Examining the temporal and spatial behavior of *Pecari tajacu* at La Selva Biological Station, Costa Rica

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Abstract

Historically, peccary populations existed in northeastern Costa Rica with relatively even proportions through the mid-1960s. However, in recent years, collared peccaries (*Pecari tajacu*) have become the dominant species in La Selva. The severe decline of apex predators like jaguars (*Panthera onca*) and pumas (*Puma concolor*), which are the primary predators of collared peccaries, has also contributed to recent peccary population growth in La Selva. This release from predation, increased exposure to humans, and tendency to congregate around human dwellings and laboratories has resulted in the collared peccaries becoming habituated to humans in and around La Selva. We established camera traps at 44 sites along a spatial gradient away from the high human traffic areas and throughout the trails of La Selva. We used the camera detection data to construct density plots of peccary diel activity patterns. We also used these data to construct binary detection histories for analyses in an occupancy modeling framework. We tested the effects of multiple habitat covariates on the probability of peccary occupancy and detection. We found that peccary activity patterns differed in areas further away from human-influenced settings when compared to wild (>3km from the lab clearing) settings. This could be a result of the lack of peccary associations with humans and increased predation risk in wild settings. In addition, we found that forest cover had the strongest effect on the probability of peccary detection. Our results suggest that peccaries alter their behavior along a gradient away from humans and in different cover types (e.g., primary forest), which we suggest might be related to increased predation pressure away from the human-shield and decreased cover availability and increased predation risk in primary forest.

Introduction

La Selva Biological Station (hereafter La Selva) is characterized by its high biodiversity and net primary productivity (Romero et al., 2013). Historically, peccary populations existed in northeastern Costa Rica with relatively even proportions through the mid-1960s (Romero et al., 2013). However, in recent years, collared peccaries (*Pecari tajacu*) have become the dominant species in La Selva. This timeline corresponds with the extirpation of white-lipped peccaries, which have not been observed in this region in over 35 years (Romero et al., 2013). This is a result of anthropogenic pressures including over-hunting and habitat loss (Peres 1996; Chiarello 1999; Cullen et al. 2000). White-lipped peccaries are competitively dominant over collared peccaries in areas of co-occurrence (Altrichter and Boaglio 2004; Keuroghlian et al.2004; Mendes Pontes and Chivers 2007). However, collared peccaries are more resilient and less susceptible to these anthropogenic pressures than the largely gregarious white-lipped peccaries (Cullen et al. 2000; Altrichter and Boaglio 2004).

The severe decline of apex predators like jaguars (*Panthera onca*) and pumas (*Puma concolor*), which are the primary predators of collared peccaries, has also contributed to recent peccary population growth in La Selva (Pardo et al., 2016). This release from predation, increased exposure to humans, and tendency to habituate readily to human encounters has resulted in the collared peccaries becoming habituated to humans in and around La Selva. This behavior reflects the human shield hypothesis which states that prey will alter their predator avoidance strategies to associate with humans due to the indirect effects of humans in deterring predators (Geffroy et al., 2015). Because of this habituation to humans it is possible that peccaries have become bold when associated with humans. This could result in the loss of collared peccaries' fear of other predators and the alteration of the perceived landscape of fear. The term "landscape of fear" is derived from the concept of the "ecology of fear" (Bleicher et al., 2017). The landscape of fear is defined as the spatial distribution of a prey species' perception of the costs and benefits associated with the acquisition of resources and risk of predation (Brown et al.1999; Bleicher et al., 2017).

There were two major objectives in this study. First, we stationed camera traps along a gradient away from human activity to estimate activity patterns of collared peccaries. We hypothesized that activity patterns would be different in peccaries further away from the lab clearing when compared to peccary activity near the lab clearing. We expected to find that peccaries further from the lab clearing have activity patterns that reflect diurnal behavior. Contrastingly, we expected to find a shift in peccary activity near the lab clearing to a crepuscular behavioral pattern. This behavior is a result of the decreased perception of predation risk and optimal foraging opportunities that arise from the peccaries' strong association with humans. Second, we used camera traps to obtain detection histories of collared peccaries to use in occupancy models. These data were used to test the indirect effects of the human shield hypothesis. We also hypothesized that distance to the lab clearing would be the covariate that had the strongest effect on the distribution of peccaries throughout La Selva. We expected peccary occurrence to be higher in areas closer to the lab clearing because of their strong association with humans.

