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Abstract

An increasing body of evidence indicates that moonlight influences the nocturnal activity patterns of tropical mammals, both predators and prey. One explanation is that brighter moonlight is associated with increased risk of predation (Predation Risk hypothesis), but it has also been proposed that nocturnal activity may be influenced by the sensory ecology of a species, with species that rely on visual detection of food and danger predicted to increase their activity during bright moonlight, while species relying on non-visual senses should decrease activity (Visual Acuity hypothesis). Lack of an objective measure of "visual acuity" has made this second hypothesis difficult to test, therefore we employed a novel approach to better understand the role of lunar illumination in driving activity patterns by using the tapetum lucidum as a proxy for "night vision" acuity. To test the alternative predictions, we analyzed a large dataset from our long-term camera trap study in Costa Rica using activity overlap, relative abundance, and circular statistical techniques. Mixed models explored the influence of illumination factors (moonrise/set, cloud cover, season) and night vision acuity (tapetum type) on nocturnal and lunar phase-related activity patterns. Our results support the underlying assumptions of the predation risk and visual acuity models, but indicate that neither can fully predict lunar-related activity patterns. With diurnal human "super predators" forcing a global increase in activity during the night by mammals, our findings can contribute to a better understanding of nocturnal activity patterns and the development of conservation approaches to mitigate forced temporal niche shifts.

Keywords

lunar phases, predation risk, visual acuity, nocturnal activity, elusive mammals, Neotropics, lunarphobic, lunarphilic

Globally, the majority of mammals are nocturnal, an ancestral character of mammals stemming from the 'nocturnal bottleneck' in the early evolution of the clade (Heesy & Hall, 2010; Hut et al., 2012). Although synapsids invaded the nocturnal niche 100 million years prior to mammals, recent studies support the essential nocturnality of ancestral mammals, including selection for dim-light vision ("night vision"), endothermy, and loss of UV protection (Angielczyk & Schmitz, 2014; Gerkema et al., 2013; Wu et al., 2017). Current evidence indicates that 69% of mammals are nocturnal, with only 20% of mammals displaying a diurnal activity pattern (Bennie et al., 2014). Recently, camera trap surveys have produced a dramatic increase in nocturnal activity data for large mammals that has sparked a renewed interest

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in the influence of moonlight on activity patterns (reviewed by Frey et al., 2017).

The time it takes for the moon to complete one revolution around the earth relative to the sun (29.5 days) is known as the synodic period or lunar month (Hafker & Tessmar-Raible, 2020). The familiar sequence of lunar phases is caused by changes in the visible portion of the moon illuminated by the sun (Andreatta & Tessmar-Raible, 2020), with illumination from the moon on the Earth's surface at night varying by three orders of magnitude over the course of a month (Kyba et al., 2017). Additionally, other factors, such as topography, cloud cover, latitude, and distance from the moon play a role in the intensity of lunar illumination. Nocturnal organisms may respond directly to changes in lunar illumination as the moon cycles through the phases; they can also anticipate changes that accompany the lunar cycle by means of an endogenous oscillator ("clock") synchronized to the ~29.5 day circalunar rhythm (Raible et al., 2017). The primary environmental cues that change with the lunar cycle are moonlight intensity and tidal force (Andreatta & Tessmar-Raible, 2020), and these cues (or 'zeitgebers') act on endogenous oscillators to regulate biological processes such as mating, feeding, activity, predator avoidance, and many others (Andreatta & Tessmar-Raible, 2020). Although it has been known for 50 years that the suprachiasmatic nucleus (SCN) of the hypothalamus acts as the master circadian clock of mammals (Krittika & Yadav, 2019; Weaver, 1998), the ecological factors regulating nocturnal activity are still incompletely understood.

The idea that fear of the dark is an adaptation to avoid predation has a long history (Darwin, 1871), and moonlight as a cue for predation risk was first studied in nocturnal desert rodents (Lockard & Owings, 1974). The literature is replete with studies linking lunar phases with activity cycles, energy acquisition, predation risk, and avoidance strategies in small mammals (Daly et al., 1992; Griffin et al., 2005; Kronfeld-Schor et al., 2013; Lockard & Owings, 1974; Price et al., 1984; Wolfe & Summerlin, 1989). According to the 'predation risk hypothesis' (Huck et al., 2017; Pratas-Santiago et al., 2017; Prugh & Golden, 2014), if predators are more successful at hunting under bright moonlight, prey species will shift activity to less bright lunar phases and become "lunarphobic" (Figure 1A). The predation risk hypothesis thus predicts that prey species will generally reduce nocturnal activity during full moon compared with dimmer phases such as new moon. However, there are some complications to the predation risk prediction: (1) bright moonlight not only gives predators an advantage in seeing their prey, but also makes it easier for prey to see predators and thus avoid them, and (2) if hunting success is influenced by moonlight, predators may adjust their activity cycle accordingly to optimize their success,
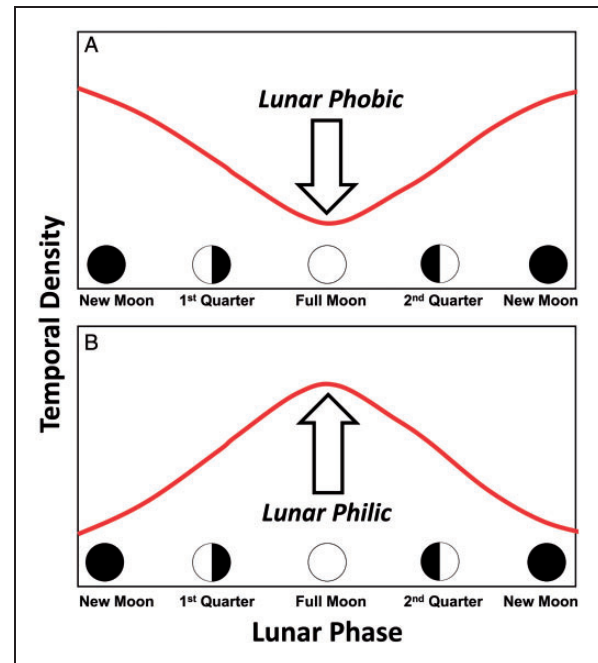

Figure 1. The Predation Risk Hypothesis Predicts That Prey Species Will Reduce Activity During Bright Lunar Illumination (A: lunarphobic), While the Visual Acuity Hypothesis Predicts That Prey Species That Depend Primarily on Vision Will Increase Activity During Bright Illumination (B: lunarphilic) but Those Species That Rely on Non-Visual Senses Like Olfaction Will Be Lunarphobic (A). Predators are predicted to reduce activity at times when prey species are less available.

as predicted by optimal foraging theory (MacArthur & Pianka, 1966).

Activity pattern is a complex decision. If predation risk outweighs the benefits of foraging during moonlit nights, prey species should reduce their activity level; conversely, if foraging success outweighs predation risk, animals should increase activity during moonlit nights (Kronfeld-Schor et al., 2013). Furthermore, predation risk is likely to be influenced by species-typical sensory ecology; species with superior nocturnal visual acuity can see clearly under low-light conditions, while those with poor night vision would benefit from bright moonlight. The 'visual acuity hypothesis' (Huck et al., 2017; Prugh & Golden, 2014) incorporates these additional factors. If moonlight increases foraging efficiency and detection of predators by prey species, the original formulation of the hypothesis states that (1) full moon luminosity provides "visually-oriented" prey species enhanced opportunity to forage and/or detect danger with the result that they are predicted to be more active during the full moon or "lunarphilic" (Figure 1B), while (2) prey species relying on non-visual senses like olfaction are predicted to be less active during bright moonlight (lunarphobic) or unaffected (Figure 1A); and (3) predators will be flexible, either less active during

bright moonlight due to reduced predation success or not affected (Prugh & Golden, 2014).

The original version of the visual acuity hypothesis was based on "visual-oriented" versus "non-visual" prey species, categories that seem rather subjective given that most mammals have well-developed visual, olfactory, and auditory senses. We believe that the lack of an objective metric to test the visual acuity hypothesis represents a significant impediment to improving our understanding of the nocturnal patterns of mammalian predators and prey. Prugh and Golden (2014) acknowledged that most species employ multiple sensory modes and that their categorization of species as visually-oriented versus non-visual was "admittedly coarse"; they recommended that future studies should "include more detailed information about the visual acuity of nocturnal predators and prey" (Prugh & Golden, 2014, p. 511). To that end and in order to effectively test the visual acuity hypothesis, we incorporated estimates of low-light visual acuity based on the *tapetum lucidum* as a proxy for the acuity of taxon-typical "night vision". The goal of this novel approach is to fill the knowledge gap regarding the role of lunar illumination in driving nocturnal activity patterns among elusive predator and prey species. Because Prugh and Golden (2014) also found a strong phylogenetic signal in their results, and tapetum structure is the result of independent evolution in different mammalian clades (Schwab et al., 2002), our analysis incorporated phylogenetic relatedness among the factors that might influence nocturnal activity.

In this study, we explored nighttime activity patterns of elusive mammals using data from our ten-year camera trap study in Costa Rica. Specifically, our goal was to (1) describe the nocturnal activity patterns of mammalian predators and prey in relation to illumination level during the four lunar phases; (2) relate the activity patterns of predators during the lunar cycle to the activity overlap and relative abundance of potential prey species so as to predict prey preferences; (3) relate nocturnal activity patterns between predators to evaluate whether time partitioning contributes to the coexistence of intra-guild competitors (Nagy-Reis et al., 2019); and (4) to test the predictions forwarded by the predation risk and visual acuity hypotheses using the tapetum lucidum as a proxy for low-light visual acuity. In accordance with Prugh and Golden (2014), we predicted that if the visual acuity hypothesis is true, prey species with poor night vision (e.g., lacking a tapetum lucidum) would decrease activity during full moon (become lunarphobic) or be unaffected by lunar phase; conversely, we predicted that prey species with superior night vision as evidenced by the presence of an efficient tapetum lucidum would increase full moon activity (become lunarphilic); finally, we predicted that predatory 'carnivorans' (members of the order Carnivora, which have excellent dim-light vision) would be flexible and either show no pattern or adjust their activity pattern to track the activity of their favored prey. Felids, which possess the most effective tapetum lucidum, would be most likely to increase activity during low-light lunar phases (e.g., new moon) to track the activity of prey species.

