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Predators in Paradise: Ecotourism and Predator-Prey Dynamics in Monteverde, Costa Rica

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Chairperson: Mark Hebblewhite

Abstract

The use of camera trap surveys is increasingly common to investigate recurring diel activity of mammals. Investigation into the temporal overlap of mammals can provide unique insights into predator-prey dynamics. Understanding this relationship is essential to effectively manage and conserve both species. Extensive research across the tropics has found that daily activities of mammals were shaped by thermoregulation and trophic location in food webs. Although broad scale studies of daily patterns of mammals have enhanced our understanding of these constraints, many study sites included were remote protected areas under strict conservation measures. Such protected areas often had full complements of native species and low levels of human activity. For example, most studies of this kind in the Neotropics include both pumas (*Puma concolor*) and jaguars (*Panthera onca*). Thus, Neotropical predator-prey activity patterns may differ in areas of higher human activity, such as private land reserves or in areas where pumas are the apex predator. To test the effect of ecotourism on temporal overlap of predator-prey species, I used remote camera trapping data collected from Monteverde, Costa Rica. The data I used was collected from 16 remote cameras deployed over 819 camera trap nights. Cameras were placed on two private land reserves in the greater Monteverde area in 2021-2022. Both sites differed significantly in their amount of human activity in the form of recreational hikers. I analyzed daily activity patterns and temporal overlap using the R package 'overlap' to test whether overlap of predator-prey species differed in areas of high human activity compared to areas of lower human activity. During my study, I detected 21 pumas, 23 ocelots *(Leopardus pardalis)*, 55 collared peccary (*Pecari tajacu*), 258 white-nosed coatis (*Nasua narica*), 674 Central American agoutis (*Dasyprocta punctata*), and 1507 humans. In general, overlap between predators and prey increased by about 23% at the site with higher human activity. For example, pumas overlapped more with agouti (by 29%) and coati (by 23%) in the site with higher human use. These results support the mutual attraction hypothesis outlined by Van Scoyoc et al. (2023) that predicts human activity will increase predator-prey overlap. My results have potential implications for ecotourism management in Monteverde and other Neotropical locales.

Keywords: Camera trapping, Costa Rica, cloud forest, ecotourism, puma, ocelot, predator-prey, diel activity, temporal activity

Introduction

The use of camera trap surveys is becoming increasingly common as researchers discover the myriad of questions they can answer (Rowcliffe & Carbone 2008, Wearn & Glover-Kapfer 2019). Camera trapping has long been used to improve estimates of species distributions, relative abundance, and even population abundance for individually recognizable species (De Luca & Rovero 2006, Sharma et al. 2010 Cove et al. 2013). Data obtained from camera trap surveys can provide a greater understanding of species behavior, niche partitioning among species, and diel activity patterns (Di Bitetti et al. 2010, Edwards et al. 2015, Vallejo-Vargas et al. 2022). Camera trap data can also provide insights into species interactions such as predator prey-dynamics (Linkie & Ridout 2011, Ramesh et al. 2012, Kachel et al. 2022).

Knowledge of predator prey-dynamics is essential to effectively manage and conserve both species, as the relationship between predator and prey has significant effects on the behavior of both species (Laundré 2010). Prey individuals choose their habitat based on resource availability and predation risk, while predators often select habitats based on prey abundance and different prey responses in those habitats (Abrams 2007). Like prey species, predators may show differences in circadian activity patterns to avoid other predators (de Stage, Teichman, & Cristescu 2017). Temporal niche partitioning is an important process for predators to avoid intraguild predation or competition (Hayward et al. 2009). It is believed that temporal partitioning is a significant factor allowing the coexistence of sympatric carnivore species (Di Bitetti et al. 2010, Edwards et al. 2015). Temporal partitioning is typically dictated by body size, with smaller species minimizing their overlap with larger dominant predators (Hayward and Slotow 2009, Edwards et al. 2015), with changes in diel activity being large or fine scale (Dröge et al. 2017, Müller et al. 2022).

Researchers often study temporal niche partitioning by estimating diel activity patterns across species (Santos et al. 2019). Diel activity refers to the distribution of a species' activity throughout the daily cycle (Vasquez et al. 2019)**.** Diel activity of predator and prey species can vary from either increasing overlap in time through attraction, or, reducing overlap through avoidance (Kamler et al. 2012, Botts et al. 2020). Recent studies have shown that such diel activity patterns of tropical mammals are constrained by thermoregulation and a species position in a trophic food web. For example, in their global analysis across 16 tropical forests**,** Vallejo-Vargas et al. (2020) showed that large herbivores are constrained chiefly by thermoregulation, focusing their activity during the cooler night. Yet mid-sized omnivores and insectivores focused their circadian patterns to minimize overlap with large predators, while large predators seek to maximize their temporal overlap with prey species, although we see variation in all classes due to human disturbance.