Methods

Study Area

La Selva is located in the northeastern lowlands of Costa Rica (10°26´N, 83°59´W). This region is composed of primary forest including areas that have been selectively logged (McDade and Hartshorn 1994). Additionally, there are successional secondary forests and uninhabited pastures and plantations in this region (McDade and Hartshorn 1994). The study area has a total area of around 16km^2 (McDade and Hartshorn 1994). The average annual rainfall is ~4m with precipitation highest in the months June-August, October and November (Clark and Clark 2010; McClearn et al. in press).

Camera Trap Data Collection

We established 44 camera traps along trails throughout La Selva. The 3 camera brands used in this study were Zopu Digital Technology, Apeman, and Victure. Each camera was set to high motion sensitivity and recorded 30 second video clips with 1 minute intervals. Each video clip also recorded the date and time when triggered. Each camera was placed at a minimum of 2 m from the focal point of the trail. Cameras were secured around sturdy trees 0.25-0.5 m above the ground and aimed either perpendicular or slightly angled to the focal point of the trail. Cameras were separated by a minimum of 250 m in a gradient moving away from the lab clearing to produce an even spatial distribution of cameras throughout La Selva (Fig 1). Cameras were moved to different locations every 7 days. Data recorded for each camera cycle consisted of the camera site, camera model, start/end date and time of camera cycle, and camera distance from focal point of trail. Additionally, individual video clip data were collected and included the date/time triggered, species/taxa recorded, group size, length of video, and whether species were adult or juvenile. In addition, we combined camera trap photos from previous 2016 REU survey data for the purpose of enlarging our sample size of peccary detections.

Activity Patterns Analysis

Camera trap data was used to estimated diel activity patterns and any shifts in peak activity along this gradient. We treated each video of peccaries as a sample from the diel time distribution (e.g., 24 hour cycle) and used those as input to fit kernel density estimates to fit activity peaks (*sensu* Lashley et al., 2018). We compared activity patterns of peccaries detected in human-influenced and wild settings. We defined the human-influenced area as within a 3 km buffer around the lab clearing and the wild setting as outside a 3 km buffer around the lab clearing. There were a total of 56 camera sites stationed in human-influenced settings and 14 camera sites stationed in wild settings throughout the course of our sampling period.

Habitat Variables and Occupancy Model Analysis

Camera trap footage was analyzed in an occupancy modeling framework (MacKenzie et al., 2002), in which we examined how the probability of peccary occurrence (ψ or psi) and detection (p) is related to 3 site-specific habitat covariates. We used satellite imagery from GoogleMaps (San Francisco, CA, USA) to measure distance from the lab clearing to each camera site. We used ArcGIS 10.0 (ESRI, Redlands, CA, USA) to overlay camera trap locations onto a digitized land cover map to quantify the forest type of each camera site (primary forest = 1, other = 0). Lastly, we recorded the number of humans detected at each camera site throughout the survey season.

We used all photo and video data from both field seasons to organize and construct binary peccary detection histories (detected = 1, not detected = 0). We partitioned detection histories into daily detection blocks for a maximum of 7-8 repeated (24-hr) surveys per site. All sampling of species were noninvasive via camera traps. We conducted all analyses in the freely available software PRESENCE and the ‘overlap’ package in R (Meredith and Ridout, 2014).

Results

Throughout the 5 week sampling period we detected 594 individual peccaries. The activity peaks derived from peccary detections in human-influenced settings reflect mostly crepuscular behavioral patterns (Fig 2). In contrast, activity peaks derived from peccary detections in wild settings reflect more diurnal behavioral patterns (Fig 2).

We also found that the number of humans detected had an influence on the occupancy probability of collared peccaries throughout La Selva (Table 1). In contrast, forest cover had a strong influence on the probability of detection of collared peccaries throughout La Selva (Table 1). Testing the influences on the probability of detection of the 3 habitat covariates alone and in combination with each other yielded high ranking models. Specifically, when testing the influences on the probability of detection, forest cover yielded the model with the lowest AIC value with a constant occupancy probability (Table 1). Interestingly, when the influence of the number of humans detected on the occupancy probability was tested in combination with the influence of forest cover on the probability of detection this yielded the top ranked model (Table 1). However, this model did not yield the absolute lowest AIC value but shared the same AIC value with a similar model. This model tested the influence of the number of humans detected on the occupancy probability in combination with the influence of forest cover and distance to the lab clearing on the probability of detection (Table 1).