Methods

Study Area

Our study was conducted predominantly within the tropical montane forest of the Talamanca Cordillera, but also included data from lowland forests of the Pacific slope (Figure 2). Both lowland and highland sites are characterized by a dry season (December-April) and a wet season (May-November), with average annual precipitation ranging from 300 to 800 cm. The average temperature in the highlands varies between 10–20°C; lowland temperatures average 24–32°C (CCSA, 2019; Herrera, 2004). 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 (Figure 2, Table 1). The landscapes ranged from primary forest in protected areas to a mosaic of primary and secondary forest fragments and agricultural lands in biological corridors. The forest types were either tropical moist forest in the Pacific lowlands or tropical montane forest in the Talamancan highlands. The lowland sites (<1000 m) included Alexander Skutch Biological Corridor, Bosque de Agua Biological Corridor, Cabo Blanco National Park, Carara National Park, La Congreja National Park, Proyecto Campanario Biological Station, and La Marta National Wildlife Refuge; Mid-elevational sites (1000–1500 m) were El Copal and part of Bosque de Agua Biological Corridor; the highland sites (>1500 m) consisted of Chirripó National Park, La Amistad International Park, Tapantí Macizo de la Muerte National Park, the Savegre Valley (Savegre Lodge Private Reserve and Los Quetzales National Park), and part of Bosque de Agua Biological Corridor (Figure 2, Table 1).

Trail Cameras

We deployed camera traps in up to 12 survey areas per year, with camera stations consisting of a single camera or paired cameras (Figure 2, Table 1). Bushnell Trophy Cam units (Bushnell Corporation, Lenexa, KS, USA) were equipped with a passive infrared sensor triggered by rapid changes in temperature, such as the body temperature of a passing mammal (Welbourne et al., 2016). Under low light conditions, the cameras utilized an infrared flash to avoid startling animals (Gibeau &
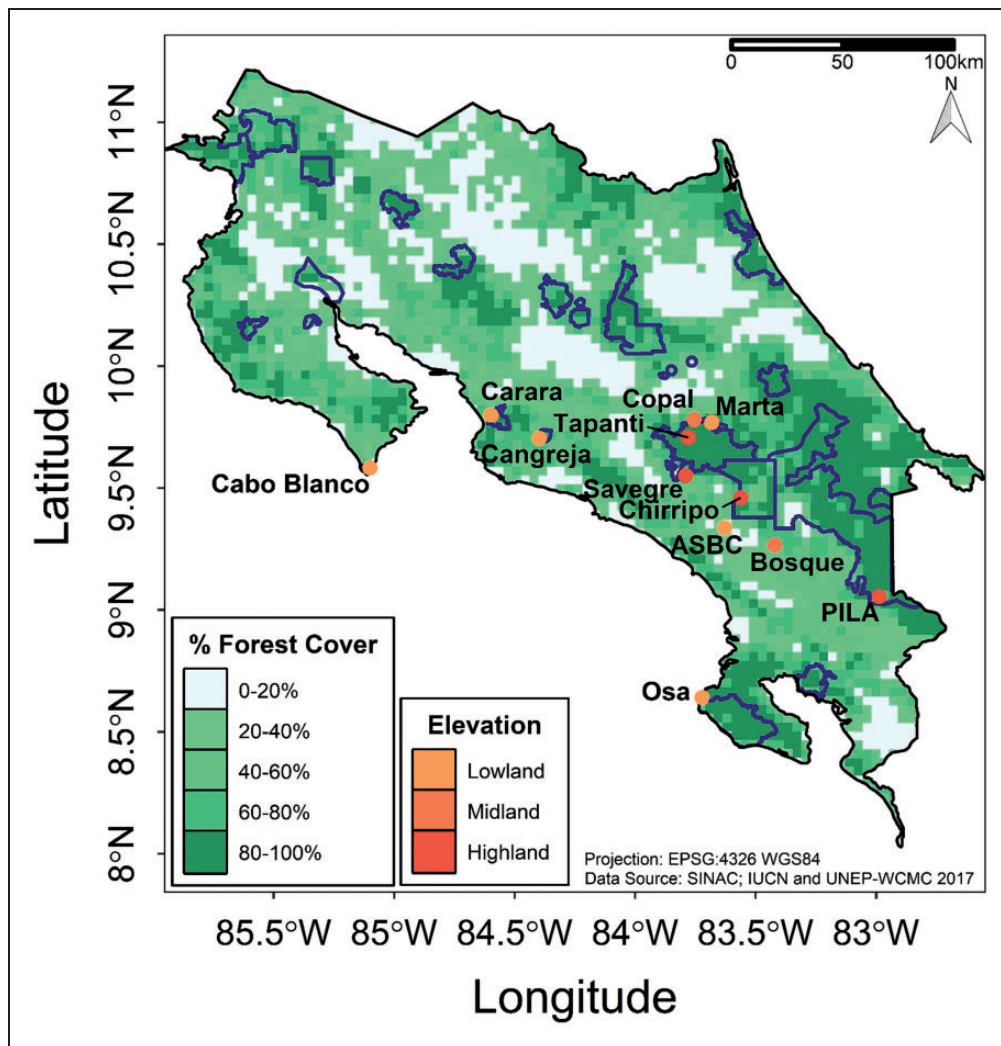
Figure 2. Map of Camera Trap Survey Sites in Costa Rica With Reference to Forest Cover and Elevation. Outlines in blue are the boundaries of the SINAC national park protected areas; forest cover is in shades of green; elevation is by color of the survey site points; and short names of the 12 survey sites are in black (see Table 1 for details).

McTavish, 2009; Meek et al., 2014, 2016; Séquin et al., 2003; Srbek-Araujo, 2018). Cameras were positioned at 1–2 km intervals, primarily along established trail systems within protected areas, which many predators tend to use as travel highways (Harmsen et al., 2010). Further details of camera trapping methodology may be found in Mooring et al. (2020).

Scent Stations

From 2012, we used a scent attractant (Calvin Klein's 'Obsession for Men'; Calvin Klein Inc., New York, NY, USA) at most camera stations to stimulate animals to stop and investigate, ensuring higher resolution photos at night for species identification (Mooring et al., 2020; Sáenz-Bolaños et al., 2019). Each station consisted of a free-standing PVC pipe (sometimes a strap attached to a tree) with sponge segments set within a 5 cm length of

clear plastic tubing; the sponges received 4–5 sprays of Obsession every time the cameras were monitored, and investigators used surgical rubber gloves to avoid leaving human scent.

Scent stations are widely used to increase photo quality for studies aimed at species and individual identification (Barea-Azcón et al., 2007; Braczkowski & Watson, 2013; Conner et al., 1983; Maffei et al., 2011; Noss et al., 2013; Polisar et al., 2014; Randel & Peace, 2010; Thorn et al., 2009; Travaini et al., 1996; Weaver et al., 2005). Unlike "baits" that provide a food reward, scent attractants (or lures) are non-reward items with a distinctive, novel scent that aim to stimulate animals to stop and investigate, resulting in more high-quality photos that can be used for individual identification (García, 2012). Experimental research on search and rescue dogs tracking scent trails has shown that odor plumes tend to

Table 1. Camera Trap Surveys With Number of Cameras, 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	–84.39206	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				

[a]Number 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.
[b]Elevational categories: Lowland < 1000 m, Midland 1000–1500 m, Highland > 1500 m.

condense under high humidity such that an odor plume reaches its detection limit for canids at around 20 m (Jinn, 2019). Given these results and the wet, humid conditions of our study sites, it is expected that the scent plume is local to the camera station and only attracts animals already near the trail. Because the scent can only be detected at short range, the scent stations would not attract animals that are not already near the trail. Recent experimental studies have tested whether scent lures could bias camera trap abundance measures by attracting animals that would not otherwise be detected. These studies have established that scent attractants do not affect the number of photographic captures, movement distances, immigration or emigration patterns, temporal activity, density estimates, and abundance measures (Braczkowski et al., 2016; García, 2012; Gerber et al., 2012) and are thus unbiased in

surveying biodiversity or prey availability (Maxwell, 2018). This supports the contention that the use of scent attractants in our study did not generate any systematic bias.

Database Creation

Once the SD memory cards were collected from cameras, the photos were manually sorted by species and loaded into Camera Base 1.7 (Tobler, 2015), along with relevant data on the camera observation. In most cases, we were unable to identify individual animals. Photographic records were considered independent if photos of a given species at a particular camera station were at least 30 minutes apart, which is a commonly used standard (Anile & Devillard, 2016; Ridout & Linkie, 2009; Si et al., 2014; Sollmann, 2018; Van Berkel, 2014). Duplicate photos of the same individual taken by

"paired" cameras were counted as a single event, as were photos in which multiple individuals of the same species were present in the same picture. Only independent captures were included in the data analysis. Collectively, we analyzed photographic records from a total of 59,919 camera trap days (Table 1).

Data Analysis

All analysis was conducted in R (R Core Team, 2019). For lunar activity overlap analysis, we considered only nocturnal activity by selecting records occurring between sunset and sunrise. 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. To account for the successive changes of the sun throughout the year (Nouvellet et al., 2012), we used the 'sunTime' function of the 'overlap' package version 0.3.2 to map times to radians for analysis (see Meredith & Ridout, 2020a for details) .

