



Circadian activity patterns of mammalian predators and prey in Costa Rica

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Temporal niche shifts can shape predator–prey interactions by enabling predator avoidance, enhancing feeding success, and reducing competition among predators. Using a community-based conservation approach, we investigated temporal niche partitioning of mammalian predators and prey across 12 long-term camera trap surveys in the Pacific slope and Talamanca Cordillera of Costa Rica. Temporal overlap and segregation were investigated between predator–prey and predator–predator pairs using overlap analysis, circular statistics, and relative abundance after accounting for differences in habitat, season, and human impact among sites. We made the assumption that predators select abundant prey and adjust their activity to maximize their temporal overlap, thus we predicted that abundant prey with high overlap would be preferred prey species for that predator. We also predicted that similar-sized pairs of predator species with the greatest potential for competitive interactions would have the highest temporal segregation. Our results supported the existence of temporal niche separation among the eight species of predators—the smaller *Leopardus* felids (ocelot, margay, oncilla) were primarily nocturnal, the largest felids (jaguar and puma) and coyote were catemeral, and the smaller jaguarundi and tayra were mostly diurnal. Most prey species (67%) were primarily nocturnal versus diurnal or catemeral (33%). Hierarchical clustering identified relationships among species with the most similar activity patterns. We discuss the primary prey and competitor species predicted for each of the eight predators. Contrary to our prediction, the activity pattern of similar-sized intraguild competitors overlapped more than dissimilar-sized competitors, suggesting that similar-sized predators are hunting the same prey at the same time. From this we conclude that prey availability is more important than competition in determining circadian activity patterns of Neotropical predators. Our results indicate the presence of a delicate balance of tropical food webs that may be disrupted by overhunting, leading to a depauperate community consisting of ubiquitous generalists and endangered specialists. With Central America a hotspot for hunting-induced “empty forests,” community-based conservation approaches may offer the best road to reduce illegal hunting and maintain the biodiversity and community structure of tropical forest systems.

Key words: activity overlap, camera trapping, Costa Rica, Neotropical mammals, predator–prey, relative abundance, Talamanca, temporal niche shift, Temporal segregation

Los cambios temporales de nicho pueden amoldar las interacciones predador-presa al permitir a la presa evadir los predadores, mejorar la eficacia de la alimentación y reducir la competición entre predadores. Mediante

muestreos con cámaras trampa en 12 sitios de la pendiente del Pacífico y la Cordillera de Talamanca de Costa Rica, investigamos la división temporal de los nichos de mamíferos predadores y presas usando un enfoque de conservación basado en la comunidad. Investigamos la superposición y segregación temporal entre pares predador-presa y predador-predador utilizando análisis de superposición, estadísticas circulares y abundancia relativa, teniendo en cuenta diferencias de hábitat, estacionales y de impacto humano entre los sitios. Asumimos que los predadores seleccionan presas abundantes y ajustan su actividad para maximizar su superposición temporal con éstas; por lo tanto, predijimos que una presa abundante con alta superposición sería una especie de presa preferida para ese predador. También predijimos que pares de especies de predadores de tamaño similar con el mayor potencial para interacciones competitivas tendrían la mayor segregación temporal. Nuestros resultados respaldaron la existencia de una separación temporal de nicho entre las ocho especies de predadores—determinamos que los felinos más pequeños del género *Leopardus* (manigordo, caucel, tigrillo) son principalmente nocturnos, los felinos más grandes (jaguar y puma) y el coyote son catemerales, y los jaguarundi y tayra más pequeños son principalmente diurnos. La mayoría de las especies de presas (67%) son principalmente nocturnas versus diurnas o catemerales (33%). Mediante análisis de agrupación jerárquica, identificamos relaciones entre especies con los patrones de actividad más similares. Para cada uno de los predadores discutimos las presas primarias predichas y las especies competidoras. Contrario a nuestra predicción, el patrón de actividad de los predadores intragremios de tamaño similar se superpone más que el de los competidores de distinto tamaño, lo que indica que los predadores de tamaño similar están cazando la misma presa y están activos al mismo tiempo. De esto concluimos que la disponibilidad de presas es más importante que la competición en cuanto a determinar los patrones de actividad circadiana de los predadores neotropicales. Nuestros resultados revelan que el delicado equilibrio de las redes tróficas tropicales puede ser interferido por la caza excesiva, lo que lleva a una comunidad depauperada compuesta por generalistas ubicuos y especialistas en peligro de extinción. Con América Central como un centro de “bosques vacíos” inducidos por la caza, los enfoques de conservación basados en la comunidad pueden ofrecer el mejor camino para reducir la caza ilegal, y mantener la biodiversidad y estructura ecológica comunitaria de los sistemas forestales tropicales.

Palabras claves: abundancia relativa, cambio temporal de nicho, Costa Rica, foto-trampeo, mamíferos Neotropicales, predador-presa, segregación temporal, superposición de actividad, Talamanca

Time is a dimension of an animal's fundamental niche that may be modified to maximize fitness benefits, minimize fitness costs, or both. Activity patterns of animals are shaped by long-term evolutionary forces, but also exhibit flexible responses to short-term environmental change (Monterroso et al. 2013). Mammalian activity patterns thus have evolved to optimize the timing of behavioral decisions (Hayward and Slotow 2009; Monterroso et al. 2013; Pratas-Santiago et al. 2016). Temporal niche shifts (synonymous with temporal niche partitioning or switching) refer to how species time their activity patterns to coexist with other species, such as by reducing competition, enhancing feeding success, or avoiding predation (Frey et al. 2017; Mugerwa et al. 2017). Species may differentiate their niches in other ways, for example, by consuming different prey or using different parts of the environment (Castillo-Ruiz et al. 2012).

Temporal niche switching is a complex phenomenon driven by many physiological–neurobiological mechanisms and evolutionary factors (Hut et al. 2012). External biotic factors driving niche shifts include competition and predator–prey relationships (Hut et al. 2012). Temporal niche shifts may enable prey species to avoid times of increased predation risk and thereby shape predator–prey interactions (Castillo-Ruiz et al. 2012; Hertel et al. 2017). The first step in the predation sequence is “overlap”—before predators can hunt prey, predators and prey must occupy the same space at the same time (Guiden et al. 2019). Optimal foraging theory predicts that

animals will forage so as to maximize net energy intake minus costs (MacArthur and Pianka 1966). But in the predator–prey arms race, prey should avoid high-risk locations and dangerous times even when this compromises energy intake (Lima 2002; Eriksen et al. 2011). A guild is a group of species that overlap significantly in their niche requirements (Simberloff and Dayan 1991). Predator guilds of similar-sized carnivores are opportunistic and often prey on the same species (Foster et al. 2013), which should lead to competitive exclusion were it not for spatial or temporal niche partitioning (Valeix et al. 2007). Interspecific competition thus may select for niche partitioning to avoid interference competition and enhance hunting efficiency via optimal foraging (Cozzi et al. 2012).

In this study, we investigated temporal niche partitioning of Neotropical predators and their prey. A significant challenge to studies of Neotropical mammals is that these animals are elusive, avoiding human observation by nocturnal behavior or hiding (Thompson 2004; Sanderson and Trolle 2005). Predatory species at the top of the trophic pyramid are both elusive and rare. Automatically triggered trail cameras (“camera traps”) have emerged as the ideal solution to the problem of elusive mammals because they are triggered by changes in the movement and body heat of mammals even in the absence of human investigators (Karanth et al. 2004). We surveyed mammalian wildlife at multiple sites over a 10-year period using a community-based monitoring approach (Danielsen et al. 2014)—these were the first systematic camera trap surveys

initiated at these study sites. Using overlap analysis, circular statistics, and relative abundance measures, we investigated predation risk and then assessed intraguild competition using hierarchical clustering to objectively identify ecological relationships among species.

Two predictions were tested: (1) We made the assumption that predators would adjust their activity cycle to be active during the same time as abundant and profitable prey (based on size and hunting efficiency); we thus predicted that predators would preferentially select profitable prey with high abundance and shift their activity to increase their temporal overlap with those species; and (2) we assumed that predators would avoid intraguild predators with the greatest potential for competitive interactions (based on diet and morphological similarity) or the highest probability of intraspecific killing, resulting in greater temporal segregation from their strongest competitors (Di Bitetti et al. 2010; Herrera et al. 2018). These predictions may work against each other insofar as it may not be possible to maximize prey overlap while simultaneously minimizing overlap with competitors.

MATERIALS AND METHODS

Study area.—Our study was carried out predominantly within the tropical montane forest of Costa Rica's Talamanca Cordillera, but also included data gathered from lowland forests of the Pacific slope. Both lowlands and highlands are characterized by two distinct seasons; the dry season (December–April) and the wet season (May–November). Rainfall largely is dependent on location in the country, leading to a range of 300–800 cm average annual precipitation among our study sites. The average temperature in the highlands varies between 10 and 20°C depending on altitude and location; lowland temperatures average 24–32°C (Herrera 2004; CCSA 2019). We

worked in collaboration with national park officials and local community volunteers in national parks, private reserves, and biological corridors from June 2010 through August 2019 (Table 1). No major changes to protection status or environmental impacts occurred during the study; differences in human impact among the survey sites are discussed below. Our study was non-interventive and we followed ASM guidelines for research on wild mammals (Sikes et al. 2016).

Trail cameras.—Camera trapping is widely used to undertake surveys that inventory biodiversity, establish species' distributions, and estimate population abundance (Frey et al. 2017). Camera traps can provide insights about animal behavior and species interactions for mammalian predators and prey, providing a relatively unbiased record of species activity patterns (Karanth et al. 2004). We deployed camera traps in up to 12 survey sites per year, with camera stations consisting of a single or paired cameras (Table 1). Bushnell Trophy Cam units (Bushnell Corporation, Lenexa, KS) using a passive infrared sensor triggered by rapid changes in temperature of a passing mammal (Welbourne et al. 2016) were used for all photos. Under low light conditions, the cameras used an infrared flash, avoiding the “white flash” that may startle animals and result in avoidance behavior (Séquin et al. 2003; Gibeau and McTavish 2009; Meek et al. 2014; Meek et al. 2016; Srbek-Araujo et al. 2018). Cameras were positioned at 1–2 km intervals, primarily along established trail systems and access roads within protected areas, which often are used as travel highways (Harmsen et al. 2010). Additional information on camera trap methodology was provided by Mooring et al. (2020).