Discussion

Top predators exhibit activity patterns that are tailored for efficient and sustainable predation strategies; whereas periods of peak prey vulnerability often reflect the activity patterns of their predators (Harmsen et al., 2010). Our cameras captured footage of 2 pumas and 1 jaguar each on different occasions. Most notably, this jaguar footage was the first detection in La Selva since 2012. These data, although insufficient to estimate population abundances, are evidence of large cat presence around La Selva. Activity patterns of collared peccaries in intact mammal communities exhibit diurnal behavior compared to the crepuscular activity patterns of collared peccaries in human-influenced settings around La Selva. This is likely a result of the difference in predator abundances across La Selva. For example, in the eastern lowlands of Belize the activity patterns of jaguars and pumas exhibit crepuscular behavior (Harmsen et al., 2010). This behavior drives the collared peccaries in this region to alter their predator avoidance strategies to exhibit more diurnal foraging behavior. The human shield of the La Selva lab clearing and field station has enabled the collared peccaries in this human-influenced area to fill this temporal niche and forage during optimal times of day (crepuscular). It is likely that the change in peccary activity in wild settings around La Selva to diurnal (less optimal) behavior is a consequence of the increased predation pressure peccaries face in wild settings due to the decreased association to humans and lack of a human shield. However, this inference should be treated with caution because some generalist predators like jaguars and pumas adapt well to humans and can remain abundant in urban settings (Geffroy et al,. 2015).

Habitat covariates did affect the probability of detection of collared peccaries. Primary forest cover had the strongest negative effect on the probability of detection. Because camera traps operate 24-hours a day, decreased detection corresponds to decreased local abundance or decreased localized activity around camera stations in primary forest (Cove et al,. 2014). These results may be a consequence of increased resource availability in secondary forest and increased vulnerability in primary forest due to decreased foliage cover. In terms of conservation and management, these data can be used to further support the protection and conservation of jaguars and other keystone species in the Neotropics. These species roles as top predators are vital for the regulation of trophic cascades in tropical ecosystems. These results can potentially support applications in management that aim to preserve the landscape of fear in similar trophic structures.

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Tables

Model	deltaAIC	AIC wqt	K
psi(humans_detected),p(forest_cover and dis_to_lab1)	0	0.1898	5
psi(humans_detected),p(forest_cover1)	0	0.1898	4
psi(humans_detected),p(forest_cover and humans_detected1)	0.68	0.1351	5
psi(humans_detected),p(forest_cover, dis_to_lab, and humans_detected1)	0.96	0.1174	6
psi(.),p(forest_cover1)	1.7	0.0811	3
psi(.),p(forest_cover and dis_to_lab1)	2.11	0.0661	4
psi(dis_to_lab),p(forest_cover and dis_to_lab1)	2.9	0.0445	5
psi(dis_to_lab and forest_cover and humans_detected),p(forest_cover, dis_to_lab, and humans_detected1)	3.45	0.0338	8
psi(.),p(forest_cover, dis_to_lab, and humans_detected1)	3.64	0.0307	5
psi(forest_cover),p(forest_cover1)	3.69	0.03	4
psi(forest_cover),p(forest_cover and dis_to_lab1)	4.06	0.0249	5
psi(dis_to_lab),p(forest_cover, dis_to_lab, and humans_detected1)	4.52	0.0198	6
psi(forest_cover and dis_to_lab),p(forest_cover and dis_to_lab1)	4.9	0.0164	6
psi(forest_cover),p(forest_cover, dis_to_lab, and humans_detected1)	5.57	0.0117	6
psi(dis_to_lab and forest_cover),p(forest_cover, dis_to_lab, and humans_detected1)	6.51	0.0073	7
psi(humans_detected1),p(.)	11.74	0.0005	3
psi(.),p(.)	12.75	0.0003	2
psi(forest_cover and humans_detected1),p(.)	13.19	0.0003	4
psi(.),p(dis_to_lab1)	13.98	0.0002	3
psi(forest_cover1),p(.)	14.43	0.0001	3
psi(.),p(humans_detected1)	14.72	0.0001	3
psi(dis_to_lab),p(forest_cover1)	40.25	0	4
psi(dis_to_lab1),p(.)	52.17	0	3
psi(dis_to_lab and humans_detected1),p(.)	54.17	0	4
psi(dis_to_lab and forest_cover1),p(.)	54.17	0	4
psi(dis_to_lab, forest_cover, and human_detected1),p(.)	56.17	0	5

Table 1: Occupancy models of collared peccaries with incorporated habitat covariates for occupancy probability and probability of detection. Models presented make up the complete candidate model set, where deltaAIC is the AIC difference, AIC wqt is the Akaike weight, and K is the number of model parameters.