The lunar activity pattern of each species was fitted non-parametrically as kernel density functions with the package "Overlap" using the default bandwidth parameters (Meredith & Ridout, 2020a,b), following the assumption that animals are equally likely to be "trapped" throughout any period of their activity (Linkie & Ridout, 2011). Circular density curves were compared using the coefficient of overlapping ('overlap coefficient' Δ), with values ranging from 0 (no overlap) to 1 (complete overlap), as proposed by Ridout and Linkie (2009). Lunar activity was characterized using the 'getMoonIllumination' function from the package suncalc (Agafonkin & Thieurmel, 2018) to obtain the moon phase for each observation based on its date. Moon phase was scaled to radians so that 0 corresponds to New Moon, $\pi/2$ as First Quarter, π as Full Moon, and $3\pi/2$ as Last Quarter. An interactive tool for exploring these analyses is available online as an R Shiny web application (https://ticomammals.shinyapps.io/ActivityBudgets/).

We estimated the overlap coefficient (Δ) for nocturnal activity between predator-prey and predator-predator species pairs, including 3 species of predators with relatively low nocturnal sample sizes because of their ecological importance: margay ($n = 25$), tayra ($n = 34$), and jaguar ($n = 45$). Because the overlap coefficient is descriptive, and the field of statistics associated with cyclical data (also referred to as "circular statistics" or "directional statistics") is not as fully developed as traditional statistics, we reported three statistical measures testing for differences between circular distributions, as 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) with *P*-values calculated through a Chi-square 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 for this statistic 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.

Using these analytical tools, we compared circadian activity between all species of predators in our survey against all prey species with ≥25 nocturnal records; jaguarundi and white-faced capuchin were not included due to low nocturnal sample size ($n = 6$ and 3, respectively). Using these criteria, our cameras recorded a total of 7 predator species and 16 prey species (Supporting Information S1). 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 Supporting Information S2. The Relative Abundance Index (RAI) is a standardized measure of how frequently a species appears on the cameras. We calculated RAI for each species using all nocturnal records from the survey sites and employing the equation:

$$RAI = [(\text{Number of Independent Records}) / (\text{Number Days Camera Was Active})] \times 1,000$$

Visual Acuity

Because of the scarcity of information on the comparative night vision abilities of different mammals (Huck et al., 2017), we used the 'tapetum lucidum' as a proxy for nocturnal visual acuity. The tapetum lucidum is an intraocular "retroreflector" that reflects back photons not initially absorbed by the eyes' photoreceptors, thus increasing the chance that light is absorbed by the photoreceptors (Michalski & Norris, 2011; Ollivier et al., 2004; Schwab et al., 2002). Three types of mammalian tapeta arose by convergent evolution during the Cenozoic era less than 60 million years ago (Table 2): (1) the *choroidal tapetum fibrosum* (CTF) is found principally in herbivorous ungulates, cetaceans, some marsupials, and a rodent, the paca; (2) the *choroidal tapetum cellulosum* (CTC) is found in seals, prosimians (primitive primates), and most carnivores (felids, canids, mustelids, procyonids, etc.); and (3) the *retinal tapetum* (RT) is found in fruit bats and opossums (Schwab et al., 2002). Some mammals have no tapetum (NT), such as monotremes (primitive mammals), most primates (including humans), most rodents (e.g., squirrels, agouti, porcupines), lagomorphs such as rabbits, suids such as pigs and peccaries, and xenarthrans such as armadillos (Alina et al., 2008; Huck et al., 2017; Ribeiro et al., 2017; Schwab et al., 2002; Table 2).

Table 2. Mammal Species Studied with Summary of Visual Acuity Information.

Common name	Species name	Tapetum lucidum[a]	Layers[a]	Main Senses[b]	Rank[c]
Predators					
Jaguar	*Panthera onca*	choroidal tapetum cellulosum	15–30	Visual, hearing	1
Puma	*Puma concolor*	choroidal tapetum cellulosum	15–30	Visual, hearing	1
Ocelot	*Leopardus pardalis*	choroidal tapetum cellulosum	15–30	Visual, hearing	1
Coyote	*Canis latrans*	choroidal tapetum cellulosum	9–15	Smell, hearing	2
Tayra	*Eira barbara*	choroidal tapetum cellulosum	7–15	Visual, smell	2
Margay	*Leopardus wiedii*	choroidal tapetum cellulosum	15–30	Visual, hearing	1
Oncilla	*L. tigrinus oncilla*	choroidal tapetum cellulosum	15–30	Visual, hearing	1
Prey					
Baird's Tapir	*Tapirus bairdii*	choroidal tapetum fibrosum	9–16	Smell	2
White-Tailed Deer	*Odocoileus virginianus*	choroidal tapetum fibrosum	9–16	Smell, hearing	2
Red Brocket Deer	*Mazama temama*	choroidal tapetum fibrosum	9–16	Smell, hearing	2
Collared Peccary	*Pecari tajacu*	no tapetum		Smell, hearing	4
Paca	*Cuniculus paca*	choroidal tapetum fibrosum	12–15	Keen eyesight	2
White-nosed Coati	*Nasua narica*	choroidal tapetum cellulosum		Smell, hearing	2
Northern Tamandua	*Tamandua mexicana*	no tapetum		Smell, poor eyesight	4
Nine-banded Armadillo	*Dasypus novemcinctus*	no tapetum		Smell, hearing, poor eyesight	4
Northern Raccoon	*Procyon lotor*	choroidal tapetum cellulosum		Smell, hearing	2
Central American Agouti	*Dasyprocta punctata*	no tapetum		Diurnal vision, smell	4
Striped Hognosed Skunk	*Conepatus semistriatus*	no tapetum		Smell, hearing	4
Mexican Hairy Porcupine	*Coendou mexicanus*	no tapetum		Non-visual	4
Common Opossum	*Didelphis marsupialis*	retinal tapetum		Vison, smell	3
Cacomistle	*Bassariscus sumichrasti*	choroidal tapetum cellulosum		Smell, hearing	2
Dice's Cottontail	*Sylvilagus dicei*	no tapetum		Smell, hearing	4
Gray 4-Eyed Opossum	*Philander opossum*	retinal tapetum		Vision, smell	3

[a]Schwab et al. 2002, p. 72.
[b]Huck et al., 2017; Prugh & Golden, 2014; Schwab et al., 2002; Ollivier et al., 2004; Michalski & Norris, 2011; McDonough & Loughry, 1995; Ribeiro et al., 2017; De Oliveira, 1998; De Farias Rocha et al., 2009.
[c]Rank is the level of nocturnal visual acuity of taxa from best (1) to worst (4).

Although the mechanisms and functional differences among the various types of tapeta lucida are incompletely understood (Ollivier et al., 2004; Schwab et al., 2002), we made two assumptions: (1) those species lacking the tapetum have poorer night vision than those possessing a tapetum, and (2) the number of cell layers making up the reflective surface of the tapetum is positively associated with its reflective efficiency and visual sensitivity under low-light conditions. It has been proposed that 5 layers of reflective material would give 75% reflection, while 20 layers should approach 100% reflectance (Ollivier et al., 2004). The reflective layer in the CTC (choroidal tapetum cellulosum) of felids is 15–30 layers (4–10 µm) and covers 50% of the fundus of the eye, compared with 9–15 layers (4 µm, 30% of fundus) for canids, 7–15 layers (3–6 µm) for mustelids, 9–16 layers (0.15 µm) for herbivorous ungulates, and 12–15 layers (8–10 µm) for the paca (Michalski & Norris, 2011; Ollivier et al., 2004). Furthermore, felid tapetal cells contain more precisely packed rodlets compared with the less efficient design of canids and mustelids, and it appears that the high number of layers coupled with efficient packing contributes to the exceptional reflectance of the feline tapetum cellulosum, estimated to reflect 130 times more light than the human eye (Ollivier et al., 2004). Table 2 summarizes the visual acuity of the species examined in this study.

Predictions

Based on the information presented above, we drew the following conclusions (Table 2): (1) the CTC (choroidal tapetum fibrosum) of carnivorans has greater light reflectance than the CTF (choroidal tapetum fibrosum) of herbivore ungulates, (2) the CTC of felids is more efficient than that of canids or mustelids, (3) opossums, paca, procyonids (e.g., raccoon, coati), and tapir (related to the horse) have good night vision, whereas (4) armadillos, skunks, and tamandua rely heavily on olfaction and have poor eyesight, and (5) lagomorphs and pigs (including peccary) lack a tapetum lucidum and thus have poor night vision. To test the predictions of the predation risk and visual acuity hypotheses, we computed the number of independent records in each quarter of the moon for each species by dividing the moon phase cycle from 0 to 2π into 4 equal quadrants centered on

each moon phase (for example: First Quarter from $1/4\pi$ to $3/4\pi$) . The percentage of records in each lunar phase for each species was calculated, with the assumption that absence of any pattern would be indicated by 25% of activity occurring during each of the four lunar phases. Deviations from 25% activity during the full moon phase was interpreted as follows: (1) species with $\leq$20% of records during full moon were classified as lunarphobic, (2) those with $\geq$30% of records during full moon were considered lunarphilic, and (3) species that did not qualify as lunarphobic or lunarphilic exhibited no pattern. We used Rao's Spacing Test (Agostinelli & Lund, 2017) to identify activity patterns that differed significantly from uniform and thus showed a preference for a lunar cycle phase (Table 2).

Mixed Effects Models

To investigate potential factors influencing activity patterns associated with the lunar cycle, we developed two models: a mixed effects model to explore factors that might influence activity during the lunar month, and a logistic mixed effects model to examine whether the lunar cycle influences activity during the circadian cycle. For the first model that explored lunar cycle activity, we asked what factors influenced an increase or decrease in activity closer to full moon (e.g., lunarphobic versus lunarphilic). For the second model that explored circadian activity, we asked what factors influenced activity changes resulting in more nocturnal or more diurnal activity. For example, if a species was less active during the full moon (lunarphobic), we asked whether that species shifted to being more active during daylight hours to compensate for the time they were less active at night during full moon.