Scent stations.—For most camera stations after 2012, we used a scent attractant (Calvin Klein's “Obsession for Men”; Calvin Klein Inc., New York, NY) to stimulate animals to stop and investigate, ensuring high photo quality for better species identification (Viscarra et al. 2011). Scent stations are widely

Table 1.—Camera trap surveys with mean number of camera stations, camera trap days, survey period, coordinates, elevation, and elevation type.

Study site (abbreviation)	Camera Stations ^a	Camera Days	Start Date	End Date	Latitude	Longitude	Elevation (m)	Elevation Type ^b
Alexander Skutch Biological Corridor (CoBAS)	6 (4–9)	3978	7/3/2012	3/30/2015	9.5633	-83.7839	338–888	Lowland
Bosque de Agua Biological Corridor (CoBBA)	4 (4)	606	6/21/2016	2/19/2017	9.2650	-83.4210	851–1672	Low/ Mid/ High
Cabo Blanco National Park (PNCB)	6 (6)	2041	7/17/2015	8/25/2018	9.5820	-85.1010	63–321	Lowland
Carara National Park (PNC)	3 (3)	653	9/26/2014	4/17/2019	9.7984	-84.5979	28–64	Lowland
Proyecto Campanario Biological Station (PC)	8 (8)	1585	7/16/2016	8/27/2017	8.6397	-83.7226	62–158	Lowland
Chirripó National Park (PNCH)	11 (6–14)	6658	6/26/2012	7/8/2019	9.4599	-83.5619	2308–3464	Highland
El Copal Private Reserve (ECR)	2 (2)	707	1/8/2013	9/17/2016	9.7804	-83.7546	1158–1225	Midland
La Amistad International Park (PILA)	17 (5–26)	7164	5/30/2017	6/25/2019	9.0539	-82.9876	2086–2308	Highland
La Congreja National Park (PNLC)	4 (4–5)	4820	10/24/2014	5/30/2019	9.7001	-84.3921	338–584	Lowland
La Marta National Wildlife Refuge (LMR)	3 (3)	1733	7/20/2013	4/26/2015	9.7685	-83.6823	747–1000	Lowland
Tapantí Macizo de la Muerte National Park (PNTMM)	16 (10–20)	9619	6/18/2012	9/17/2018	9.7068	-83.7793	1506–2803	Highland
Savegre Valley / Los Quetzales National Park (PNLQ)	14 (9–31)	20,355	6/29/2010	8/16/2019	9.5502	-83.7911	2112–3118	Highland
Total = 12 Sites	94 (64–131)	59,919	6/29/2010	8/16/2019				

^aNumber of camera stations is the mean (range) of stations deployed during a sampling period, with stations made of one or two cameras. For example, during summer 2010 there were 10 camera stations operating in the Savegre Valley, but 31 stations in summer 2011.

^bElevational categories: Lowland <1000 m, Midland 1000–1500 m, Highland >1500 m.

used to increase photo quality for studies aimed at species identification (Conner et al. 1983; Travaini et al. 1996; Weaver et al. 2005; Barea-Azcón et al. 2007; Thorn et al. 2009; Randel and Peace 2010) without impacting temporal activity, distance traveled, or total photographic captures (Braczkowski 2016). Scent station methodology was discussed by Mooring et al. (2020).

Data analysis.—Images were loaded into Camera Base 1.7 (Tobler 2015). Only one independent event was recorded for each species observed within a 30-min time window. Collectively, we analyzed photographic records from a total of 59,919 camera trap days (Table 1).

The daily activity patterns of each species were fitted nonparametrically as kernel density functions, and the coefficient of overlapping (Δ) between each (Ridout and Linkie 2009) was estimated using the package “Overlap” (Meredith and Ridout 2020a, 2020b) in the R programming language (R Core Team 2018). The overlap coefficient is a measure of the similarity between two circular density curves, with values ranging from 0 (no overlap) to 1 (complete overlap). The overlap function assumes that animals are equally likely to be “trapped” throughout any period of their activity (Linkie and Ridout 2011). We used Dhat1 when the sample size was >20 and ≤ 75 , which was more conservative for small samples than the cutoff of ≤ 50 recommended by Ridout and Linkie (2009); we used Dhat4 for samples >75 as per Ridout and Linkie (2009). In calculating the overlap coefficient, we used a default bandwidth parameter of one to specify the “smoothness” of the kernel densities. Three different circular statistics were used to compare temporal distributions, because no single method is currently accepted as the standard.

The first statistic we report is Watson’s two-sample U^2 test with Ties (Zar 1999: section 27.6). A P -value for this statistic was calculated through a χ^2 approximation of the U^2 distribution (Tiku 1965). The second statistic we report is W_r , a uniform scores statistic (Fisher 1993: section 5.3.6), with P -values calculated according to the recommendations of Fisher (1993). The third statistical method we used was Fisher’s Exact Test (Upton 1992) with P -values calculated using 1,000 Monte Carlo replicates. Further details were provided by Mooring et al. (2020). All the R code used in this analysis and an interactive tool for exploring these analyses is available for review online at Github (<https://github.com/rbotts/OverlapAnalysis>).

Hierarchical clustering was used to identify groups of species occupying similar temporal niches using the Ward method on the square distances as described in Murtagh and Legendre (2014). The hierarchical clustering was based on overlap estimates, with overlap coefficients of all species pairs turned into measures of dissimilarity using $1 - \Delta$, with dissimilarity between the same species being 0. Hierarchical clustering groups species into successively larger groups with most similar temporal niches separated by the shortest branch lengths (Murtagh and Legendre 2014).

Influence of confounding factors.—Besides prey abundance and intraguild competition, circadian activity patterns might be influenced by differences in habitat, seasonal climate, or human impact among study sites (Di Bitetti et al. 2010). We

therefore explored whether these additional factors might influence temporal activity by comparing circadian activity patterns between seasons (wet versus dry), habitat (montane versus lowland tropical forest), and human impact (high versus low). To measure activity pattern, we used two measures: Activity level (Rowcliffe et al. 2014; Rowcliffe 2019) and percent nocturnal activity (%Night). For the seasonal comparison, dry season was defined to be from December to April, and wet season was from May to November. We used elevation as a surrogate for habitat, because all the high elevation sites are in montane tropical forest and all the low elevation sites are lowland tropical forest. Sites below 1,000 m were considered lowland (lowland rainforest), sites above 1,500 m were considered highland (montane tropical forest), and the mid-elevation sites (Bosque Agua, El Copal) were omitted (Table 1).

For human impact, we scored each study site on the relative level of protection based on protected area category, evidence of illegal hunters, vandalism of camera traps, volume of human traffic, and remoteness from roads and villages. Protected area categories represent a rough gradation in naturalness and “stringency of protection” that is associated with greater biodiversity (Dudley 2008; Di Bitetti et al. 2010; González-Maya et al. 2015; Nagy-Reis et al. 2019b). In Costa Rica, national parks may contain the greatest species richness compared with areas of lower protection status because they prohibit human alterations, whereas other protected area categories may allow resource extraction and other human activities (González-Maya et al. 2015; Sáenz-Bolaños et al. 2020). Based on the above-mentioned factors, we rated large, remote national parks with low human traffic and low evidence of hunting (PNCH, PILA, PNLQ) as high protection, while all other sites (PNCB omitted) were rated low protection.

We approached the analysis of factors influencing overall activity using two approaches. We first undertook bivariate comparisons using the nonparametric Mann–Whitney test (Siegel and Castellan 1988). In addition, because some factors are likely to covary (e.g., montane sites were larger and more remote than lowland sites), we fit Linear Mixed Models (LMMs) in which all three factors (habitat, season, protection) were included as fixed effects, with a random effect to control for species-specific differences. Separate models were built for “Activity” and “%Night” as the response variables. LMMs were fit with the lmer function of the lme4 library (Bates et al. 2011). Likelihood ratio tests were used to identify significant factors using the forward stepwise (“add-one”) model selection approach outlined in Zuur et al. (2009). We began with a minimal model having only species as a random effect and no fixed effects. We then assessed whether adding a particular fixed effect to the model resulted in a significantly better model fit via likelihood ratio tests. Extended models not significantly different indicated that a fixed effect had little predictive power on the response and were not added, while fixed effects that were significantly better were added to the model. We sequentially added one variable at a time, updating the best fit model until adding any additional fixed effect did not result in a significantly

better model fit. Significance thresholds of 0.05 were used for all tests.

Activity patterns and relative abundance.—To characterize activity patterns, records between sunrise and sunset were categorized as daytime, while records between sunset and sunrise were regarded as nighttime. In the tropics, the clock time of sunrise/sunset changes slightly over the course of the year depending on distance from the equator and time of year. For this reason, we used “sun time” rather than “clock time” to analyze day/night activity patterns (Nouvellet et al. 2012). Species were classified as diurnal (<10% of records at night), nocturnal (≥90% of records at night), mostly diurnal (10–29% of records at night), mostly nocturnal (70–89% of records at night), or cathemeral (30–69% of records at night), as per Azevedo et al. (2018). To account for successive changes of the sun’s position throughout the year (Nouvellet et al. 2012), we used the “sunTime” function of “overlap” version 0.3.2 as detailed below (Meredith and Ridout 2020a, 2020b). Additional details on these techniques were provided by Mooring et al. (2020).