It is well understood that anthropogenic effects can also have a significant effect on the diel activity of mammals. An extensive meta-analysis of 76 studies across six continents found that mammals worldwide are increasingly becoming nocturnal due to human activities, including non-consumptive activities such as hiking (Gaynor et al. 2018). Furthermore, a review of 246 studies by Seveque et al. (2020) found 46 reported effects of human disturbance specifically on carnivore niche portioning regarding trophic status, spatial use, and diel activity. The shifting of mammalian diel activity may have profound effects on temporal overlap of predator and prey species (Murphy et al. 2021). Patterns of avoidance known as “human shields” occur in which prey species are attracted to areas of human presence to find relief from predators (Berger 2007). An analysis of 19 studies encompassing 178 predator-prey dyads found 4 four behavioral pathways by which humans increase or decrease predator-prey spatiotemporal overlap: predator attraction, mutual attraction, mutual avoidance, and prey refuge (Van Scoyoc et al. 2023, Figure 1). Mutual attraction and mutual avoidance cause an increase in temporal overlap, while prey refuge and predator attraction decrease overlap of predator and prey species. (Figure 1; reproduced from Van Scoyoc et al. 2023)

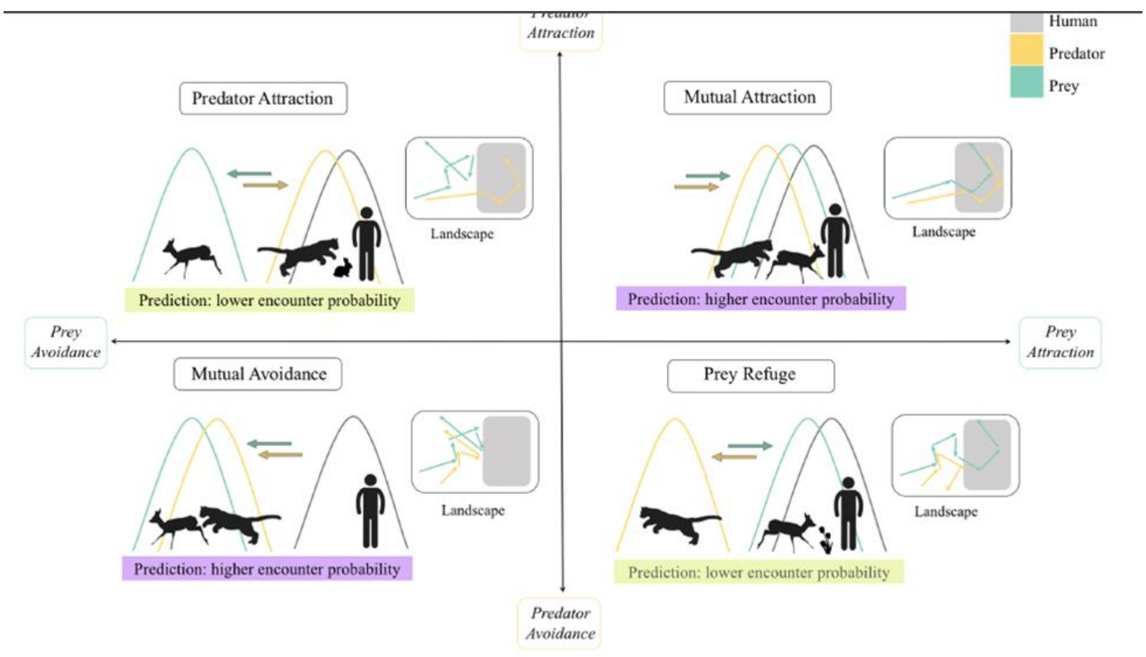


Figure 1: Potential effects of shifts in diel activity patterns of predator-prey species in response to human activity, ranging from mutual attraction/avoidance to predator/prey attraction or avoidance. Reproduced from Van Scoyoc et al. 2023.

The ecotourism industry's rapid growth has raised questions about its effects on wildlife in the Neotropics (Dunstone & O'Sullivan 1996, Blangy & Mehta 2006, Zambrano, Broadbent, and Durham 2010, Das 2011). Ecotourism is defined as "responsible travel to natural areas that conserves the environment, sustains the well-being of the local people, and involves interpretation and education." (TIES 2015). Research on ecotourism as a tool for conservation and its effects on wildlife show positive and negative effects, with many studies showing behavioral changes due to human presence (Grossberg et al. 2003, Cunha 2010, Das & Chatterjee 2015, Geffroy et al. 2015). Human activity within popular ecotourism areas can have profound effects on the diel-activity patterns of mammals (Kobayashi 2021). Nocturnal species may experience less of a hindrance than diurnal and cathemeral species because tourist activity is typically highest during the day, which was demonstrated by Ouboter et al. (2021) in Brownsberg Nature Park, Suriname. In that study, predatory species such as jaguars *(Panthera onca)* and pumas *(Puma concolor)* showed an increase in nocturnal activity due to human presence. Alternatively, diurnal prey species such as the Amazonian brown brocket deer *(Mazama nemorivaga)*, red acouchi *(Myoprocta acouchi)*, and red-rumped agouti *(Dasyprocta leporina)* showed an increase in early morning activity, likely to avoid the larger crowd of hikers in the evenings. Human presence through ecotourism may alter temporal overlap of predator-prey species, resulting in decreased foraging efficiency of predators and significant effects on the structure, function, and biodiversity of the ecosystem (Kerley et al. 2002, Kobayashi 2021). These effects may be most profound in popular ecotourism countries such as Costa Rica.