For the first model, we employed a Linear Mixed-Effects Model (LMM) using only nocturnal data with 'time from full moon' as the response variable and season (wet season vs. dry season), elevation (lowland tropical rainforest vs. montane cloud forest), type of tapetum lucidum (possessed by the species as a proxy for night visual acuity), cloud cover, and the interaction between tapetum lucidum and cloud cover (to identify how varying levels of darkness impact activity differently for the different tapetum types) as fixed effects. Note that 'time from full moon' was used as the response variable to transform the circular lunar phase variable to a linear scale as required by the model (Norris et al., 2010). For the second model, we performed a Logistic General Linear Mixed-Effects Model (GLMM) with the designation of day or night as the binary response variable (0 = Day, 1 = Night) and season, elevation, type of tapetum lucidum, Moonlight Risk Index (MRI; see below), and the interaction between MRI and tapetum lucidum

included as fixed effects. Both models contained random effects to control for species and camera site.

We calculated an index of nocturnal luminosity called the 'Moonlight Risk Index' (MRI) as described (albeit by different names) by Schwitzer et al. (2007), Norris et al. (2010), and Gigliotti and Diefenbach (2018) by multiplying the proportion of the moon illuminated, the proportion between sunset and sunrise that the moon was above the horizon, and the proportion of the sky covered in clouds between 0 (overcast) and 1 (clear). Lunar illumination was obtained with the 'getMoonIllumination' function and moonrise/set with the 'getMoonTime' function, both from the 'suncalc' package (Thieurmel & Elmarhraoui, 2019). Sunrise/set were obtained with the 'sunriset' function from the 'maptools' package (Bivand & Lewin-Koh, 2019) and cloudcover with the 'NCEP.interp' function from the 'RNCEP' package (Kemp et al., 2012) to access the NCEP Reanalysis data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site at http://www.esrl.noaa.gov/psd/ (Kalnay et al., 1996). The MRI was normalized to the average over the study.

For the tapetum variable used to gauge the role of night vision acuity in an animal's activity decisions, we tested several measures that characterize the tapetum lucidum: average number of reflective layers, binary presence/absence of a tapetum, and the type of tapetum possessed by a given taxon based on their evolutionary history (Table 2). We chose to use 'type of tapetum' in the model development: the choroidal tapetum fibrosum (CTF), choroidal tapetum cellulosum (CTC), retinal tapetum (RT), and no tapetum (NT).

We fitted the models with the 'lmer' function and the 'glmer' function, respectively, from the 'lme4' package (Bates et al., 2015). For the GLMM, the MRI fixed effect was square root transformed to increase normality and the optimizer 'bobyqa' was used. Following the top-down "drop one" model selection approach outlined in Zuur et al. (2009), we began with the full model of all possible variables that could affect the response variables. We then removed each fixed effect, one at a time, and compared the resulting model to the full model using likelihood ratio tests to determine if dropping the variable produced a significantly worse model. The fixed effect with the least significant *P*-value was eliminated from the full model, which was then treated as the new full model, and the process was repeated until all the remaining variables produced significantly worse models when removed. The resulting final full model was the 'best fit' model that explained the variables with a significant influence on the response variables pertaining to lunar cycle and circadian cycle activity patterns. The best fit models were then analyzed to determine the effects of each variable. Confidence

intervals for the coefficients in the final model were calculated using the 'confint' function from the 'Stats' package (included in the base R). Details of all intermediate models tested can be found in Supporting Information S3. For this analysis, we omitted the mid-elevation sites Bosque de Agua Biological Corridor and El Copal Private Reserve to avoid optimization errors. The threshold for statistical significance (alpha) was set at 0.05 for all tests utilized in this paper. All of the R code used in this analysis has been made available at https://github.com/rbotts/Lunar.

Results

Mixed Models

The details of the mixed model analyses may be inspected in Supporting Information S3-S6; S3 describes the modelling details, and S4-S6 displays overlap plots for all species based on comparison of elevation (S4), season (S5), and day-night (S6). Based on the final model coefficients for the lunar cycle mixed model (Table 3A), the best fitting model showed that higher cloud cover was associated with activity closer to full

Table 3. Results of (A) the Optimal Mixed Effects Regression Model of the Time Until Full Moon for Nocturnal Activity and (B) the Optimal Mixed Effects Logistic Regression Model of Nocturnal/Diurnal Activity.

Fixed Effects[a]	95% CI for β	
A. Lunar Cycle Model		
Tapetum CTF	−0.018	0.040
Tapetum NT	−0.016	0.037
Tapetum RT	0.008	0.086
Cloud Cover	−0.071	−0.024
Tapetum CTF : Cloud Cover	0.011	0.084
Tapetum NT : Cloud Cover	−0.019	0.058
Tapetum RT : Cloud Cover	−0.080	0.037
B. Circadian Cycle Model		
Season	−0.204	−0.013
Tapetum CTF	−1.350	2.425
Tapetum NT	−0.633	2.572
Tapetum RT	0.337	4.737
MRI	0.048	0.263
Tapetum CTF : MRI	−0.813	−0.420
Tapetum NT : MRI	−0.299	0.094
Tapetum RT : MRI	−0.440	1.877

95% bootstrap confidence intervals for the fixed effects regression coefficients are reported.
[a]*Fixed Effects abbreviations*: Tapetum CTF (choroidal tapetum fibrosum), NT (no tapetum), and RT (retinal tapetum) are all in reference to Tapetum CTC (choroidal tapetum cellulosum); Cloud Cover (proportion of sky covered in clouds between 0 = overcast and 1 = clear); Season (wet season versus dry season); MRI (Moonlight Risk Index = proportion of moon illuminated × proportion moon above horizon between sunset and sunrise × proportion of sky covered in clouds).

moon (95% CI β: −0.071, −0.024). Cloud cover also had differing effects across the tapetum types, with higher cloud cover having a significant association with activity further away from the full moon for the CTF tapetum type (95% CI β: 0.011, 0.084), while cloud cover did not have significantly different effects on activity patterns for the other tapetum types compared to the CTC tapetum type (95% CI β not tapetum: −0.019, 0.058, 95% CI β RT: −0.080, 0.037). However, the direct effects of tapetum type on activity from full moon showed that only the RT type tapetum had activity further away from the full moon than the CTC type tapetum (95% CI β: 0.008, 0.086), while the other tapetum types were not significantly different (95% CI β CTF: −0.018, 0.040, 95% CI β NT: −0.016, 0.037).

The best fitting logistic mixed model for circadian activity (Table 3B), indicated that season, type of tapetum, MRI, and the interaction between the type of tapetum and MRI were all significant factors determining nighttime versus daytime activity. The final coefficients in the model revealed that MRI is associated with higher levels of nocturnal activity (95% CI β: 0.048, 0.263). The interaction terms between MRI and tapetum type indicated that the CTF type has lower levels of nocturnal activity on bright nights (95% CI β: −0.813, −0.420). However the other tapetum types did not have a significantly different circadian activity at higher levels of MRI (95% CI β NT: −0.299, 0.094, 95% CI β RT: −0.440, 1.877). Overall, only the RT tapetum type had significantly higher nocturnal activity (95% CI β: 0.337, 4.737), while the other tapetum types were not significantly different from CTC (95% CI β CTF: −1.350, 2.425, 95% CI β NT: −0.633, 2.572). See Supporting Information S3-S6 for further details of the analysis.

General trends in activity by species with the different tapetum types are shown for lunar cycle activity (Figure 3A) and circadian activity (Figure 3B). There was a trend for species with the CTF and RT tapetum types (ungulates and opossums) to exhibit a lunarphobic response, being less active at full moon compared with species with the CTF type (carnivorans) or no tapetum (most rodents, rabbits, and peccary; Figure 3A). Possession of the RT (opossums) and CTF (ungulates) tapetum types was associated with nocturnal activity, while possession of the CTC type (carnivorans) or no tapetum was associated with a cathemeral or more diurnal activity pattern (Figure 3B).

Some species exhibited a 'trade-off' shift between nocturnal and diurnal activity at the time of the full moon, presumably to compensate for the change in nocturnal foraging behavior resulting from "lunarphobic" or "lunarphilic" trends (Figure 4). While some species showed an increase in nighttime activity simultaneous with a decrease in daytime activity during the full moon (coyote, puma, raccoon; Figure 4A to C), other
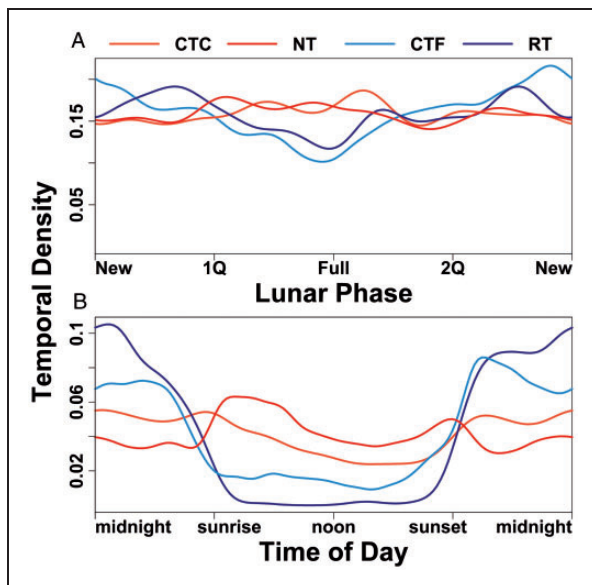
Figure 3. Activity Trends by Species With Different Tapetum Types. For lunar phase (A): CTF and RT species tended to be lunarphobic compared with CTF or NT. For circadian cycle (B): RT and CTF was associated with nocturnal activity, while CTC and NT was associated with a more diurnal activity pattern. Tapetum type abbreviations: CTC = choroidal tapetum cellulosum, NT = no tapetum, CTF = choroidal tapetum fibrosum, RT =retinal tapetum; see Table 2 for details.

species exhibited the opposite pattern, decreasing activity at night while increasing daytime activity (oncilla, brocket deer, tapir; Figure 4D to F). Jaguar were unusual in exhibiting both patterns, shifting from low to high nocturnal activity (and high to low diurnal activity) midway through the full moon phase (Figure 4G). To view plots of species-typical circadian activity shifts, see Supporting Information S6.