Using these analytical tools, we compared circadian activity between all species of predators in our survey against all prey species with ≥ 27 records (so as to include margay and jaguarundi). Using these criteria, our cameras recorded a total of eight predator species and 16 prey species (Supplementary Data SD1). Because we did not have dietary data from scat samples or kills, we searched the literature for the prey species typically hunted by predators in our study. Typical prey species for each predator are listed in Supplementary Data SD2. Relative abundance index (RAI) is a standardized metric of how frequently a species appears on the cameras. We calculated RAI for each species from all survey sites using the equation:

$$\text{RAI} = [(\text{number of independent records}) \\ / (\text{number days camera was active})] * 1000.$$

Although the RAI assumes that capture rates are the same across species and sites, unequal probability of detection is common in camera trap surveys. To assess whether these assumptions were reasonable, we calculated the RAI for each camera station, and computed the mean and standard deviation of the RAI for cameras within a given site (Supplementary Data SD3), as suggested by Di Bitetti et al. (2010). Mann–Whitney tests were used to check for significant differences in RAI for all species across habitats: high elevation (montane tropical forest, $n = 96$) versus low elevation (lowland rainforest, $n = 144$). The results showed RAI was not significant ($U = 6541$, $P = 0.48$), supporting the assumption.

Prediction of major prey and competitor species.—For each predator, we predicted its major prey species and intraguild competitors. The basis of this prediction process was the assumption that these predators are opportunistic and tend to select the most frequently encountered of appropriate prey species. The frequency of encounter is a combination of the prey’s abundance and the extent to which the predator and prey are at the same place at the same time. Thus, encounter

frequency with prey was estimated from a combination of relative abundance and activity overlap. Specifically, we examined the activity overlap (coefficient of overlapping Δ and associated statistical tests) of each predator with all potential prey species (according to Supplementary Data SD1) plus its RAI to predict the most preferred prey species; a similar process was used to predict the most likely intraguild competitors. We assumed that predators and prey were using approximately the same areas consistent with the overlap estimates, supported by the comparison of site RAI across habitat (see previous section).

We predicted that morphologically similar intraguild competitors would have less activity overlap (greater temporal segregation) than pairs of dissimilar size, and that the degree of overlap would depend on the activity cycle of the most important prey species (Di Bitetti et al. 2010; Herrera et al. 2018). To test this prediction, Mann–Whitney tests were used to compare the mean coefficient of overlapping ($\Delta \pm \text{SD}$) between the most similar-sized predators (jaguar versus puma, jaguarundi versus tayra, oncilla versus margay, puma versus ocelot, puma versus coyote) and dissimilar-sized predators (jaguar versus ocelot/coyote/oncilla/margay, puma versus oncilla/margay, oncilla versus jaguarundi/tayra, margay versus jaguarundi/tayra). Degree of morphological similarity was obtained by reference to Di Bitetti et al. (2010; Table 1).

RESULTS

Survey Site Comparisons.—Prior to activity overlap analysis, we compared sites to assess if there were any significant differences that would prevent us from pooling sites for analysis. Mann–Whitney tests showed no difference in species-typical activity patterns across habitat and elevation (%Activity: $n = 23$, $U = 231.5$, $P = 0.48$; %Night: $n = 23$, $U = 256.5$, $P = 0.88$; Supplementary Data SD4), across seasons (%Activity: $n = 24$, $U = 278.5$, $P = 0.85$; %Night: $n = 24$, $U = 270.0$, $P = 0.72$; Supplementary Data SD5), or across levels of protection (%Activity: $n = 22$, $U = 237.0$, $P = 0.91$; %Night: $n = 22$, $U = 235.5$, $P = 0.89$; Supplementary Data SD6). Linear mixed effects models were used to test whether any of these three variables were good predictors either of %Night or Activity level. For this analysis, individual stations were summarized by season for each species with a minimum of 20 observations, resulting in $n = 213$ total data points. Neither elevation ($\chi^2_{(1)} = 0.00$, $P = 0.99$), season ($\chi^2_{(1)} = 0.29$, $P = 0.59$), nor protection levels ($\chi^2_{(1)} = 0.80$, $P = 0.37$), were significant predictors of activity level. In addition, neither elevation ($\chi^2_{(1)} = 0.10$, $P = 0.74$), season ($\chi^2_{(1)} = 1.50$, $P = 0.22$), nor protection levels ($\chi^2_{(1)} = 2.41$, $P = 0.12$), were significant predictors of %Night. Because there was no significant difference in Activity level or %Night across sites, we pooled data from all the sites in subsequent analyses.

Details of species records are located in Supplementary Data SD1. Overall, the most common predator species were coyote (*Canis latrans*), puma (*Puma concolor*), and ocelot (*Leopardus pardalis*); less common predators were jaguar

(*Panthera onca*), tayra (*Eira barbara*), and oncilla (*Leopardus tigrinus onca*), with jaguarundi (*Herpailurus yaguarondi*) and margay (*Leopardus wiedii*) being uncommon. The common prey species were Dice's cottontail (*Sylvilagus dicei*), Baird's tapir (*Tapirus bairdii*), red brocket deer (*Mazama temama*), Mexican porcupine (*Coendou mexicanus*), common agouti (*Dasyprocta punctata*), nine-banded armadillo (*Dasypus novemcinctus*), white-tailed deer (*Odocoileus virginianus*), gray four-eyed opossum (*Philander opossum*), northern tamandua (*Tamandua mexicana*), white-headed capuchin (*Cebus capucinus*), collared peccary (*Pecari tajacu*), paca (*Cuniculus paca*), common opossum (*Didelphis marsupialis*), white-nosed coati (*Nasua narica*), northern raccoon (*Procyon lotor*), and striped hog-nosed skunk (*Conepatus semistriatus*).

Circadian activity patterns.—We examined the circadian (24-h) activity pattern of each predator and prey species from all sites of the camera trap survey. The activity patterns of the predators (Fig. 1; Supplementary Data SD1) are suggestive of intraguild temporal niche separation insofar as the smaller *Leopardus* felids (oncilla, margay, ocelot) were mostly nocturnal (70–89% of records at night), the large felids (puma, jaguar) and coyote were cathemeral (30–69% of records at night), and the smaller jaguarundi and tayra were diurnal or mostly diurnal (<30% of records at night). Likewise, the activity patterns of prey species (Fig. 2; Supplementary Data SD1 and SD7) indicated temporal niche separation, with species either nocturnal or mostly nocturnal (>70% of records at night) or mostly diurnal or diurnal (<30% of records at night). Interestingly, only red brocket deer was cathemeral (30–69% of records at night), being significantly active both day and night (Fig. 2; Supplementary Data SD7). Of the 16 prey species for which adequate records were available, 69% ($n = 11$) were active primarily at night versus only 31% ($n = 5$) that were active primarily during the day or cathemeral (Supplementary Data SD1). In contrast, 50% of the eight predator species were most active at night, 25% were most active during the day, and another 25% were cathemeral (Supplementary Data SD1). Thus, both predators and prey species show evidence of having partitioned their temporal niches primarily by night or day. Hierarchical clustering analysis confirmed these results, with species tending to broadly group into diurnal and nocturnal clusters, with cathemeral species interleaved at the transition between the two clusters (Fig. 3).

Activity overlap and relative abundance.—We compared circadian (24-h) activity patterns between each of the eight predator species and all other species from our camera trap survey using the overlap statistic (Supplementary Data SD8). The sample size, relative abundance index (RAI), overlap estimates ($\Delta \pm 95\%$ confidence intervals), and three tests of statistical significance (Watson's U^2 , W , Fisher's Exact) are listed in Supplementary Data SD9 for all sites for jaguar (Supplementary Data SD9-1), puma (Supplementary Data SD9-2), ocelot (Supplementary Data SD9-3), coyote (Supplementary Data SD9-4), jaguarundi (Supplementary Data SD9-5), tayra (Supplementary Data SD9-6), margay (Supplementary Data SD9-7), and oncilla (Supplementary Data SD9-8). As expected,

the three statistical techniques for assessing significantly different overlaps were not always in agreement. In particular, they had differing levels of sensitivity to sample size and variation in distribution. In general, cases with the highest overlap (> 0.83) were shown to be not significantly different temporal distributions by one or more of the tests. In cases where the three tests did not agree, typically at least one of the species had a small sample size. We predicted that known prey species (based on Supplementary Data SD2) with the highest overlap/abundance combination would be the primary prey species, and the similar-size intraguild predator with the highest abundance (regardless of overlap) would be the primary competitor. For the smallest felids (margay and oncilla), we predicted that the medium-sized competitors (coyote and ocelot) that had the highest overlap were more likely to be their primary competitors rather than the more abundant and much larger puma—we reasoned that puma would not compete for the smaller vertebrate prey (e.g., rodents) that is an important component of the diet of these small cats, although not documented by the camera traps. Although we cannot validate these predictions with dietary analyses, our predictions are reasonable given the extensive literature review of predator diets (Supplementary Data SD2). The predicted primary prey and competitor species are listed in Table 2 and illustrated by Fig. 4.

Large felids.—Our data showed that jaguar (80 kg) and puma (50 kg) had a modest coefficient of overlap ($\Delta = 0.76$) and significantly different activity patterns ($P < 0.05$ for all measures; Table 2; Supplementary Data SD9-1 and SD9-2). Although both were cathemeral, dividing their activities between day and night, jaguar were significantly more diurnal than puma (daytime activity 57% versus 35%; Supplementary Data SD1). The prey with the highest overlap with jaguar were red brocket deer, white-tailed deer, and peccary, while paca and collared peccary were predicted to be the primary prey species for puma (Supplementary Data SD9-1 and SD9-2; Fig. 4). Peccary (RAI = 27.8) and paca (RAI = 30.9) were the most abundant prey, while brocket deer (RAI = 10.8) had the highest activity overlap with jaguar ($\Delta = 0.84$) and puma ($\Delta = 0.78$). We predicted the strongest intraguild competitor of jaguar would be the slightly-smaller and common puma (RAI = 16.1) which is predicted to select similar prey, but the strongest predicted competitor of puma was not jaguar but coyote. This makes sense because jaguar were relatively rare at most survey sites (RAI = 1.8) whereas coyote were both abundant (RAI = 47.5) and often travelled in groups of 2–3 and thus were capable of hunting larger prey. For jaguar and puma, a smaller mesopredator (coyote and ocelot, respectively) was predicted to be the second most important competitor due to abundance and dietary overlap (Supplementary Data SD9-1 and SD9-2; Fig. 4).