Monteverde is a town located in the Cordillera de Tilarán mountain range approximately 140 kilometers northwest of the capital, San Jose, Costa Rica This isolated mountain town with a population of 4,155 people (in 2011) hosts a growing ecotourism industry as the regions primary source of income, with 150,000-200,000 visitors a year (INEC Costa Rica 2011, Nadkarni & Wheelwright 2014). The Monteverde Cloud Forest Preserve is a 4025-hectare private preserve that welcomes 70,000-80,000 visitors per year. With increased visitation, infrastructure upgrades to the existing 13 kilometers of public trails include expansion of the trail network, trail widening and hardening, adding a hanging bridge, and a waterfall viewing platform (Nadkarni & Wheelwright 2014). Ninety-Seven percent of the preserve has absolute protection; 1% is zoned for special use and 2% is for public use. The Monteverde Cloud Forest Preserve has become the core reserve of a growing private land refuge network including many other private reserves such as Curi-Cancha Wildlife Refuge, the Crandell Reserve, and other lands managed for biodiversity tourism.

To test the effects of human presence on diel activity of neotropical mammals, I analyzed camera trap data from 2 private land reserves in Monteverde, Costa Rica, an area with significant human presence in the form of ecotourism. Operating under the assumption that predators will seek to maximize temporal overlap with abundant prey and that ecotourism will affect mammalian diel activity patterns, I hypothesize human activity in the form of ecotourism will cause increased nocturnal activity in predators and a peak of early morning activity by prey species. I tested the prediction that sites of greater human presence in the form of hikers will show greater nocturnal activity of carnivores and a peak in early morning activity by prey species, an example of prey refuge as outlined by Van Scyoc et al. (2023) in Figure 1. I also considered alternative hypotheses of mutual attraction, mutual avoidance, and predator attraction (Figure 1)

Methods

Study Area

I investigated these questions in two private nature reserves adjacent to the larger Monteverde Cloud Forest Preserve lands in the Monteverde region. First, I studied diel activity of mammalian predators and prey on the Crandell Memorial Reserve (MVI), a 32-acre conservation land trust administered by the Costa Rica Conservation Foundation (MVI 2022). It comprises secondary regenerating tropical cloud forest rising in an elevation gradient from 1400m-1500m with some of our study area on the largest private land reserve in the Monteverde region, the Bosque Eternos de los Ninos (Figure 2). Second, I studied lands owned by the Centro de Educacion Creativa Cloud Forrest School (CEC). The Cloud Forest School is an independent school located on 106 acres of cloud forest adjacent to the town of Santa Elena (Centra de Educacion Creativa 2022). CEC lands also encompass regenerating secondary tropical forest at elevations ranging from 1450m-1550m. Both study areas include a series of trails open to the public and used for outdoor education of large groups of students. The data for this study was collected by Mark Hebblewhite from 2021-2022 as part of an effort to evaluate the application of camera trap surveys in Costa Rica.

Species

The greater Monteverde area hosts at least 90 species of mammals (Nadkarni & Wheelwright 2014). During these camera trap surveys, I only detected and identified the following species: puma *(Puma concolor)*, ocelot *(Leopardus pardalis)*, jaguarundi *(Herpailurus yagouaroundi)*, tayra *(Eira barbara)*, coyote *(Canis latrans)*, collared peccary *(Pecari tajacu)*, white-nosed Coati (*Nasua narica*), Central American agouti (*Dasyprocta punctata*), nine-banded armadillo (Dasypus novemcinctus), opossums (*Didelphis* sp.), and various species in order Rodentia. Due to high mammal diversity and low image quality, many images were impossible to classify to species, such as *Didelphis* sp. and order Rodentia. Photos of unknown species were sent to M. Hebblewhite, H. Robinson, or other experts for consultation. I identified possible prey species for each predator with the following studies on scat analysis or overlap in diel activity: puma, (Aranda & Sanchez-Cordero 1996, Foster et al. 2010, Gomez-Ortiz & Monroy-Vilchis 2013, Rueda et al. 2013, Avila-Najera et al. 2018) ocelot, (Moreno et al. 2006, Bianchi et al. 2010, Rocha-Mendes et al. 2010) coyote, (Aranda et al. 1995, Moreno et al. 2006, Cruz-Espinoza et al. 2010, Martinez-Vasquez et al. 2010) and margay, (Bianchi et al. 2011, Seibert et al. 2015, Rinaldi et al. 2015).