Nocturnal Activity Patterns of Predators and Prey

We examined the lunar activity patterns of seven predators for which we had sufficient nocturnal records (Table 4). With the exception of lunarphilic margay, no predators exhibited a clear lunarphobic or lunarphilic activity pattern (Figure 5). Puma and coyote (Figure 5B and D) exhibited a fairly uniform level of activity across the four lunar phases, whereas jaguar and tayra (Figure 5A and E) had an irregular activity pattern. Tayra activity (Figure 5E) demonstrated a wave that may be the result of small sample size ($n = 26$), whereas jaguar lunar activity (Figure 5A) had elements of both lunarphobia and lunarphilia with a marked peak in activity during the second half of full moon into the last quarter, and lowest activity during the second half of new moon into the first quarter. Ocelot (Figure 5C) and oncilla (Figure 5G) had a dip in activity during full moon but also during the second quarter and the new moon,

respectively. Margay (Figure 5F) exhibited a clear lunarphilic pattern with 40% of activity occurring during full moon; nocturnal activity showed a dramatic peak in the second half of the first quarter and first half of full moon. Lunar activity patterns of coyote, ocelot, and puma were significantly non-random by Rao's spacing test (coyote: $U_{2136} = 231.0$, $P < 0.001$; ocelot: $U_{505} = 182.0$, $P < 0.001$; puma: $U_{633} = 189.1$, $P < 0.001$), while the Rao's P-values for the activity patterns of predators with smaller sample sizes were non-significant (tayra: $U_{26} = 129.8$, *NS;* oncilla: $U_{157} = 142.5$, *NS*; margay: $U_{25} = 158.8$, *NS*; jaguar: $U_{46} = 15.0$, *NS*; Table 4, Figure 5).

We next examined the lunar activity patterns of the 16 prey species with sufficient nocturnal records (Figure 6, Table 4). Only four of 16 prey species (25%) exhibited a lunarphobic activity pattern that conformed to the ≤20% cutoff for full moon records, with the lowest level of activity during full moon. These species were the paca, nine-banded armadillo, gray four-eyed opossum, and Mexican hairy dwarf porcupine (Figure 6A to D). All lunarphobic activity patterns were significantly non-uniform according to Rao's spacing test (paca: $U_{1815} = 213.9$, $P < 0.001$; armadillo: $U_{304} = 172.2$, $P < 0.001$; four-eyed opossum: $U_{149} = 158.4$, $P < 0.001$; porcupine: $U_{66} = 152.3$, $P < 0.05$; Table 4, Figure 6A to D).

Four of the prey species (25%) exhibited a lunarphilic activity pattern (Table 4). These were tamandua, raccoon, cacomistle, and Dice's cottontail (Figure 6E to H). For these species, peak activity occurred during the full moon phase and activity declined during less bright phases. According to Rao's spacing test, lunarphilic activity patterns were significantly non-uniform for all species except for cacomistle (tamandua: $U_{110} = 146.8$, $P < 0.05$; raccoon: $U_{468} = 182.0$, $P < 0.001$; cacomistle: $U_{39} = 140.0$, *NS;* Dice's cottontail: $U_{1254} = 196.8$, $P < 0.001$; Figure 6E to H, Table 4).

Eight prey species (50%) exhibited no clear pattern of nocturnal activity based on percent activity during full moon phase (Figure 6, Table 4). These species were Baird's tapir, agouti, striped hognosed skunk, white-tailed deer, red brocket deer, collared peccary, common opossum, and white-nosed coati (Figure 6I to P). It is notable that four of the species are cathemeral or mostly diurnal (agouti, white-tailed deer, brocket deer, and peccary) and are thus most active during the day (Supporting Information S1). Although these lunar activity patterns did not qualify as lunarphobic or lunarphilic, tapir, skunk, brocket deer, and common opossum had their lowest activity during full moon, while agouti, white-tailed deer and peccary had their lowest activity during a less illuminated lunar phase (Figure 6I to P). Lunar activity was significantly non-uniform for all species according to Rao's spacing test (tapir: $U_{1437} = 192.3$, $P < 0.001$; agouti: $U_{223} = 152.6$, $P < 0.001$;
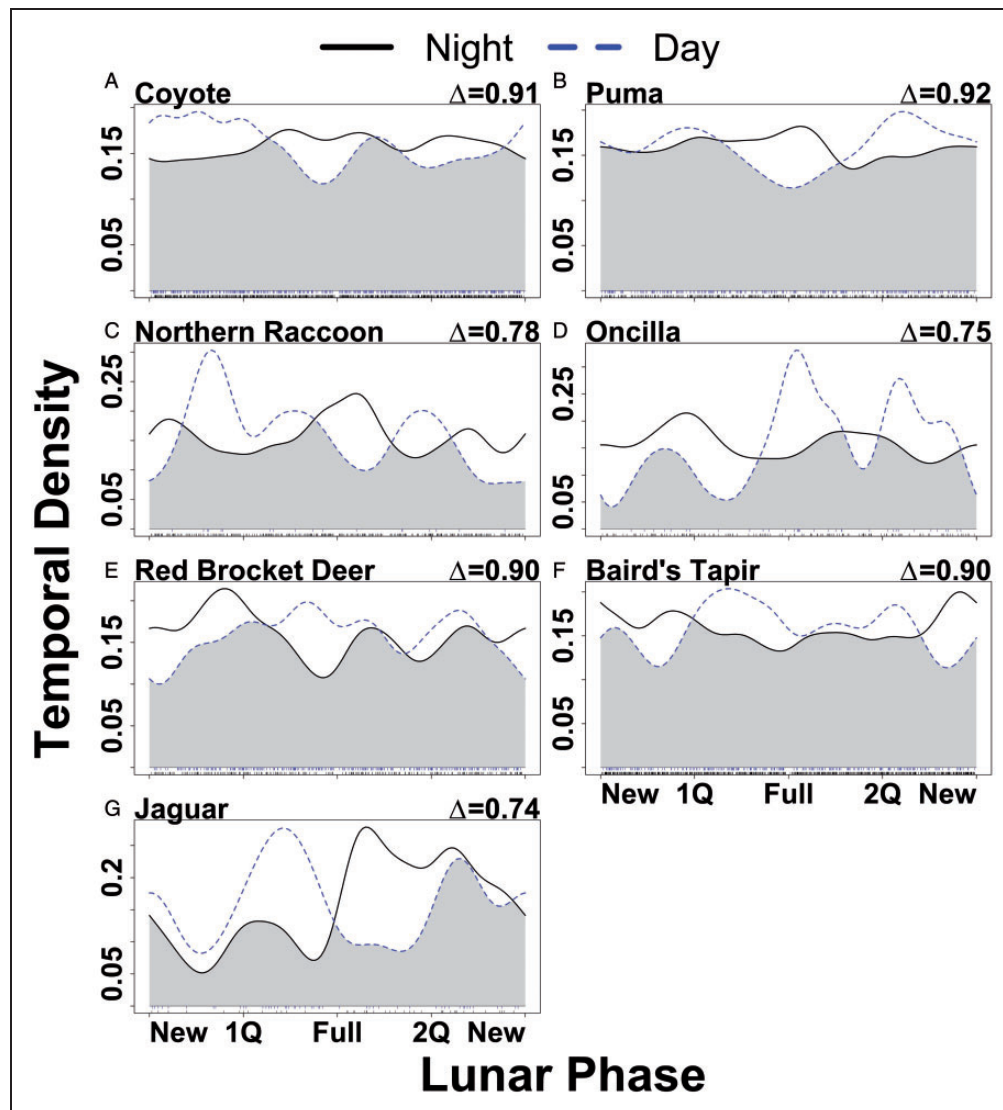
Figure 4. Activity Shifts Between Nocturnal and Diurnal Activity During the Full Moon. Species that increased nocturnal activity and decreased diurnal activity during the full moon: (A) coyote, (B) puma, (C) raccoon; species that decreased nocturnal activity and increased diurnal activity at full moon: (D) oncilla, (E) brocket deer, (F) tapir. Jaguar (G) showed both patterns, shifting from decreased to increased nocturnal activity (and increased to decreased diurnal activity) midway through full moon phase. The logistic mixed model showed that factors that influence nocturnal illumination by the moon and tapetum type (reflecting night vision acuity) had a significant effect on whether animals were active during the night versus day. Temporal density of nocturnal activity (solid line), diurnal activity (broken line), and overlap between the two (shaded area). The coefficient of overlapping (Δ) on top right of frame; lunar phases are New Moon (New), First Quarter (1Q), Full Moon (Full), and Second Quarter (2Q).

skunk: $U_{237} = 145.1$, $P < 0.05$; white-tailed deer: $U_{84} = 153.5$, $P < 0.05$; brocket deer: $U_{303} = 144.2$, $P < 0.01$; peccary: $U_{415} = 164.5$, $P < 0.001$; common opossum: $U_{731} = 186.7$, $P < 0.001$; Figure 6I to P, Table 4).

Activity Overlap With Prey and Competitors

We predicted the most commonly selected prey species based on a combination of RAI, overlap, and appropriate size (Supporting Information S2 and S7-S13; Figure 7). Four prey species were predicted to be the most

commonly selected by predators hunting at night: common opossum, Dice's cottontail, paca, and peccary (Figure 7). Common opossum were predicted to be selected by 5 of the 7 predators (71%), while Dice's cottontail and paca were predicted to be primary prey for 4 of the predators (57%). All three prey species are highly nocturnal, being active 96–98% of the time at night (Supporting Information S1). Opossum are moderately abundant (RAI = 12) and exhibited moderate to high overlap with predators (Δ = 0.76–0.94; mean Δ = 0.86). Dice's cottontail were predicted prey for the smaller

Table 4. Mammal Species Studied With Predicted and Observed Lunar Activity Patterns.