Mesopredators.—The mid-sized mesopredators (10–12 kg) in our survey were ocelot and coyote, which were mostly nocturnal in their activity patterns and overlapped extensively ($\Delta = 0.89$) (Table 2; Supplementary Data SD9-3 and SD9-4). Ocelot were mostly active at night (86%), while coyote were slightly less so (75%). However, ocelot were invariably solitary

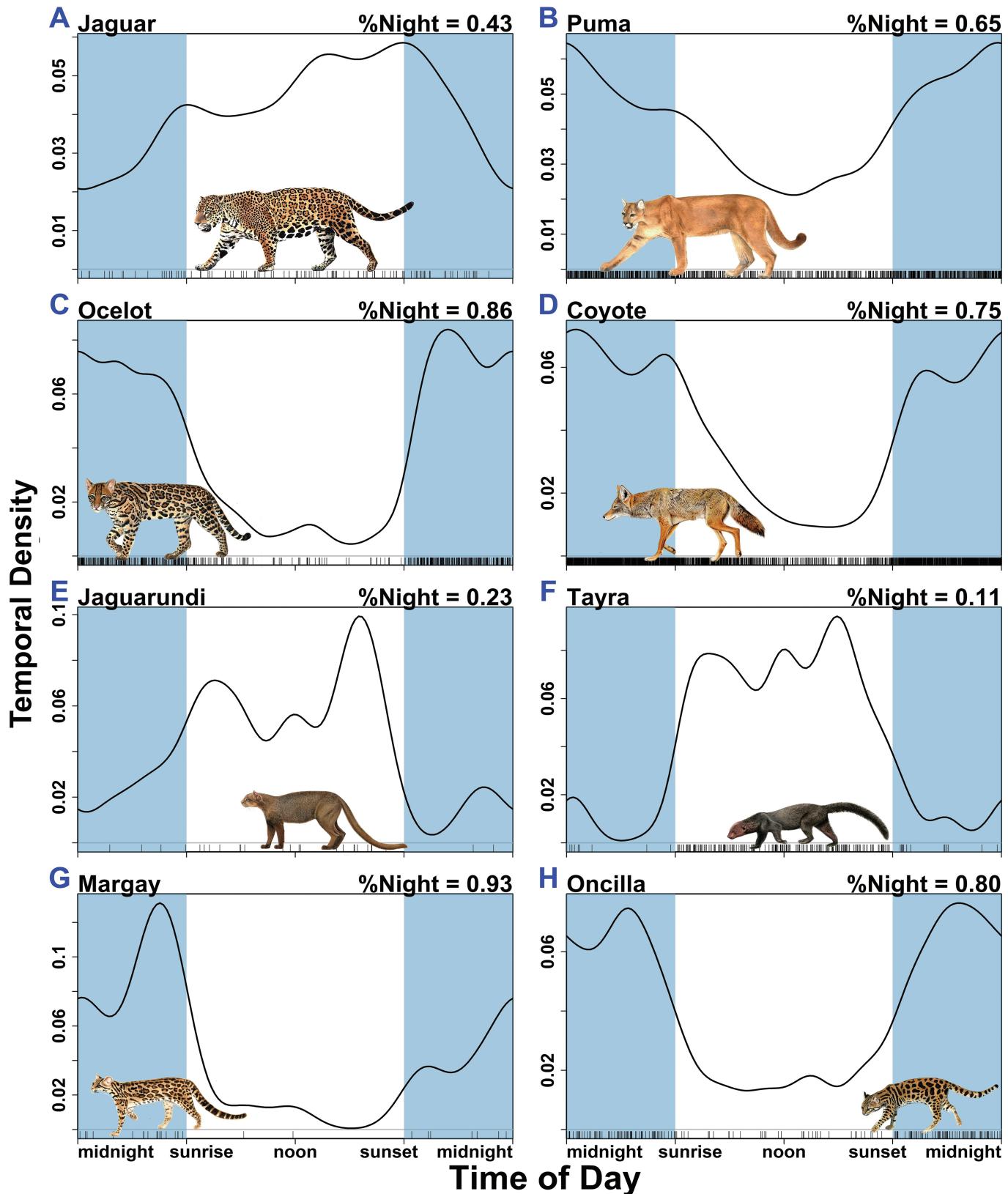


Fig. 1.—Circadian activity patterns for the eight species of predators recorded on the camera trap survey from all survey sites 2010–2019: (A) jaguar, (B) puma, (C) ocelot, (D) coyote, (E) jaguarundi, (F) tayra, (G) margay, and (H) oncilla. Temporal density is the density distribution of independent photo records; blue shading indicates night based on sunrise/sunset. The large jaguar and puma were cathemeral, the mid-sized ocelot and coyote were mostly nocturnal, the small jaguarundi and tayra were mostly diurnal, and the smallest *Leopardus* felids (margay and oncilla) were nocturnal. The number of records for margay and jaguarundi was small ($n = 27$ and 28, respectively), therefore, their activity patterns should be interpreted conservatively.

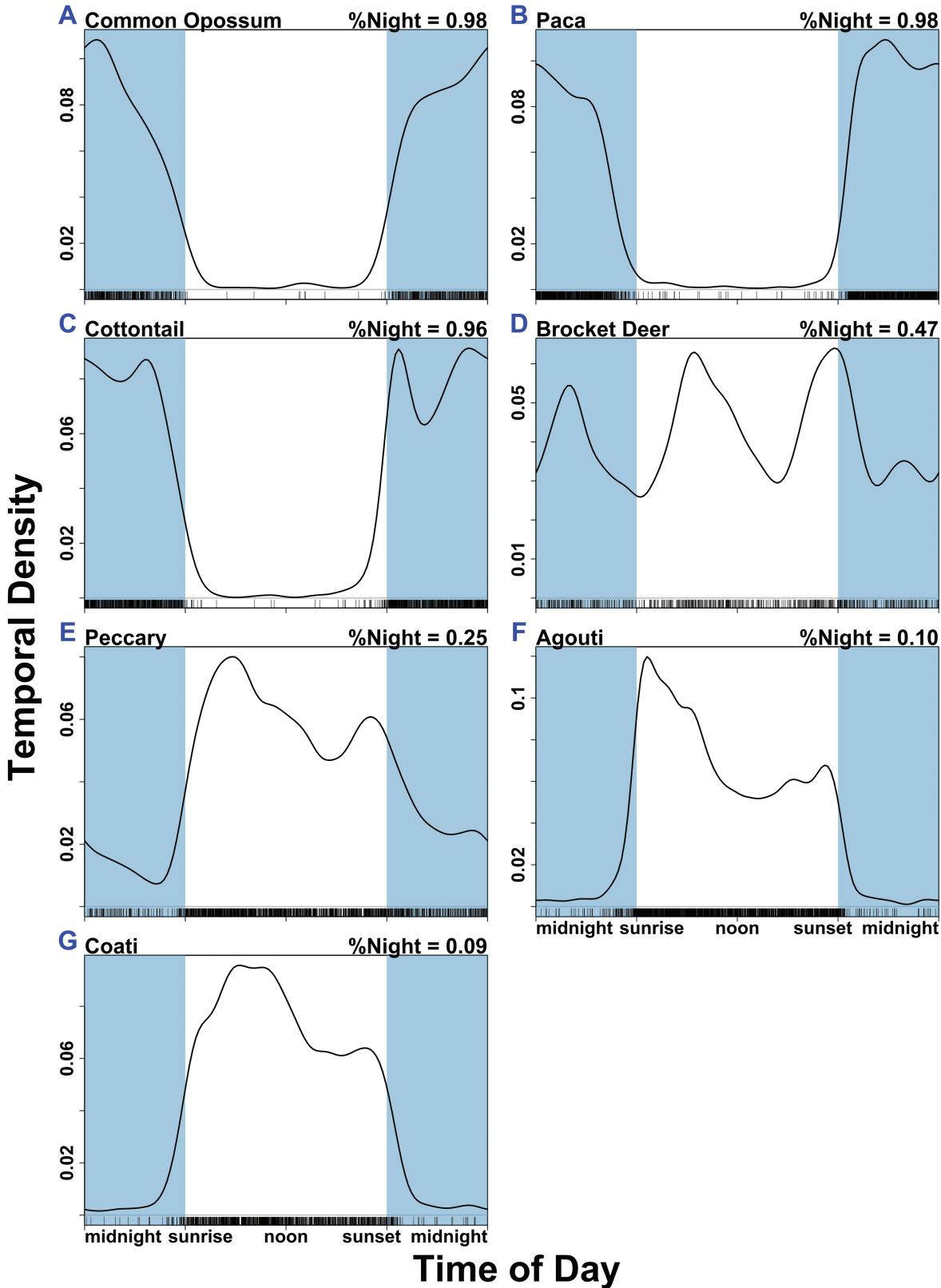


Fig. 2.—Circadian activity patterns for the seven major prey species recorded on the camera trap survey from all survey sites 2010–2019 and listed as primary and secondary prey species in **Table 2**: (A) common opossum, (B) paca, (C) Dice's cottontail, (D) red brocket deer, (E) collared peccary, (F) agouti, and (G) white-nosed coati. Percent nocturnal activity (%Night) is indicated on the top right of each frame; blue shading represents night based on actual sunrise and sunset.