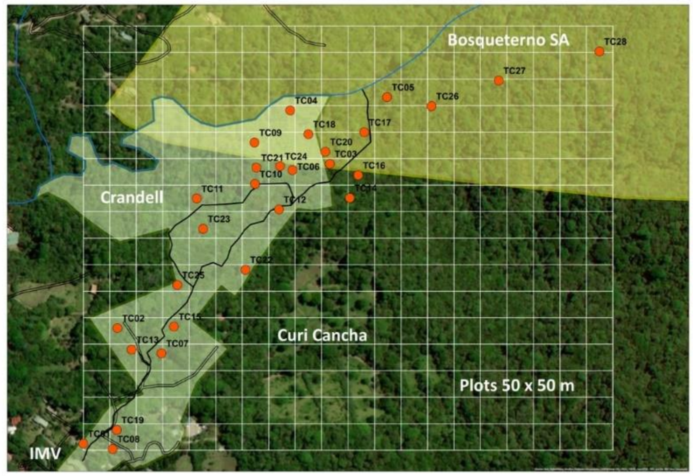


Figure 2: Camera trap sites on the Monteverde Institute Site (MVI) from 2021/2022 to investigate the effect of increased human presence on temporal overlap of predator-prey species.

Camera Array

Camera trap locations were selected by choosing random locations along trails in a 50x50 meter sampling grid within each of the two study sites. For example, Figure 2 shows the camera trap sampling design for the Crandell Nature Reserve field site. (Figure 2). The nearest suitable tree was selected (within ~50 meters of the trail) that would allow a single camera to detect at least 10 meters. Cameras were faced in the direction of the least vegetation and typically faced along trails, not perpendicular. This was done to maximize the time the animal was in the frame. If cameras were placed on a slope, the camera was faced so that it would traverse the slope, as opposed to facing up or down hill. Trail cameras were placed at knee height (approximately 50cm) and vegetation within approximately 5 meters was cleared.

The two study sites had differing numbers of cameras of differing sampling duration. At MVI, I used data from 11 cameras over 305 days. Conversely, at CEC I used 5 cameras set on a video setting- which influenced my classification approach. Cameras collecting video footage were out for 514 days.

Image Classification

For the Crandell Reserve site (MVI), I classified 5,002 images using the artificial intelligence (AI) classification systems developed by Wildlife Insights. Wildlife Insights is a public platform that utilizes machine learning models to manage, analyze, and share camera trap data (Ahumada et al. 2020, Wildlife Insights 2023). Photos are placed into one sequence based on the time between photos, allowing researchers to classify multiple photos simultaneously and record multiple photos as one occurrence or capture. Features such as these greatly streamline the classification process and reduce time in classifying species. Researchers are given the AI recommended species identification for each 'sequence' and can manually correct misclassified species. Preliminary data suggests species were correctly classified > 95% of the time, even in Monteverde. Example species that Wildlife Insights struggled to correctly classify margay versus ocelot, opossums, and rodents. Manually correcting the few incorrect classifications took minimal time investment compared to classifying all 5,002 images without Wildlife Insights.

At the Cloud Forest School (CEC) site, I processed 4,335 videos using Timelapse software (Greenberg & Godin 2012**)**. Timelapse is a free software that allows researchers to create a Graphic User Interface (GUI) template that specifies what data should be taken from each image, how that data should appear in the user interface, and how data output should be organized (Greenberg & Godin 2012).

Statistical Analysis

To analyze camera trap data from both sites for temporal overlap of predator-prey species, I used the program R package "overlap" (Ridout & Linkie 2009). This R package easily converts circular circadian activity patterns recorded in hours and minutes to more easily analyzed geometric data. The amount of temporal overlap is then estimated using kernel smoothing and/or bootstrapping and estimates "coefficient of overlapping", or Δ. The coefficient of overlapping measures the amount of agreement of two probability distributions from 0 (no overlap) to 1 (complete overlap) (Schmid & Schmidt 2006). Because overlap data are not often normally distributed, I used bootstrapping methods to estimate the overlap statistic (Δ -hat) and to estimate a 90% confidence interval, I ran a bootstrap test with 1,000 repetitions and used the "bootCIlogit" function appropriate for binomial 0-1 data within the "overlap" package. Because I used the bootstrap Δ-hat statistic, I used the corresponding bias-corrected confident interval using the "basicθ" estimator in Linkie and Ridout (2009) column.

To test my hypothesis regarding differences in predator-prey overlap between areas of high and low human presence, I tested for significant differences in overlap statistics for the same predator-prey dyads at both sites. For example, I compared overlap between puma and agouti at both sites, then tested whether overlap changed significantly. I calculated overlap for each predator-prey dyad at each site from the mean of the bootstrap distribution (Δ-hat). Differences between sites were deemed significant if the average margin of error of the two distributions was less than ½ of their agreement as outlined in Rule 4 of Cumming et al. (2005). However, for some species (see results) with few detections, I calculated overlap statistics for predators and prey pooled across study sites to test whether patterns of predator-prey overlap were consistent with previous studies.