Species name	Predicted	Observed (20/30 Rule)	Rao's Test	Rao's P-value	Chi² P-value	Supports Prediction[a]	Literature review[b]
Predators							
Panthera onca	Flexible	–	135.0	NS	0.037	Yes	No pattern
Puma concolor	Flexible	–	189.1	0.001	NS	Yes	No pattern
Leopardus pardalis	Flexible	–	182.0	0.001	NS	Yes	No pattern
Canis latrans	Flexible	–	231.0	0.001	NS	Yes	
Eira barbara	Flexible	–	129.8	NS	NS	Yes	
Leopardus wiedii	Flexible	Lunarphilic	158.8	NS	0.001	Yes	
L. tigrinus oncilla	Flexible	–	142.5	NS	NS	Yes	
Prey							
Tapirus bairdii	Lunarphilic	–	192.3	0.001	NS	No	Lunarphobic
Odocoileus virginianus	Lunarphilic	–	153.5	0.05	NS	No	
Mazama temama	Lunarphilic	–	144.2	0.01	NS	No	Lunarphilic / No pattern
Pecari tajacu	Lunarphobic	Unaffected	164.5	0.001	NS	Yes	
Cuniculus paca	Lunarphilic	Lunarphobic	213.9	0.001	0.026	No	Lunarphobic
Nasua narica	Lunarphilic	–	154.9	0.01	NS	No	
Tamandua mexicana	Lunarphobic	Lunarphilic	146.8	0.05	NS	No	
Dasypus novemcinctus	Lunarphobic	Lunarphobic	172.2	0.001	0.001	Yes	Lunarphobic / No pattern
Procyon lotor	Lunarphilic	Lunarphilic	182.0	0.001	NS	Yes	
Dasyprocta punctata	Lunarphobic	Unaffected	152.6	0.001	NS	Yes	Lunarphobic
Conepatus semistriatus	Lunarphobic	Unaffected	145.1	0.05	NS	Yes	Lunarphilic
Coendou mexicanus	Lunarphobic	Lunarphobic	152.3	0.05	NS	Yes	
Didelphis marsupialis	Lunarphilic	–	186.7	0.001	NS	No	No pattern
Bassariscus sumichrasti	Lunarphilic	Lunarphilic	139.9	NS	0.001	Yes	
Sylvilagus dicei	Lunarphobic	Lunarphilic	196.8	0.001	NS	No	Lunarphobic/philic
Philander opossum	Lunarphilic	Lunarphobic	158.4	0.001	NS	No	Lunarphilic

[a]Supports the prediction of the visual acuity hypothesis that (1) prey species with poor night vision will be lunarphobic or be unaffected by lunar phase, and (2) prey species with good night vision will be lunarphilic.
[b]See text for details of the literature review (Harmsen et al., 2011; Huck et al., 2017; Michalski & Norris, 2011; Pratas-Santiago et al., 2017; Sánchez-Pinzón et al., 2020).

predators (coyote to oncilla), and they were both common (RAI = 21) and had moderate to high overlap ($\Delta = 0.79$–0.93; mean $\Delta = 0.87$). Paca were predicted to be prey for both small and large predators (oncilla to jaguar), were extremely common at night (RAI = 30), and exhibited very little variation in overlap ($\Delta = 0.81$–0.85; mean $\Delta = 0.835$). Collared peccary, predicted to be an important prey species for coyote, are mostly diurnal, and although they had a high overlap with coyote ($\Delta = 0.97$), they were less common than the other prey at night (RAI = 7).

Coyote was the most frequently predicted intraguild predator at night, being listed as a primary or secondary competitor for 6 out of 7 predators (86%). Coyote were generally very common (RAI = 36) and had moderate to high overlap with other predators ($\Delta = 0.78$–0.96; mean $\Delta = 0.88$). Ocelot was a predicted competitor with 5 of the intraguild predators (71%), and although they were less abundant than coyote (RAI = 8) they had a similar overlap ($\Delta = 0.73$–0.94; mean $\Delta = 0.874$). Puma were of intermediate abundance (RAI = 11) and moderate to high overlap ($\Delta = 0.79$–0.96; mean $\Delta = 0.90$), and were

predicted to be an important competitor for 3 of the predators (43%).

Ocelot exhibited a dip in activity at full moon, matching a similar activity dip with its primary lunarphobic prey species (common opossum and paca) with which ocelot had high overlap ($\Delta = 0.85$–0.94; Figure 7). Predators whose activity level remained fairly constant across the lunar phases (puma, coyote) did not appear to be tracking any particular prey species nor avoiding any particular competitor. Tayra were primarily diurnal and thus had a small sample size of nocturnal records ($n = 34$), most of which were crepuscular (within an hour of sunrise or sunset). The tayra's lunar activity pattern exhibited a wave pattern with no discernable association with the lunar phases. Like the puma and coyote, their nocturnal pattern did not track specific prey or competitor species. Margay were nocturnal but uncommon in our surveys ($n = 25$), thus their nocturnal activity is represented by a small sample size that should be interpreted with caution. Margay exhibited a major peak in their activity during the lunar first quarter and full moon phases (lunarphilic), but this pattern did not
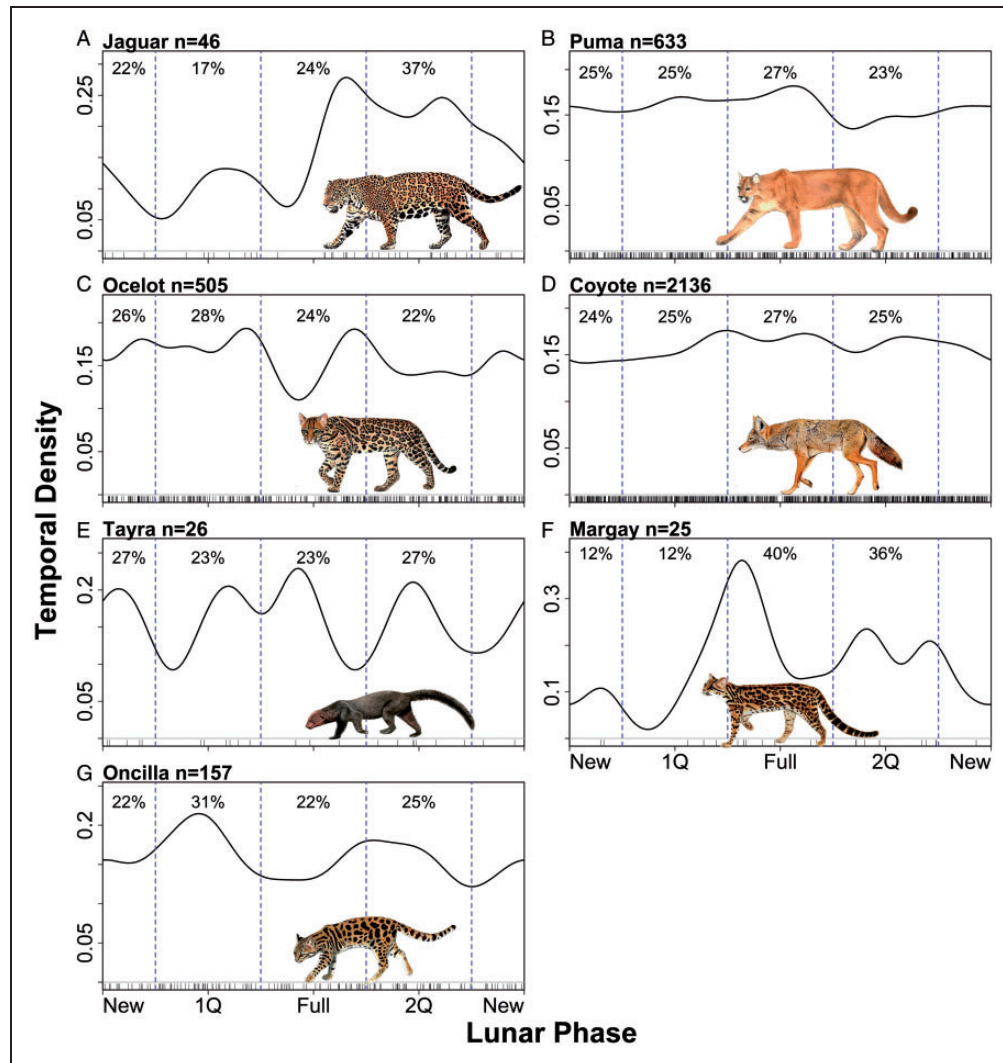
Figure 5. Lunar Phase Activity Patterns of the Predators Examined in This Study: (A) jaguar, (B) puma, (C) ocelot, (D) coyote, (E) tayra, (F) margay, and (G) oncilla. Temporal density of nocturnal records is shown, sample size (n) is indicated on top of frame, lunar phases are New Moon (New), First Quarter (1Q), Full Moon (Full), and Second Quarter (2Q). No discernable pattern was seen for any species except margay, which was lunarphilic. Lunar activity patterns of coyote, ocelot, and puma were significantly non-random by Rao's spacing test.

overlap with the margay's major prey species or intra-guild competitors (Figure 7).

Discussion

Nearly all living organisms have the ability to anticipate and adapt to environmental changes associated with periodic cycles such as the circadian day or the lunar month (Krittika & Yadav, 2019). Like all biological rhythms, regulation of the mammalian circalunar rhythm is regulated by environmental cues/zeitgebers (e.g., lunar illumination) that involve an internal time keeper made up of sensory receptors (e.g., photoreceptors) that communicate with a master clock/oscillator (the SCN) that triggers adaptive behavioral and metabolic responses

(Hafker & Tessmar-Raible, 2020; Krittika & Yadav, 2019). How the circalunar activity rhythm is regulated by mammals in the wild remains an ecological and evolutionary enigma, but the increasing number of studies of nocturnal activity made possible by camera trap surveys is starting to provide some clues.