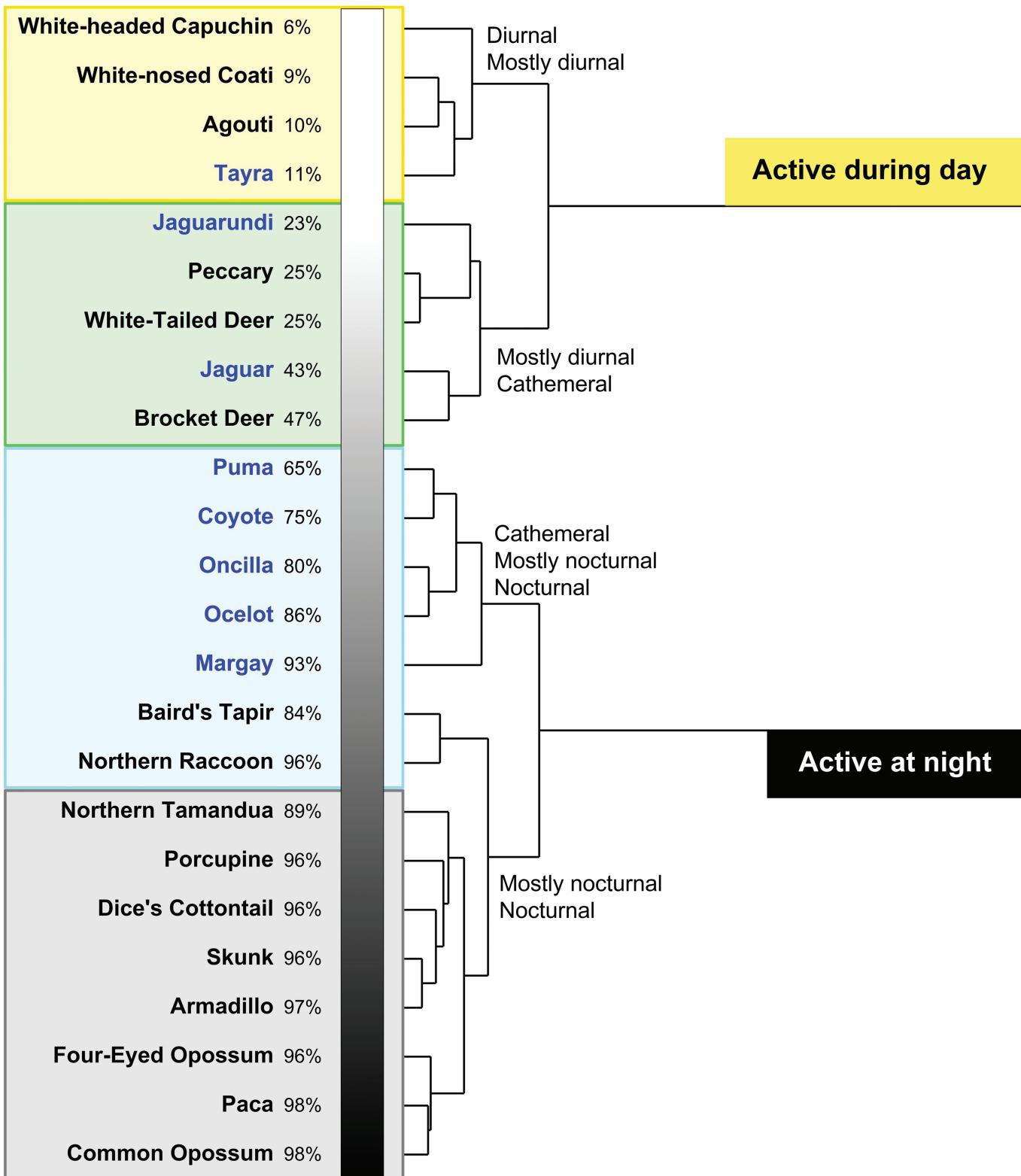


Fig. 3.—Dendrogram from Ward's hierarchical clustering based on activity overlap among species (predators in blue font, prey in black). Species grouped into clusters active mostly during the day or mostly at night, with cathemeral species at the transition between the diurnal and nocturnal clusters. The percent nocturnal activity (%Night) is listed beside the species common name, with the shaded bar indicating the trend from diurnality (top) to nocturnality (bottom).

Table 2.—Predicted primary prey species and intraguild competitors for each of the eight predators in the camera trap survey, gleaned from Supplemental Data SD9.

Predator	Scientific name	Mass (kg)	Primary Prey	Secondary Prey	Primary Competitor	Secondary Competitor
Jaguar	<i>Panthera onca</i>	80.0	Collared peccary	Brocket deer	Puma	Coyote
Puma	<i>Puma concolor</i>	50.0	Paca	Collared peccary	Coyote	Ocelot
Ocelot	<i>Leopardus pardalis</i>	12.0	Dice's cottontail	Paca	Coyote	Puma
Coyote	<i>Canis latrans</i>	10.0	Dice's cottontail	Collared peccary	Puma	Ocelot
Jaguarundi	<i>Herpailurus yaguarondi</i>	5.0	Agouti ^a	Paca ^a	Coyote	Puma
Tayra	<i>Eira barbara</i>	5.0	Coati ^a	Agouti ^a	Coyote	Puma
Margay	<i>Leopardus wiedii</i>	3.5	Dice's cottontail ^a	Common opossum ^a	Coyote	Ocelot
Oncilla	<i>Leopardus tigrina oncilla</i>	2.0	Dice's cottontail ^a	Paca ^a	Coyote	Ocelot

^aSmall rodents are important prey for small predators, but were not recorded in the camera trap survey. Thus, the listed prey species are predicted to be the most important larger prey species.

hunters, whereas coyote frequently were seen in groups of 2–3. This would suggest that coyote could potentially hunt larger prey species than ocelot, but the overlap data indicate that both ocelot and coyote should choose Dice's cottontail as their primary prey, with paca and peccary for secondary prey—the more nocturnal ocelot was predicted to hunt the completely nocturnal paca, while the more diurnal coyote was predicted to hunt the diurnal peccary (Fig. 4). The most important intraguild competitors predicted for ocelot and coyote were each other (Supplementary Data SD9-3 and SD9-4; Fig. 4). Interestingly, these mesopredators also overlapped with the two small nocturnal felines (margay and oncilla) in their predicted preference for Dice's cottontail and paca. Thus, mesopredators and small nocturnal felids may be hunting the same prey at the same time; Dice's cottontail and paca also were the two most abundant nocturnal prey species (RAI cottontail = 21.7; RAI paca = 30.9).

Small predators.—The small predators (≤ 5 kg) recorded in our camera trap surveys included three felids (jaguarundi, margay, oncilla) and the mustelid tayra (Table 2; Supplementary Data SD9-5 to SD9-8; Fig. 4). Margay and oncilla were mostly nocturnal and showed a modest activity overlap ($\Delta = 0.78$), although their activity patterns were not significantly different from each other ($P > 0.07$ by all measures; Supplementary Data SD9-5 to SD9-8). Jaguarundi and tayra were diurnal or mostly diurnal and had high overlap ($\Delta = 0.83$), and their activity patterns were not significantly different ($P > 0.28$ by all measures; Supplementary Data SD9-5 and SD9-6; Fig. 4). These small predators had high overlap with Dice's cottontail and agouti, which were very abundant, and also with paca, opossum, and coati. The nocturnal oncilla and margay were predicted to hunt the nocturnal cottontail, paca, and opossum (Fig. 4), while the diurnal jaguarundi and tayra were expected to prefer hunting the diurnal agouti and coati (Fig. 4). Note that these are the largest prey species predicted to be preferred by these small predators, which are reported to hunt small rodents that are not recorded by the camera traps. Interestingly, the most prominent intraguild competitor predicted for all four small predators was the coyote due to its abundance and generalist diet. Although ocelot (RAI = 9.8) were less abundant than coyote (RAI = 47.5) or puma (RAI = 16.1), the smaller body size of ocelot (12 kg) compared with puma (50 kg) suggests that ocelot would compete more for the smaller prey hunted by margay

and oncilla (2–5 kg). The activity overlap between the smallest predators and their potential secondary competitors varied greatly: coyote: $\Delta = 0.40 – 0.88$; puma: $\Delta = 0.49 – 0.59$; ocelot: $\Delta = 0.79 – 0.91$ (Supplementary Data S9-5 to S9-8; Fig. 4). Table 2 summarizes the results.

Variation in temporal activity between predators.—We predicted that morphologically similar intraguild competitors would exhibit greater temporal segregation, overlapping less in their activity patterns than pairs of dissimilar size, with the degree of overlap depending on the most important prey species. Contrary to our prediction, similar-sized predator pairs (jaguar versus puma, jaguarundi versus tayra, oncilla versus margay, puma versus ocelot, puma versus coyote) had a higher mean overlap ($\Delta = 0.811 \pm 0.053$) compared with dissimilar-sized predator pairs (jaguar versus ocelot, jaguar versus coyote, jaguar versus oncilla, jaguar versus margay, puma versus oncilla, puma versus margay, oncilla versus jaguarundi, oncilla versus tayra, margay versus jaguarundi, margay versus tayra; $\Delta = 0.544 \pm 0.180$), which was a significant difference (Mann–Whitney U : $n_1 = 5$, $n_2 = 10$, $U = 4.00$, $P = 0.008$). Overall, similar-sized competitors had the highest overlap (i.e., less temporal separation) and the most dissimilar-sized competitors had lower overlap. Further examination of the predator pairs revealed that in all cases, similar-sized pairs shared the same activity pattern designation (e.g., cathemeral–cathemeral, nocturnal–nocturnal, diurnal–diurnal), whereas dissimilar-sized pairs had different activity patterns (e.g., cathemeral–nocturnal, nocturnal–diurnal; Supplementary Data SD1).