Results

At MVI I had a total of 3,394 images from 11 cameras over 305 camera nights. At MVI I detected and classified 4 puma, 6 ocelot, 2 margay, 1 coyote, 185 agouti, 10 collared peccary, 36 white nosed coati, 5 opossums, and 51 humans (Table 1). At CEC I had a total of 1606 images from 5 cameras and 4,335 10 second videos over 514 camera nights. At this site I detected and classified 17 puma, 17 ocelot, 18 margay, 217 coyote, 489 agouti, 45 collared peccary, 222 white-nosed coati, 37 opossums, and 1,456 humans (Table 1). Based on these data, I classified CEC as the site of high human presence and MVI as the site of low human presence.

Table 1. Total camera detections of each species at MVI and CEC from the 2021/2022 camera trap project in Monteverde, Costa Rica.

Species	MVI	CEC
Puma	4	17
Ocelot	6	17
Margay	2	18
Coyote	1	217
Agouti	185	489
Collared Peccary	10	45
White-nosed Coati	36	222
Armadillo	51	75
Opossum	5	37
Rodent	49	1
Human	51	1456

There was a total of 21 puma detections during this study (Table 1). When compared to MVI, pumas at CEC had significantly increased overlap with agouti (29%) and collared peccary (44%) (Table 2, Figure 2). Pumas also showed a 26% increase in overlap with humans at CEC. An increase in overlap of pumas with white-nosed coati (10%) and with armadillos (22%) was recorded at CEC when compared to MVI but overlap values larger than ½ the margin of error suggests these differences are not significant (Table 2, Figure 2).

There was a total of 23 ocelot detections during this study (Table 1). At CEC ocelots showed a significant increase in overlap with agouti (29%), white-nosed coati (25%), and collared peccary (41%)

when compared to MVI (Table 2, Figure 3). Ocelot-human overlap also increased at CEC compared to MVI by 28% (Table 2, Figure 3). Ocelots also showed an increase in overlap with armadillos (8%), but an overlap greater than ½ the margin of error suggests that the result is not significant.

I captured a total of 20 margay and 218 coyotes (Table 1). I was unable to compare the overlap between sites because of the small number of captures at MVI. Between both sites margay had the highest overlap with opossums (Δ-hat= 0.722), armadillos (Δ-hat=0.680), and small rodents (Δ-hat=0.645) (Table 3). Coyotes had the highest overlap with peccary (Δ-hat=0.800), armadillos (Δ-hat=0.686), and small rodents (Δ-hat=0.667) (Table 3).

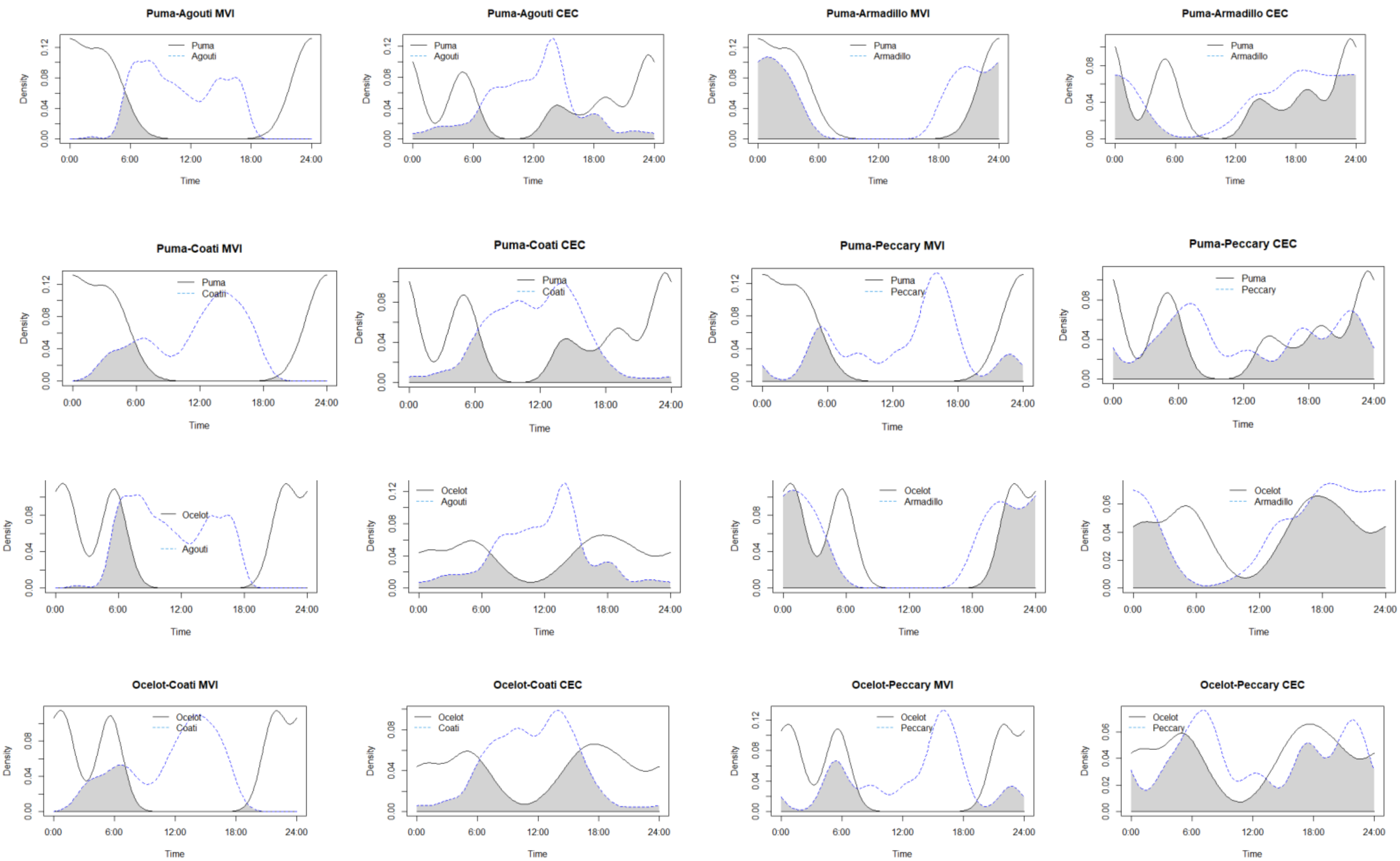
Table 2 – Statistical summaries comparing predator-prey and human-wildlife temporal overlap calculated using the R package 'overlap' at two sites in Monteverde, Costa Rica, the Monteverde Institute (MVI) and Cloud Forest School (CEC), 2021/2022.