Our results identified a diversity of lunar activity patterns: lunarphobic, lunarphilic, and patterns not obviously associated with the lunar cycle. Only one predator out of seven (14%) exhibited a nocturnal activity pattern (lunarphilic margay), while 50% of the prey species were lunarphobic or lunarphilic by our definition, supporting the notion that the threat of predation is a strong influence on nocturnal activity patterns. Of the 16 prey species analyzed, eight (50%) had their
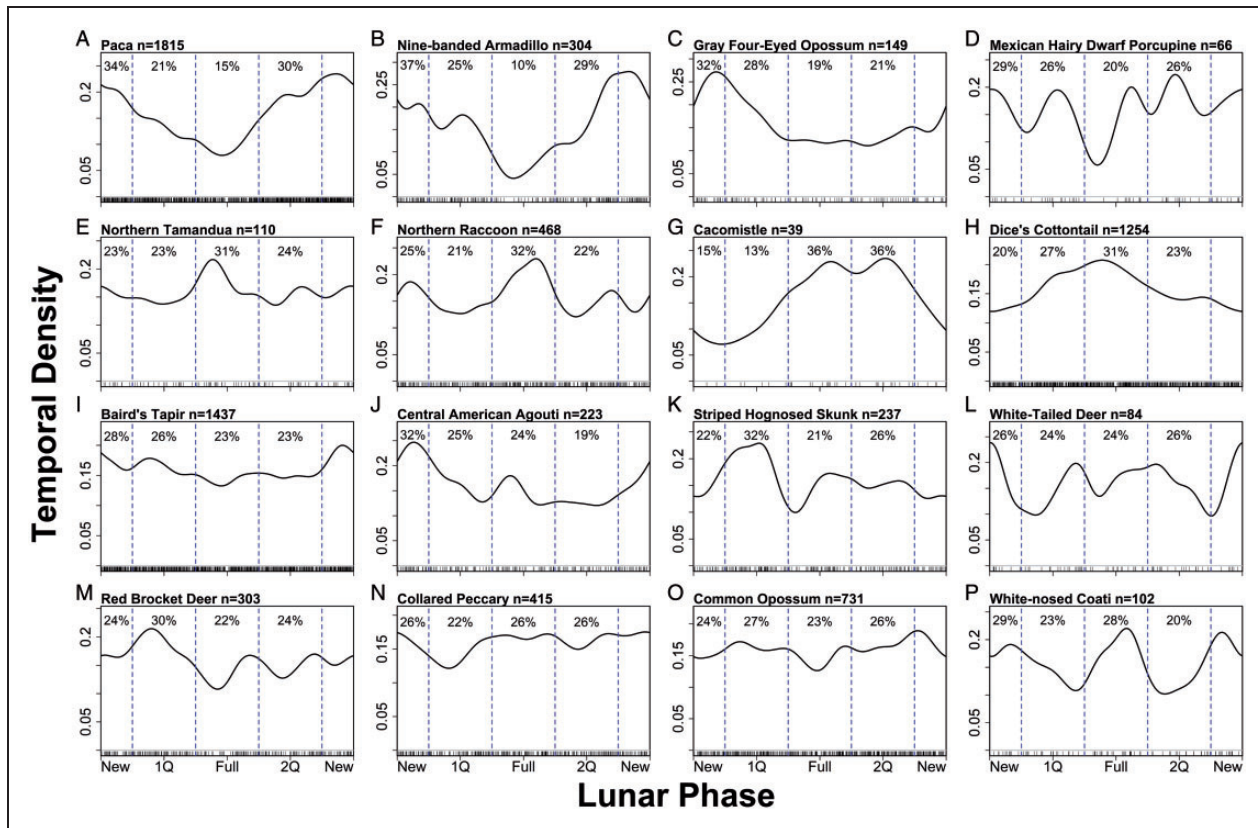
Figure 6. Prey Species Examined in This Study Arranged According to Activity Pattern. Temporal density of nocturnal records with sample size (n) on top of frame. Lunarphobic: (A) paca, (B) nine-banded armadillo, (C) gray four-eyed opossum, and (D) Mexican hairy dwarf porcupine; lunarphilic: (E) northern tamandua, (F) northern raccoon, (G) cacomistle, and (H) Dice's cottontail; no pattern: (I) Baird's tapir, (J) Central American agouti, (K) striped hognosed skunk (L) white-tailed deer, (M) red brocket deer, (N) collared peccary, (O) common opossum, and (P) white-nosed coati. Lunar phases: New Moon (New), First Quarter (1Q), Full Moon (Full), and Second Quarter (2Q).

lowest activity during the full moon (only four of which met the criteria for lunarphobic), four species (25%) were lunarphilic, and four (25%) had no clear pattern. Our results agree with previous research showing that mammals often adapt their nocturnal activity to the level of lunar illumination (e.g., Huck et al., 2017; Pratas-Santiago et al., 2017; Prugh & Golden, 2014). However, only seven of the 16 prey species (44%) supported the predictions of the visual acuity hypothesis, implying that this model does not incorporate all of the relevant factors that determine nocturnal activity.

Review of the Literature

A review of the literature indicated a diversity of nocturnal activity patterns in Neotropical mammals, many of which differed from our observations (Tables 4 and 5, Figure 7). Other investigators found as we did that paca exhibit lunarphobic activity (Harmsen et al., 2011; Michalski & Norris, 2011). As in our study, neither jaguar nor puma in Belize showed a lunar pattern, and both armadillo and paca exhibited lunarphobic behavior (Harmsen et al., 2011). Pratas-Santiago et al. (2017) also found that pacas and armadillos in Brazil were lunarphobic, while brocket deer, opossum, and pumas had a uniform activity pattern. Ocelot in Argentina did not exhibit a strong relationship between moon phase and activity with perhaps a slight tendency to be more active on brighter nights (Huck et al., 2017), while in our study ocelot had no pattern but were less active at full moon. Huck et al. (2017) showed that brocket deer and opossum were lunarphilic, while armadillo showed no distinct pattern; in our study, these species also had no pattern. Matos Dias (2017) found that the striped hognosed skunk was more active on bright moonlit nights (i.e., lunarphilic), in contrast to our finding that skunks had no pattern. Unlike our study, in which Baird's tapir exhibited no pattern, tapir in Mexico had a lunarphobic pattern (Sánchez-Pinzón et al., 2020).

Some predators may have shifted their nocturnal activity to track the activity of their main prey species (Table 4, Figure 7). Most notably, the dip in full moon
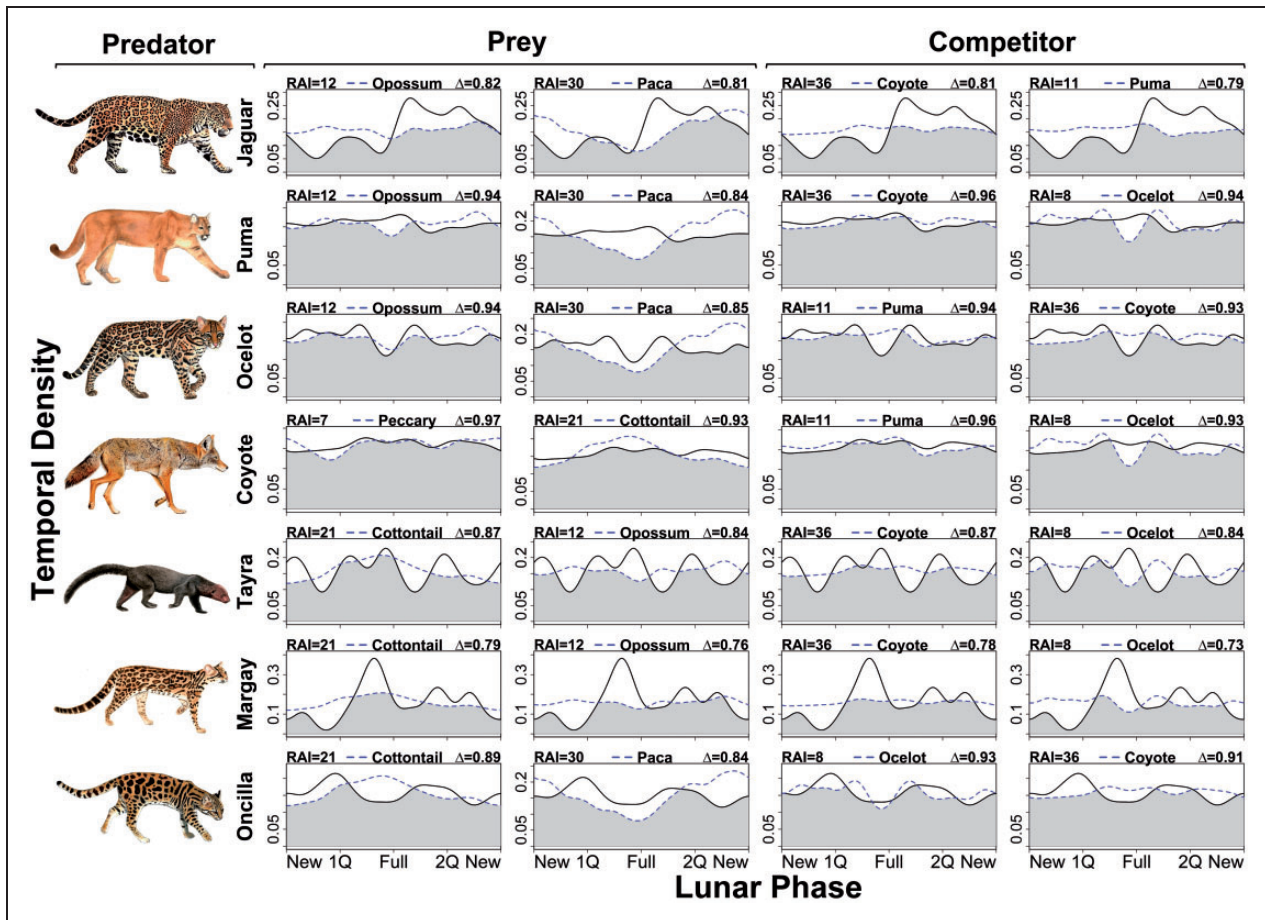
Figure 7. Activity Overlap Plots for Each of the Seven Predators in the Study (Predator) With the Predicted Primary and Secondary Prey Species (Prey) and the Predicted Primary and Secondary Competitors (Competitor) for That Predator. For each plot, temporal density is represented by the solid line (Predator) and broken line (Prey or Competitor); 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 Supporting Information S3–S9 for further details.