Consistency across sites.—Generally, the activity patterns of a given species was consistent across sites with no significant discrepancies (Supplementary Data SD10; Fig. 5 shows the examples of coyote and puma). The predominant activity pattern (nocturnal, diurnal, cathemeral) of most species was consistent across seasons and sites. There was one exception—puma tended to be least active in the middle of the day (12:00 noon) at almost all sites, with the Tapantí and PILA survey sites being an exception (Fig. 5). At Tapantí in particular, puma ($n = 93$) showed a distinctive activity peak at noon compared with all other sites ($n = 968$). This may be because red brocket deer, a cathemeral prey species active during the day, was especially abundant at Tapantí compared with the average for all sites (RAI Tapantí = 32.4, RAI All Sites = 10.8). The more diurnal activity pattern of puma

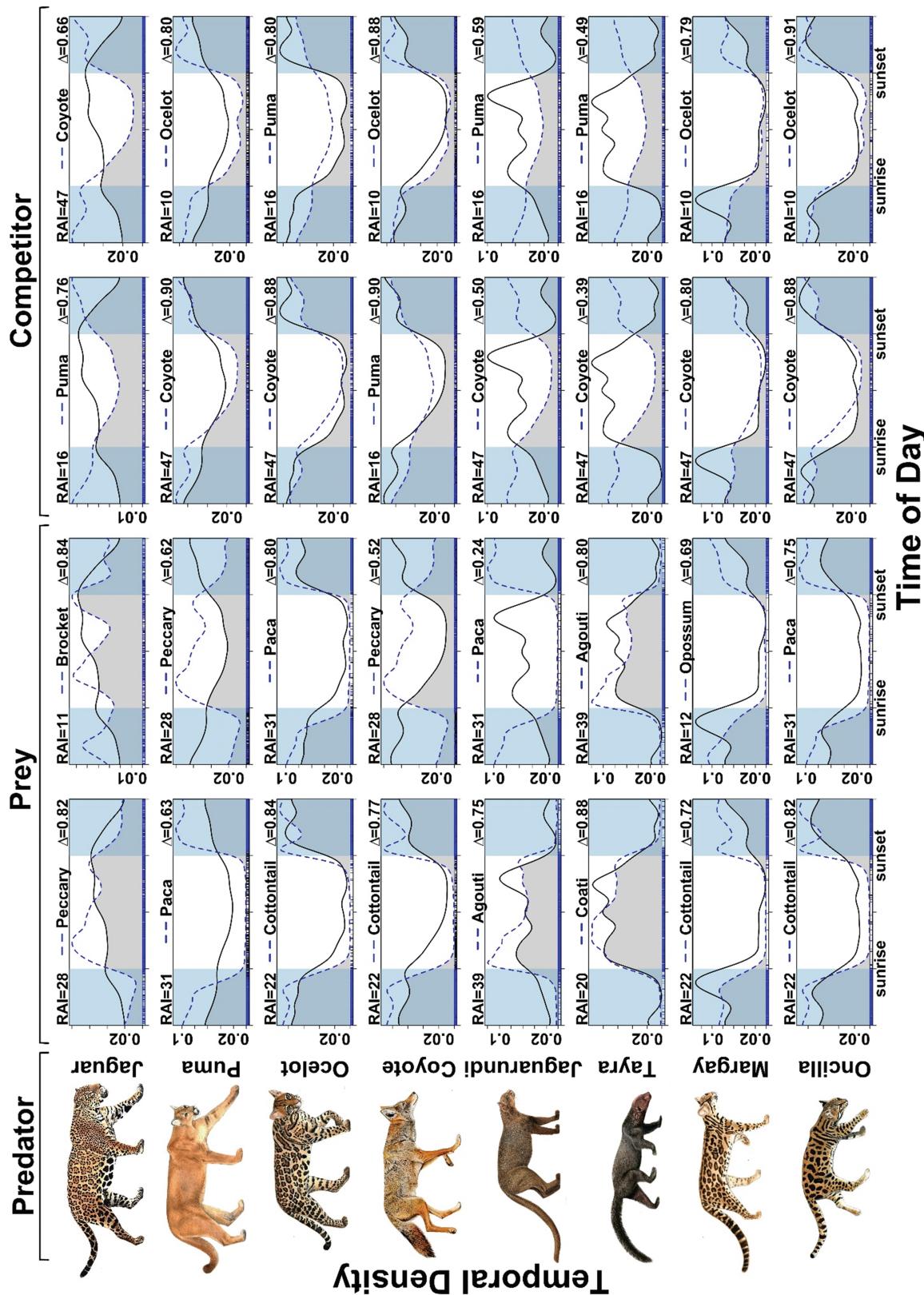
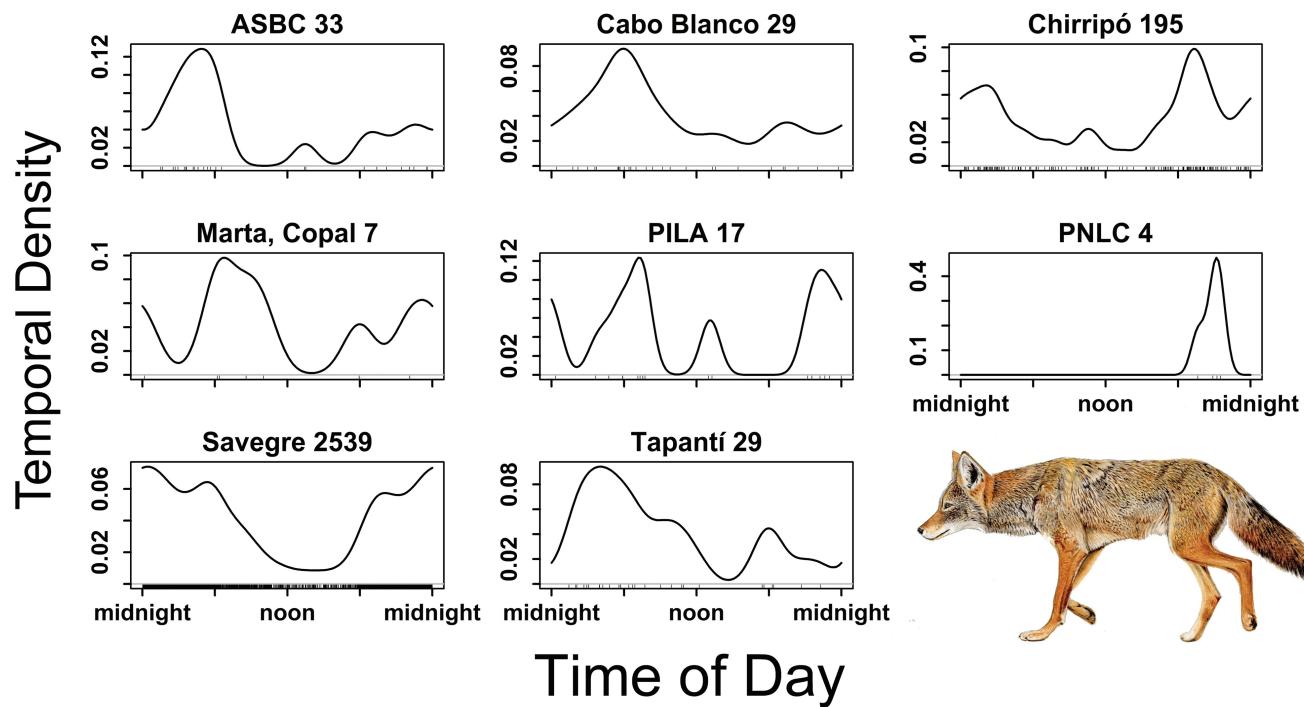


Fig. 4.—Activity overlap plots for each of the eight predators in the study (Predator) with the predicted primary and secondary prey species (Prey) and the predicted primary and secondary competitors (Competitor) for that predator. For each plot, temporal density is represented by the solid line (Predator) and broken line (Prey or Competitor); light blue shading represents night based on sunrise/sunset, while gray shading represents the area of overlap; the Relative Abundance Index (RAI) of the prey or competitor species is indicated on the top left of each frame, and the coefficient of overlapping (Δ) between the predator and its prey/competitor is indicated on the top right of the frame. See the text and [Supplementary Data SD9](#) for further details.

A Coyote activity patterns across sites



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B Puma activity patterns across sites