Species	Species 2	Δ hat - MVI	90% CI - MVI	Δ hat - CEC	90% CI - CEC	Difference	Statistical Significance
Puma	Agouti	0.141	0.011-0.346	0.43	0.288-0.541	0.289	Significant
Puma	Armadillo	0.586	0.408-0.880	0.683	0.522-0.828	0.097	No difference
Puma	Coati	0.182	0.044-0.400	0.408	0.262-0.528	0.226	No difference
Puma	Peccary	0.227	0.054-0.595	0.673	0.536-0.809	0.446	Significant
Ocelot	Agouti	0.214	0.038-0.404	0.499	0.347-0.604	0.285	Significant
Ocelot	Armadillo	0.621	0.425-0.859	0.702	0.614-0.863	0.081	No difference
Ocelot	Coati	0.239	0.095-0.408	0.493	0.338-0.625	0.254	Significant
Ocelot	Peccary	0.294	0.108-0.586	0.707	0.602-0.880	0.413	Significant
Human	Agouti	0.594	0.469-0.720	0.81	0.764-0.840	0.216	Significant
Human	Armadillo	0.192	0.073-0.245	0.333	0.241-0.373	0.141	Significant
Human	Coati	0.671	0.572-0.827	0.831	0.784-0.872	0.16	Borderline
Human	Ocelot	0.099	0.007-0.138	0.383	0.228-0.480	0.284	Significant
Human	Peccary	0.582	0.442-0.815	0.487	0.369-0.561	0.095	No difference
Human	Puma	0.061	0.001-0.152	0.318	0.191-0.428	0.257	Significant

Table 3. Temporal overlap of ocelot and coyote with potential prey species pooled across MVI and CEC.

Species 1 (All Locations)	Species 2	Δ	Δ-hat	90% CI
Margay	Armadillo	0.679	0.680	0.528-0.800
Margay	Coati	0.195	0.237	0.128-0.285
Margay	Opossum	0.749	0.722	0.598-0.859
Margay	Rodent	0.652	0.645	0.478-0.805
Coyote	Agouti	0.540	0.573	0.488-0.589
Coyote	Armadillo	0.663	0.686	0.594-0.733
Coyote	Coati	0.546	0.564	0.488-0.601
Coyote	Peccary	0.808	0.800	0.725-0.877
Coyote	Opossum	0.585	0.590	0.474-0.687
Coyote	Rodent	0.639	0.667	0.545-0.737

Figures 2 & 3. Temporal overlap of predator-prey species at MVI and CEC from Monteverde, Costa Rica camera trap survey 2021/2022. Solid black lines are predator activity, dotted blue lines are prey activity, and the grey shaded region is the overlap in temporal activity.



Discussion

Pumas are considered cathemeral "generalists" in that they will alter their diel activity to maximize their overlap with abundant prey species (Botts et al. 2022). Conversely, ocelots are typically nocturnal throughout their range with the ability to adjust their activity slightly to extrinsic factors (Sandoval-Serés et al. 2022). In my study, there were only enough detections of puma and ocelot to test for differences in overlap between these predators and their prey between both sites. Both puma and ocelot showed increased daytime activity with increased human presence resulting in a significant increase in overlap between humans and prey species. These results show that ocelots at CEC may not be typically nocturnal, as commonly reported for this species (Sandoval- Serés et al. 2022). These results do not support my hypothesis that carnivores would show increased nocturnal activity in response to human presence, resulting in a "prey refuge" effect where overlap of predator-prey species is decreased (Van Scoyoc et al. 2023). Instead, my results are more consistent with the "mutual attraction" hypothesis as in Figure 1 by Van Scoyoc et al. (2023)