activity by ocelot corresponded to the lunarphobic pattern of their main prey (opossum and paca) with which they had high temporal overlap. This pattern supports the prediction that predators should reduce activity at times when major prey species are less active, in accordance with both the visual acuity and optimal foraging model (MacArthur & Pianka, 1966; Prugh & Golden, 2014). By reducing full moon activity, ocelot could also potentially reduce overlap with intraguild competitors such as puma and coyote, which have uniform activity patterns; however, the high overlap with those species (Δ = 0.94–0.95) suggests that intraguild competition may be less important than prey abundance in determining activity. If prey are abundant, predators may track their activity patterns regardless of high temporal overlap with competitors. Herrera et al. (2018) also found that temporal overlap occurred among jaguar, puma, and ocelot, and that the activity of jaguar and puma had strong overlap with medium- and large-sized prey,

while the activity of ocelot matched that of small-sized prey. They concluded that these felids synchronized their activity with that of their prey, and prey availability was a stronger predictor of predator activity than avoidance of competitors (Herrera et al., 2018). Similarly, a study of landscape use and co-occurrence patterns of three Neotropical spotted cats (ocelot, margay, and oncilla) failed to find evidence that any one species influenced the habitat use of any other species (Nagy-Reis et al., 2017). Also, a study of eight Neotropical forests concluded that prey availability was more important for space use of felids (jaguar, puma, ocelot) than species interactions (Santos et al., 2019).

Mixed Model Analysis

The two mixed models produced interesting and important insights. The lunar cycle model revealed that both cloud cover (which modifies moonlight) and tapetum

type (which reflects differences in night vision acuity) have a significant influence on when some animals are active at night during the lunar cycle. Opossums (which have an RT tapetum) would tend to be less active at full moon compared with carnivorans (with the CTC tapetum), while ungulates like deer and tapir (with the CTF tapetum) would reduce activity on cloudy nights under the full moon. Similarly, the logistic mixed model revealed that factors that influence lunar illumination (MRI and season) in conjunction with night vision acuity (associated with tapetum type) have a significant effect on whether animals are active during the night versus day. There was an overall trend for animals to be more active at night during brighter moonlight, although species with the CTF tapetum (deer, tapir, paca) tended to be less active during full moon; the opossums (with RT tapetum) were significantly associated with nocturnal activity. Although we readily acknowledge the complexity involved in these behavioral decisions, the tapetum lucidum plays a significant role in the timing of activity patterns. Regardless of the exact relationship among cloud cover, tapetum type, and nocturnal activity, the key factors identified by the predation risk and visual acuity hypotheses (moonlight and visual acuity, respectively) have been confirmed to play a role in regulating mammalian activity during both circadian and lunar cycles.

Predictions of the Alternative Hypotheses

Of the two hypotheses proposed to explain lunar activity patterns – the predation risk hypothesis and the visual acuity hypothesis – neither was completely supported by our results. The predation risk hypothesis predicts that, if predation is more successful under bright moonlight, prey species will become lunarphobic by reducing full moon activity. Although 50% of the prey species exhibited the reduction in full moon activity predicted by the predation risk model, the remaining species were either lunarphilic or exhibited no lunar activity pattern.

Our test of the visual acuity model incorporated the differential costs and benefits of lunar illumination given the taxon-specific night vision acuity indicated by tapetum type (Prugh & Golden, 2014). We predicted that prey with well-developed tapeta (superior night vision) would be lunarphilic whereas species lacking a tapetum (poor night vision) would be lunarphobic or unaffected by lunar phase (Prugh & Golden, 2014). Although the visual acuity model successfully predicted the flexible lunar activity of predators, it was only successful in predicting the nocturnal activity of 44% of prey species (7 out of 16 species). The mixed model analysis confirmed that tapetum type (as a proxy for night vision acuity) plays a significant role in determining the lunar activity

patterns of Neotropical mammals, thus providing partial support for the visual acuity model.

The significant influence of tapetum type on both circadian and lunar phase cycle indicates that lunar activity patterns may have a phylogenetic signal, the tendency of related species to resemble each other more than species drawn at random (Wu et al., 2017). An analysis of 1,914 tetrapod species revealed that diel activity patterns are phylogenetically conserved, with closely related species tending to share similar activity patterns (Anderson & Wiens, 2017). Prugh and Golden (2014) found a significant phylogenetic signal in the effect of illumination on nocturnal activity in their analysis. In a meta-analysis of 62 species, they found that moonlight had a lunarphobic effect on the taxonomic orders of Carnivora, Lagomorpha, and Rodentia regardless of visual acuity (Prugh & Golden, 2014). However, most of the 62 species in their analysis were rodents ($n = 38$) followed by primates and bats ($n = 18$), with only a single lagomorph, a single ungulate, and two carnivores – these results should therefore be most accurate for rodents. Interestingly, two of three rodent species in our study (paca and porcupine, but not diurnal agouti) exhibited a lunarphobic pattern (Table 4).

Another way to test the role of phylogeny would be to compare the lunar activity patterns of species from different geographical populations. If lunar activity is strongly constrained by genetic inheritance, we predict that different geographic populations of the same species will exhibit similar patterns. Table 5 tabulates all the relevant studies we were able to locate. To summarize, we identified 10 species for which lunar activity pattern was reported in two populations ($n = 5$), three populations ($n = 3$), and four populations ($n = 2$; Table 5). The comparison revealed only four species with complete cross-population agreement of activity pattern (jaguar, puma, tapir, cottontail), four species with partial agreement (ocelot, brocket deer, paca, armadillo), and two species that completely disagreed across populations (common opossum, four-eyed opossum). Thus, 40% of species surveyed support a strong phylogenetic signal indicated by a fixed lunar activity pattern in geographically separated populations. For example, all three puma populations exhibited no lunar pattern, and both cottontail populations exhibited a lunarphilic pattern (Table 5). But 60% of species displayed different lunar activity patterns in different populations, suggesting that many species exhibit behavioral plasticity in their lunar activity. We conclude that neither phylogenetic signal, tapetum lucidum as proxy for visual acuity, nor lunar illumination are able to reliably predict lunar activity patterns for all species, and natural selection may favor behavioral flexibility in nocturnal activity.

Table 5. Observed Lunar Activity Patterns of Mammals from Different Studies.

Species name	This Study	Harmsen et al. 2011	Michalski & Norris, 2011	Huck et al. 2017	Pratas-Santiago et al. 2017
Predators					
Panthera onca	No pattern	No pattern			
Puma concolor	No pattern	No pattern			No pattern
Leopardus pardalis	No pattern	No pattern		Lunarphobic	
Canis latrans	No pattern				
Eira barbara	No pattern				
Leopardus wiedii	Lunarphilic				
L. tigrinus oncilla	No pattern				
Prey					
Tapirus bairdii	No pattern	No pattern			
Odocoileus virginianus	No pattern				
Mazama temama	No pattern			Lunarphilic	No pattern
Pecari tajacu	No pattern				
Cuniculus paca	Lunarphobic	Lunarphobic	No pattern / Lunarphilic?		Lunarphobic
Nasua narica	No pattern				
Tamandua mexicana	Lunarphilic				
Dasypus novemcinctus	Lunarphobic	Lunarphobic		No pattern	Lunarphobic
Procyon lotor	Lunarphilic				
Dasyprocta punctata	No pattern				
Conepatus semistriatus	No pattern				
Coendou mexicanus	Lunarphobic				
Didelphis marsupialis	No pattern			Lunarphilic	
Bassariscus sumichrasti	Lunarphilic				
Sylvilagus dicei	Lunarphilic			Lunarphilic	
Philander opossum	Lunarphobic			No pattern	

Implications for Conservation

As diurnal "super predators", humans dominate 75% of Earth's land surface and are driving increases in nocturnal activity in medium- and large-bodied mammals (Benítez-López, 2018). A recent meta-analysis of 76 studies of 62 mammalian species on six continents (Gaynor et al., 2018) revealed a strong effect of human presence on the temporal activity of wildlife, with an average 36% increase in nocturnal activity in response to human disturbance. Nocturnal activity increased in response to a wide range of human impacts, lethal and nonlethal, including hunting, farming, and hiking; this suggests that animals perceive humans as threats whether or not they pose a lethal risk (Gaynor et al., 2018). Even seemingly innocuous ecotourism activities may cause mammals to shift to greater nocturnal behavior and decreased diurnal activity. The authors concluded that "fear of humans is the primary mechanism driving the increase in wildlife nocturnality" (p. 1233), which may have indirect effects on fitness, reproduction, survival, trophic interactions, and population persistence (Benítez-López, 2018; Gaynor et al., 2018). Thus, a better understanding of the nocturnal activity of mammals in relation to the lunar phase cycle can contribute to more holistic approaches and conservation tools to address the consequences of human encroachment on wildlife populations (Benítez-López, 2018).

Using a diversity of computational tools to analyze our robust dataset, this study has made two advances towards understanding the nocturnal behavior of wild mammals: (1) species are unlikely to practice a single fixed pattern of nocturnal activity across geographical ranges, but appear to exhibit behavioral plasticity in response to the unique combination of factors facing each population, and (2) a nexus of factors influence circalunar activity rhythms, including lunar illumination (as modified by lunar phase, moonrise/set, cloud cover, and season), night vision acuity (of which the tapetum lucidum provides but one measure), predation risk (as influenced by the previous factors plus the abundance and temporal overlap of predators), food availability, potential competitive interference, and perhaps phylogenetic signal.

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Supplemental Material

Supplemental material for this article is available online.

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