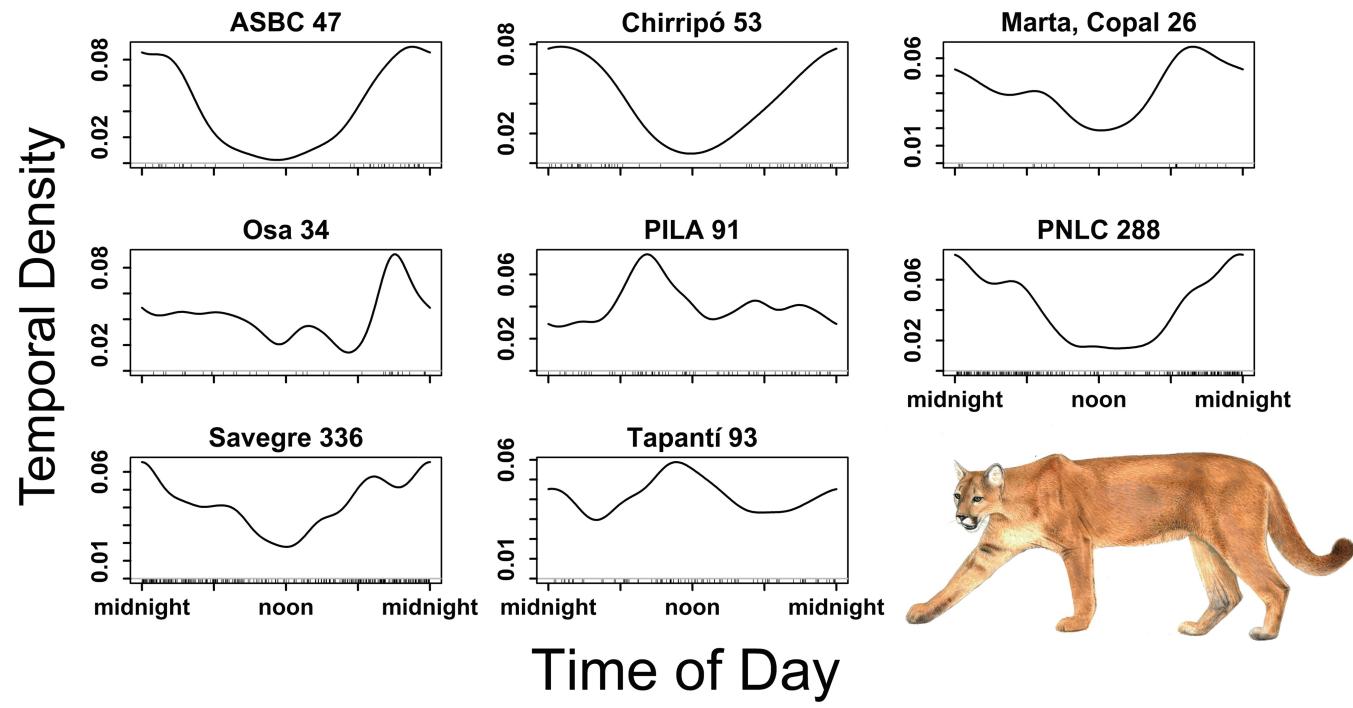


Fig. 5.—Examples of variability in activity patterns across sites for (A) coyote ($n = 2853$) and (B) puma ($n = 968$). Number of independent records per site are indicated at the top of the frame. Activity patterns were consistent across sites, with expected variability for sites with few records. However, puma had an anomalous peak at midday at Tapantí ($n = 93$) and a morning peak at PILA ($n = 91$) compared with the low diurnal activity pattern observed at other sites.

at Tapantí resulted in a higher overlap with brocket deer ($\Delta = 0.83$) compared with all sites ($\Delta = 0.78$).

DISCUSSION

We predicted that (1) predators adjust their activity cycle to overlap with abundant and profitable prey, and (2) predators avoid intraguild competition by temporal segregation with larger or similar-sized predators. All else being equal, higher temporal segregation should occur between intraguild predators that engage in stronger competitive interference and more intraguild killing (Di Bitetti et al. 2010; Santos et al. 2019). However, our results suggest that similar-sized predators hunting equivalent prey are selecting the most abundant prey of appropriate size regardless of activity overlap with competitors. We reasoned that a high overlap between two predators indicated that competitive interference was less important to fitness than obtaining the shared food resources, with the degree of activity overlap between competitors depending on the activity pattern and abundance of the selected prey. Given that dissimilar-sized predators were temporally segregated, we also cannot rule out the possibility that small predators are evading overlap with apex competitors capable of intraguild killing.

Temporal Niches.—Our camera trap surveys supported the temporal niche shift hypothesis (Cozzi et al. 2012) insofar as the majority of mammals chose to pursue a restricted temporal niche by limiting activity to day or night. Hierarchical clustering (Fig. 4) showed that prey species clustered with prey of similar activity, and similar-sized predators appeared to have similar activity patterns. The mid-sized and small *Leopardus* felids (ocelot, margay, oncilla) were mostly nocturnal, the small jaguarundi felid and tayra mustelid were diurnal or mostly diurnal, and the largest felids (jaguar, puma) and the canid coyote were cathemeral and thus active day and night. The implication is that the smaller felids were focused on nocturnal prey, the jaguarundi and tayra selected diurnal prey, and the dominant jaguar and puma spread their activity out throughout the 24-h cycle to encounter more and larger prey (a generalist strategy). These results are supported by many other studies of Neotropical mammals, as mentioned below (de Oliveira 2002; Scognamillo et al. 2003; Harmsen et al. 2011; Foster et al. 2013; Rueda et al. 2013; Gutiérrez-González and López-González 2017; Pérez-Irineo et al. 2017; Ávila-Nájera et al. 2018; Dias et al. 2018; Herrera et al. 2018; Marinho et al. 2018, 2020; Massara et al. 2018; García-R et al. 2019; Nagy-Reis et al. 2019a; Santos et al. 2019).

Predicted prey and competitors.—We predicted that the combination of high activity overlap (Δ) and high relative abundance (RAI) between potential predator–prey pairs would reflect the most important prey species for that predator, and high relative abundance between similar-sized predator–predator pairs would reflect the most important intraguild competitors. A full half of the predator species surveyed (oncilla, margay, ocelot, coyote) were predicted to hunt Dice's cottontail as their primary prey item based on the rabbit's high

abundance and temporal overlap with these mostly nocturnal predators, while the small diurnal predators (jaguarundi, tayra) were predicted to prey mostly on the abundant, diurnal agouti (Supplementary Data SD9; Fig. 4). Because small felids also are known to prey on small rodents that were not recorded in our surveys (Supplementary Data SD2), it would be more accurate to state that rabbits and agouti were the predominant large mammal prey for these predators. The two large apex predators (puma, jaguar) were predicted to prey largely on collared peccary, with brocket deer and paca being secondary prey for jaguar and puma, respectively (Supplementary Data SD9; Fig. 4). Peccary and deer were active both day and night, and they were abundant at many sites, while paca were abundant but entirely nocturnal in our surveys. Because many predators are food generalists, it is likely that individuals consumed a variety of prey depending on the encounter frequency of prey in the specific area.

Comparison with previous studies

Jaguar and puma.—We compared the activity patterns observed in our Costa Rica survey sites with the published literature from other regions. Pumas and jaguars are more likely to compete for food because they have similar body sizes (Santos et al. 2019), and they appear to exhibit dietary partitioning. Jaguars are thought to prey mostly on ungulates and larger prey >2 kg, while pumas select a wider range of medium-sized prey (Scognamillo et al. 2003; Di Bitetti et al. 2010).

In our surveys and elsewhere in Costa Rica, jaguar and puma have cathemeral activity patterns (Herrera et al. 2018). Jaguar and puma in our surveys exhibited a modest overlap ($\Delta = 0.76$) with significantly different activity patterns, which was in general agreement with another study from Costa Rica showing jaguar and puma to overlap 75–80% although hunting many of the same prey (Herrera et al. 2018). Dias et al. (2018) also found that puma in Brazil exhibited a cathemeral activity pattern such as we observed. In contrast to evidence for modest temporal partitioning in Costa Rica, other studies have concluded that jaguar and puma have high activity overlap. A study of sympatric jaguar and puma in four Brazilian biomes (Foster et al. 2013) showed that both were highly nocturnal and crepuscular in their activity patterns, with little temporal segregation and high overlap ($\Delta = 0.86$). The investigators concluded that temporal partitioning probably was not a mechanism of coexistence between Brazilian jaguars and pumas, and suggested that partitioning of habitat and food resources may have played a larger role in enabling their coexistence (Foster et al. 2013). Similarly, no temporal partitioning was observed for sympatric jaguar and puma in Belize and Venezuela (Scognamillo et al. 2003; Harmsen et al. 2011), with both species exhibiting similar nocturnal activity patterns. Some authors have suggested that the activity patterns of jaguars and pumas are determined by the daily activity patterns of their prey species (Emmons 1989; Núñez et al. 2000, Scognamillo et al. 2003; Harmsen et al. 2011). As in our study, these studies found a significant overlap in activity between both predators and their main prey, lending support to the notion that predators adjust their activity

to optimize energy intake and reduce energy expenditure when foraging.

De Oliveira (2002) reviewed 23 dietary studies of jaguar and puma, of which eight studies involved sympatric populations in five Neotropical countries. Although prey use was extremely variable, the trends were consistent with dietary segregation to minimize competition in the sympatric populations. Mean prey weight was positively correlated with predator body size: jaguars consumed more medium-sized (1–15 kg) and large-sized mammals (>15 kg), whereas puma ate mostly medium-sized mammals. Peccary and deer were the preferred prey species of jaguar, with these prey found in jaguar diet in every study area and mostly as the major prey (**De Oliveira 2002**). The review reported that the main components of puma diet were deer, paca, armadillos, peccaries, and lagomorphs (**De Oliveira 2002**). This supports our results which predicted that collared peccary and brocket deer would be the primary prey species of Costa Rican jaguar, while paca and collared peccary would be the primary prey species of puma (Table 2). **Gutiérrez-González and López-González (2017)** found that the presence of sympatric jaguar and puma was positively correlated with the presence of peccary prey. Other studies have also indicated that jaguar and puma prefer to consume peccary and deer (**Rueda et al. 2013**; **Ávila-Nájera et al. 2018**).

Mesopredators.—Ocelot and coyote are medium-sized predators: ocelot diets are composed of small- to medium-sized vertebrates, while coyote in the tropics also consume small rodents, reptiles, and fruit (**Hidalgo-Mihart et al. 2009**; **Di Bitetti et al. 2010**). Ocelot and coyote activity in this study strongly overlapped ($\Delta = 0.89$), with ocelot being mostly nocturnal (86% activity at night). Previous studies also have shown that ocelot are predominantly nocturnal (**Marinho et al. 2020** and references therein). Puma, often assumed to be the major competitor with ocelot, exhibited a cathemeral activity pattern in this study (66% activity at night), and this difference was significant ($P < 0.0001$). In our study, ocelot activity had an 80% overlap with puma but only a 57% overlap with jaguar, whereas **Herrera et al. (2018)** found that ocelot elsewhere in Costa Rica had less overlap with puma (64–73%) and more overlap with jaguar (81–82%). As in this study, **Massara et al. (2018)** found that sympatric ocelots and pumas in Brazil showed evidence of temporal segregation, with ocelots being nocturnal and puma exhibiting cathemeral activity. Furthermore, ocelots increased their nocturnal activity in sites where probability of occupancy by pumas was high, suggesting that temporal segregation allowed coexistence between ocelot and puma. Medium-sized ocelot and coyote exhibited temporal niche overlap with the small felines (margay, oncilla) in being mostly nocturnal. For example, ocelot and margay in our study had an activity overlap of $\Delta = 0.79$. Sympatric ocelot and margay in Mexico also displayed predominantly nocturnal activity, with a similar coefficient of overlapping of $\Delta = 0.75$ (**Pérez-Irineo et al. 2017**). Our study concluded that the nocturnal paca should be an important prey species for the nocturnal ocelot (Table 2). Other studies have found a marked temporal overlap between ocelot

and paca, with paca in Colombia being mainly nocturnal and paca in Brazil being strictly nocturnal during the rainy season and predominately nocturnal during the dry season (**Dias et al. 2019**; **García-R et al. 2019**).