Similarly, Morris (2005) highlighted an example of "mutual attraction" (Van Scoyoc et al. 2023) in Canada's boreal forest. Supplemental feeding of red-backed voles (*Clethrionomys gapperi*) increased their overlap with black bears (*Ursus americanus*), resulting in increased predation. Additionally, Murphy et al. (2021) found increased spatiotemporal overlap of predators and prey in response to human disturbance in Pennsylvania. Black bears and white-tailed deer fawns (*Odocoileus virginianus*), bobcats (*Lynx* rufus) and fawns, and coyotes (*Canis latrans*) and adult male deer had significantly higher spatiotemporal overlap because of anthropogenic change. On the contrary, Kobayashi (2021) demonstrated an example of "prey refuge" in Peninsular Malaysia. High human activity caused increased nocturnality in carnivores and an increase in diurnal activity of mouse deer (*Tragulus sp.*), resulting in decreased temporal overlap of both species. Furthermore, a study in southwest Alberta revealed that trails with greater than 32 humans per day yielded three times the abundance of prey species, while trails with greater than 18 humans per day showed a significant decrease in predator abundance (Muhly et al. 2011). Berger et al. (2007) coined the term "human shield" (prey refuge in Figure 1) after he recorded female moose (*Alces alces*) shifting birthing sites closer to roads to avoid brown bears (*Ursus arctos).* In my study area, there was no visible feeding like Morris (2005) implemented in the boreal forest, but increased overlap of humans occurred raising the question of how? The differences in prey abundances between sites may have been driving the activity patterns of predators.

Studies have shown differing changes in spatiotemporal activity of pumas in response to human activity. Increased human activity in the Atlantic Forest of Argentina caused increased nocturnality of pumas (Paviolo et al. 2009). Inversely, Figel et al. (2020) found that pumas in Colombia make relatively small changes in response to human activity, especially when compared to jaguars. Increase in overlap with humans is not likely a product of pumas directly seeking out humans, but more likely an effect of differential prey selection between the two sites. Armadillo captures were abundant in both sites, but peccary captures were limited at MVI (Table 1). As armadillos and peccary are important prey items for pumas (Aranda & Sanchez-Cordero 1996, Foster et al. 2010, Gomez-Ortiz et al 2013 Rueda et al. 2013, Avila-Najera et al. 2018), pumas may be maximizing their overlap with armadillos at MVI, leading to increased nighttime activity, resulting in less overlap with humans. Pumas maximizing their overlap with peccary at CEC would increase their daytime activity, therefore increasing overlap with humans and agouti. Similar changes in temporal activity were seen in ocelots.

Ocelots also showed increased daytime activity with increased human presence leading to a significant increase in overlap with humans. Ouboter et al. (2021) found that ocelots were positively correlated with numbers of hikers and postulated that this shift in behavior is due to release of competition or predation from pumas and jaguars. This is unlikely to be the case in Monteverde as jaguars were absent or occurred at very low densities and pumas did not show patterns of temporal avoidance of humans. The increase in daytime activity of predators may be a product of differences in prey availability between the two sites. At MVI, there were 49 captures of small rodents, whereas there was 1 capture of small rodents at MVI (Table 1). As small rodents have been shown to be a significant portion of ocelot diet (Bianchi et al 2010, Rocha Mendes et al. 2010) and as all rodent captures occurred at night in my study, it is possible that the lack of rodents at CEC caused ocelots to select more abundant diurnal prey species, such as coati and agouti, thus increasing their overlap with humans.

It is unclear why many prey species had increased overlap with humans at CEC. Although I saw no evidence of wildlife feeding by humans, it is possible that it may have played a role in increased overlap with humans. Craighead et al. (1995) observed grizzly bears in Yellowstone National Park expand their home range by five-fold when the dump within the park was closed, suggesting that human food sources were a significant attractant. Additional patterns of wildlife attraction to human food sources have been seen in Manuel Antonio National Park in Costa Rica (Farrera 2016). Racoons (*Procyon lotor*) within the park have decreased their range in recent years and have increased their diurnal behavior to overlap with peaks of human activity (Farrera 2016). Monkeys and raccoons within the park commonly steal food from tourists and have even learned to open tourists' bags in search of food. Increased overlap of prey species may also be a result of strict hunting laws and environmental protections in Costa Rica, as human hunting has been shown to elicit behavioral changes as methods to avoid humans (Reimers et al. 2009, Marantz et al. 2016, Brown et al. 2020). For example, Carrillo et al. (2000) showed that areas in Costa Rica with less strict hunting laws and less supervision had consistently lower mammalian species abundance and diversity. Hunting was largely banned in 2012 in Costa Rica except for the cases of population control, wildlife research, and subsistence hunting (Asamblea Legislativa de la República de Costa Rica 2012). This law was created as a Law of Popular Initiative, in which citizens submit laws directly to Congress (Mckinney 2012) and represents the country's history of disapproval of sport hunting (Drews 2002, Murillo & Huson 2014). It is unknown whether a country's history of hunting protections have long term effects on wildlife behavior. This gap in knowledge highlights an opportunity for further research on the effects of historical wildlife management on temporal predator-prey overlap in Costa Rica compared to other Neotropical areas.

