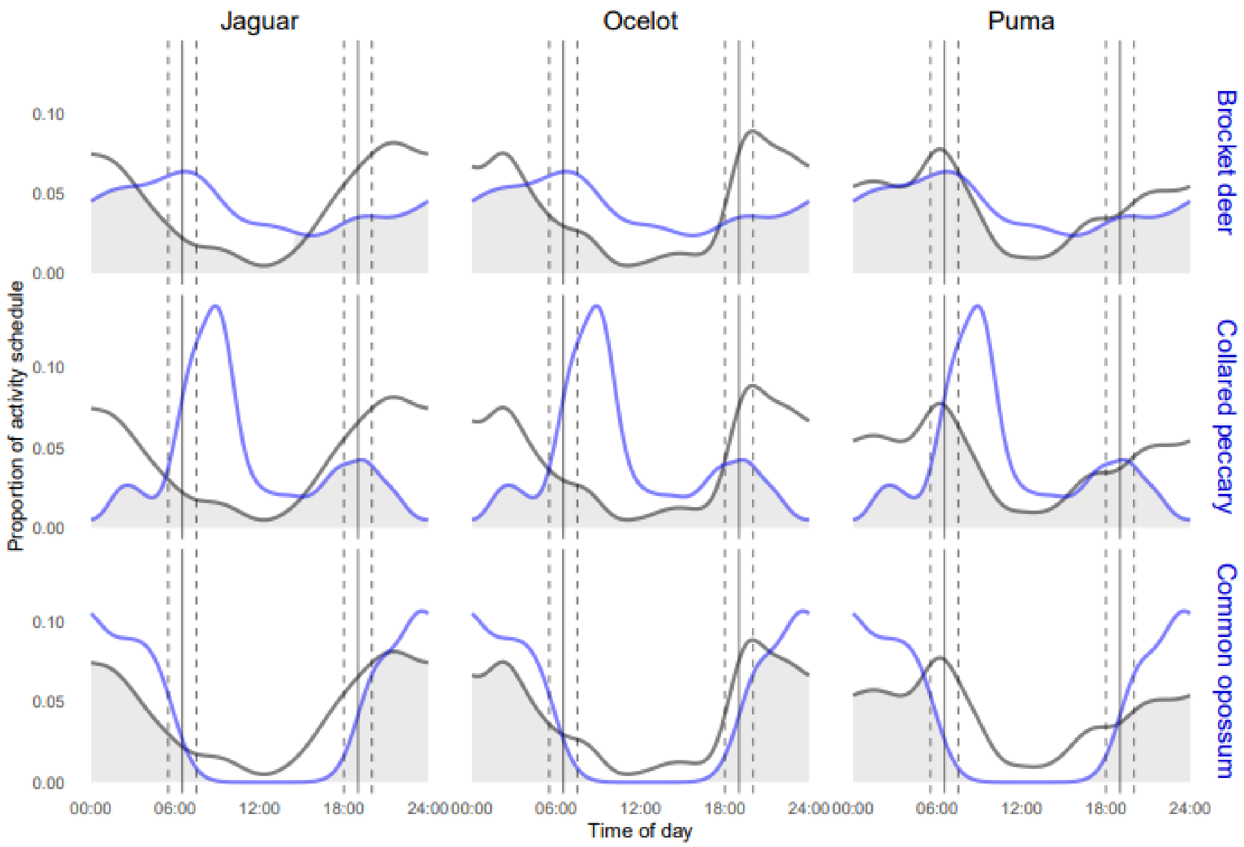

FIGURE 4. *Activity patterns of predators (black) and three representative potential common prey species (blue). Grey shading shows overlap in pairwise species activity patterns; dawn and dusk are shown (vertical, solid lines) with 30-minute seasonal variation around these time periods (vertical, dashed lines). Prey species were chosen as they are likely common prey species of jaguars (collared peccary) and pumas (brocket deer) and common ocelots (opossums).*

ACKNOWLEDGEMENTS

Data collected for this study was approved by the Mexican federal government with research permits awarded to Pronatura Peninsula de Yucatan (PPY) in collaboration with Operation Wallacea. We thank Patricio Canul Chuc from PPY, David Sima-Panti, and all personnel from CONANP working at the CBR for assistance with fieldwork, and Dr Evelyn Piña-Covarrubias for contributing camera traps and scientific advice. We also thank Operation Wallacea for logistical support with field work. We are very grateful to Dr. Lon Grassman for his comments on the draft and Luis P. Pratas-Santiago for comments on earlier drafts. This study was supported by grants to C. A. V. from the Rufford Foundation and Mexico's Consejo Nacional de Ciencia y Tecnologia (CONACyT) Becas al Extranjero programe.

DISCLOSURE STATEMENTS

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

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