Small predators.—The three small felids (jaguarundi, margay, oncilla) overlap extensively in body size and have broadly similar diets composed mainly of small rodents, birds, and reptiles, suggesting potential food competition (**Di Bitetti et al. 2010**), while the mustelid tayra consumes fruit and small vertebrates (**Presley 2000**). All these small predators take larger prey as well (Supplementary Data SD2). We found that oncilla in Costa Rica were mostly nocturnal (80% activity at night). Likewise, **Marinho et al. (2020)** and references therein found that the northern tiger cat (subspecies of *L. tigrinus*) in Brazil were primarily nocturnal, and **Marinho et al. (2018)** found that *L. tigrinus* had a high coefficient of overlapping ($\Delta = 0.75$) with small mammals (<1 kg) presumed to be their major prey, which also were strongly nocturnal. A study in Brazil (**Nagy-Reis et al. 2019a**) found that oncilla and margay were cathemeral, jaguarundi were diurnal, and ocelot were nocturnal, resulting in low to moderate temporal overlap between these three species and potentially decreasing interspecific encounters. This differed from our study, in which oncilla and margay were mostly nocturnal; however, it agreed with our finding that jaguarundi were diurnal and ocelot were nocturnal (Supplementary Data SD1). Small predators of the Caatinga dry forest of Brazil exhibited similar activity patterns as our observations in Costa Rica, with the northern tiger cat (of which oncilla are a subspecies) being nocturnal-crepuscular, ocelot being nocturnal, and jaguarundi being diurnal (**Marinho et al. 2020** and references therein); apart from the diurnal jaguarundi, these species failed to show strong temporal segregation (**Marinho et al. 2020**).

Interestingly, southern tiger cats (*Leopardus guttulus*) of the Atlantic Forest of Brazil (ecological equivalent of oncilla in Costa Rica) were nocturnal when margay, ocelot, or puma were absent, but became more diurnal or cathemeral when these other felids were present (**Oliveira-Santos et al. 2012**). This suggests that temporal partitioning contributed to the co-existence of this Neotropical small-felid assemblage (**Nagy-Reis et al. 2019a**). **Marinho et al. (2020)** found in the Brazilian Caatinga that the three felid species assumed to be the strongest competitors due to their ecological similarities (ocelot, jaguarundi, northern tiger cat) exhibited partial avoidance from each other, being segregated at least during their activity peaks. While they failed to find strong temporal segregation among these mesocarnivores, they concluded that partial temporal segregation might contribute to interspecific coexistence by reducing that chance of intraguild killing by the dominant ocelot (**Marinho et al. 2020**).

Variation in temporal activity.—Our prediction that similar-sized intraguild competitors would exhibit more temporal segregation (less overlap) than pairs of dissimilar size was not supported; indeed, similar-sized competitors overlapped more and dissimilar-sized competitors were more segregated. In all cases, the similar-sized competitor pairs in our study shared the same activity pattern, whereas the dissimilar-sized pairs had

different patterns ([Supplementary Data SD1](#)). These results contrast with the findings of [Di Bitetti et al. \(2010\)](#) and [Herrera et al. \(2018\)](#), who found that the species pairs with the highest morphological similarity (puma–jaguar and puma–ocelot) had less temporal overlap (greater temporal segregation) compared with morphologically distinct species. While it appears logical that temporal segregation among more similar intraguild predators would be effective in reducing competition and enabling coexistence among the predator guild, additional mechanisms may be important for niche segregation. In fact, [Herrera et al. \(2018\)](#) concluded that temporal segregation of activity patterns did not appear to be the principal mechanism for the coexistence of jaguars, pumas, and ocelots in their study sites. Rather, they proposed that space use or prey availability might play the fundamental role in intraguild coexistence, with fine-scale adjustments in activity peaks contributing to community equilibrium ([Herrera et al. 2018](#)).

We conclude that the similar-sized predators we studied in Costa Rica are eating similar prey and are thus more likely to be active at the same time and to have high activity overlap. This suggests that prey availability is more important than competition in determining predator activity patterns. Others have suggested that activity of prey is a stronger predictor of the activity of predators ([Herrera et al. 2018](#)). This does not mean that morphologically similar predators will not adjust their activity to increase temporal separation. Although jaguar and puma in our study were both catemeral, they still exhibited a significant niche separation, with jaguar being more active during the day and puma more active at night, and were thus able to exploit a slightly different prey base. A study of eight Neotropical camera trap sites ([Santos et al. 2019](#)) described the spatiotemporal organization of six sympatric felids (jaguar, puma, ocelot, jaguarundi, margay, oncilla) and also concluded that prey abundance was more important than species interactions in governing the local occurrence and spatial distribution of the felids, with patterns of habitat-use by jaguar, puma, and ocelot best explained by prey availability.

Although the predominant activity pattern for most predators was consistent across seasons and sites, puma activity at Tapantí appears to be an exception. Whereas puma were least active at midday at most sites, puma at Tapantí had a noontime activity peak that coincided with high activity overlap with brocket deer, a catemeral prey species that tends to be active during midday and was especially abundant at Tapantí. The greater availability of this diurnal prey species may be the most likely explanation for the aberrant daytime activity of Tapantí puma, and suggests that typical predator activity patterns are subject to temporal niche shifts when local food resources are sufficiently abundant.

Human impacts.—With deforestation no longer occurring within protected areas in Costa Rica ([Sanchez-Azofeifa et al. 2003](#)), the level of illegal hunting is likely to be the greatest human impact threatening the biodiversity and ecological integrity of our study sites. Camera trap surveys, field observations, and retrospective interviews have demonstrated that the abundance of hunted mammals within protected areas is significantly

reduced in zones of high hunting pressure versus areas of lower hunting activity, especially for the larger mammal species ([Carrillo et al. 2000](#); [Daily et al 2003](#); [Altrichter and Carbonell 2013](#)). In the Talamanca Bri bri-Cabecar Indigenous Reserve, species abundance is 17 times greater at the sites with low subsistence hunting compared with sites with high hunting pressure ([Altrichter and Carbonell 2013](#)). Twenty kilometers from the protected La Amistad International Park, tapir and other species are intensively hunted for their meat ([Daily et al. 2003](#)). Near Carara National Park, only 3% of families are involved in illegal hunting for subsistence and commercial benefits, yet these 23 families kill >5,000 animals annually, including 145 pacas per month ([Molina Murillo and Huson 2014](#)). Although hunting in the Alexander Skutch Biological Corridor has declined since the 1970s, it still occurs for sport, bushmeat, and profit, with large mammals like deer, peccary, paca, and tapir, being the primary targets ([Maguire 2017](#)).

Our results suggest that predators adjust their activity patterns primarily based on the abundance of appropriate and profitable prey rather than to avoid competition. If true, a disturbing implication is that the reduction of prey populations via widespread (though seldom documented) illegal hunting activities will inevitably increase intraguild competition. The commonly accepted idea that environmental change produces winners and losers suggests that, as prey populations decline, there will be winners and losers among predators. The predator species most likely to lose under a scenario of declining prey and intensified competition for limited food resources are (1) the larger predators that rely on the popular game species preferred by hunters (jaguar and puma), and (2) the specialists reliant on a limited range of prey. We suggest that the more specialized jaguars and ocelots may be pitted in opposition to the more generalized pumas and coyotes. The prey base of smaller predators might be little impacted by hunting activity, but the fact is: we do not really know what would happen.

In conjunction with other investigations, our study suggests that tropical predator–prey communities are in a delicate balance that can be disrupted by the “unintended consequences” of overhunting, resulting in a depauperate landscape consisting of ubiquitous generalists and endangered specialists. The most insidious aspect of this dilemma is that illegal hunting is generally unseen, undocumented, and “out of sight”—and thus largely “out of mind” in conservation planning. Central America has become known as a global hotspot for hunting-induced “empty forests” ([Benítez-López et al 2019](#)), and top-down approaches such as enacting stricter laws against hunting may not be effective without significantly expanded enforcement capabilities requiring more staff and funding by central government.

Our study used a community-based monitoring framework to survey the large mammal fauna at multiple sites over a 10-year period. By empowering local partners to monitor the camera trap surveys, this approach enabled us to capture long-term data from remote sites comparable to that collected by professional scientists ([Danielsen et al. 2014](#)) while at the same time providing social benefits from increased engagement of local communities in wildlife conservation ([Danielsen et al. 2014](#);

Lavariega et al. 2020). Compared with top-down attempts to regulate hunting, community-based conservation approaches that emphasize environmental education, citizen science, and the socio-economic benefits of sustainable development offer a more comprehensive road to reduced hunter defaunation that can maintain the biodiversity and community structure of tropical forest systems.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Percentage photo records.

Supplementary Data SD2.—Predatory diets.

Supplementary Data SD3.—Relative Abundance Index by site.

Supplementary Data SD4.—Elevational comparison.

Supplementary Data SD5.—Seasonal comparison.

Supplementary Data SD6.—Protection comparison.

Supplementary Data SD7.—Single species activity patterns of prey.

Supplementary Data SD8.—Two species activity overlaps.

Supplementary Data SD9.—Activity overlap by predator species.

Supplementary Data SD10.—Site comparisons.

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