Although coyote and margay detections were too low at MVI to compare predator-prey overlap between sites, analysis of overlap between both species and their possible prey showed congruencies to Botts et al. (2020), a thorough study of diel activity patterns of mammalian predators and prey in Costa Rica. Because opossums and small rodents are a principal food source for margay (Binachi et al. 2011, Seibert et al. 2015) it was not surprising to find a high degree of overlap between margay and both species. Additionally, margay had a high degree of overlap with armadillos, which was surprising and has not been reported before. As peccary and small rodents are common food items for coyotes (Moreno, Kays, & Samudio 2006, Martinez-Vazquez et al. 2010) it was expected to see a high degree of overlap between coyotes and the two species. Like margay, coyotes had a relatively high degree of overlap with armadillos.

The reason for the difference in detections of coyotes and margay between sites is not entirely clear. As previously stated, several species of opossum are often important prey items for margay (Bianchi et al. 2011, Seibert et al. 2015). The difference in detections between sites may therefore be due to low abundances of their main prey species, such as small rodents and opossums (Table 1). Alternatively, as margay commonly prey on arboreal species (Rinaldi et al. 2015), a lack of terrestrial species may have forced margay at MVI to switch to arboreal species resulting in fewer detections on the ground. The lack of detections of coyotes at MVI may be due to constraints in denning behavior. Coyotes at CEC seemed to use the CEC grounds for a rendezvous site and could be heard howling frequently (M. Hebblewhite, pers comm). Little is known about den site selection by coyotes in the Neotropics, however, it could be a fruitful topic of study to further our understanding of coyote breeding habits in the region. This is especially noteworthy as coyotes have only recently expanded to all of central America, and are poised to colonize south America (Hody and Kays 2018)

My study had several additional limitations that created difficulties when attempting to draw strong conclusions. A sample size of 819 camera trap days is the chief limitation of this study. Previous studies in Costa Rica investigating overlap of predator-prey species had sample sizes of 10,581-59,919 camera trap days by comparison (Herrera et al. 2018, Botts et al. 2020). Kays et al. (2020) recommends 3-5 weeks of surveying across 40-60 sites to precisely estimate species richness, occupancy, and detection rates in tropical forests. An additional limitation of this study is the lack of analysis of spatial overlap of predator-prey species, as human presence can affect both the use of time and space by wildlife. For example, Griffiths & Van Schaik (1993) found that in Sumatra, large mammals actively avoided areas of greater human presence and carnivores such as the tiger (*Panthera tigris sumatrae)* and sun bear (*Helarctos malayanus)* increased their nocturnal activity in response to humans. The marked increase in detections at CEC compared to MVI may also be due to greater survey time (305 days vs. 514 days). Additionally, increased detection at CEC compared to MVI may be a result of cameras at CEC recording 10 second videos as opposed to still images, although research suggests that detection rates between photo and video do no differ significantly (Green et al. 2022). Both sites were also similar in their vegetation history, as they were both regenerating secondary forests adjacent to higher elevation primary montane cloud forests, but there may have been other unmeasured differences between sites that affected my study. Finally, whether my results – mutual attraction – hold at private wildlife reserves such as the Monteverde Cloud Forest Preserve with higher human visitation rates remains to be tested. Hopefully my study inspires such broader scale comparisons in the Monteverde region.

In this study I used camera trap data from Monteverde, Costa Rica to investigate the effects of ecotourism on temporal overlap of predator-prey species. I found that increased human presence resulted in increased predator-prey overlap and increased overlap of carnivores and humans. Several prey species also showed increased overlap with humans, exhibiting an example of mutual attraction. This finding did not support my prediction that higher human presence would cause increased nocturnality of carnivores and distinct early morning peaks of activity by prey species, a pattern of mutual avoidance. These findings did not agree with previous studies showing patterns of prey refuge in response to increased human presence at ecotourism sites (Kobayashi 2021, Ouboter et al. 2021). It is unlikely that increased diurnal activity of carnivores was a function of carnivores actively seeking out humans, but instead may be a function of carnivores selecting the most abundant prey at both sites, with nocturnal prey being more abundant at MVI and diurnal prey being more abundant at CEC. The cause for the increase in temporal overlap of humans and prey species is unclear, but it is possibly due to prey species attraction to human food sources or the country's strict hunting laws and history of environmental protection. Regardless of the mechanisms, these results suggest that ecotourism in Monteverde does not decrease temporal overlap of carnivores and their principal prey species at these 2 private wildlife reserves. Therefore, ecotourism may be a sustainable avenue to protect, conserve, and restore wildlife habitats without detriment to temporal overlap of predator-prey species.

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