Figures

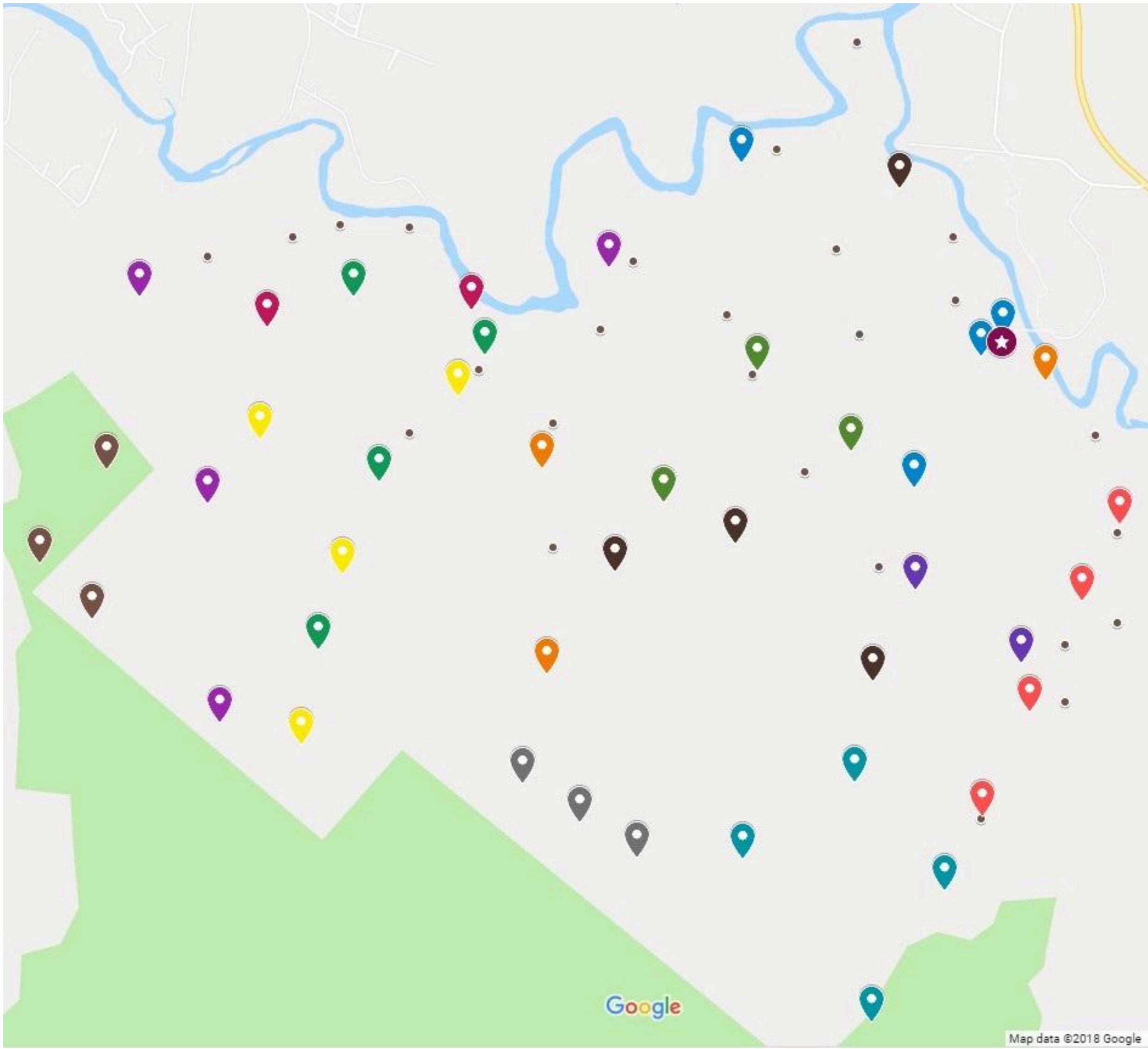

Figure 1: Map of camera trap survey sites within La Selva Biological Station, Costa Rica. Colored markers indicate location of camera trap sites from 2018 survey season. Small brown points indicate location of camera trap sites from 2016 survey season.

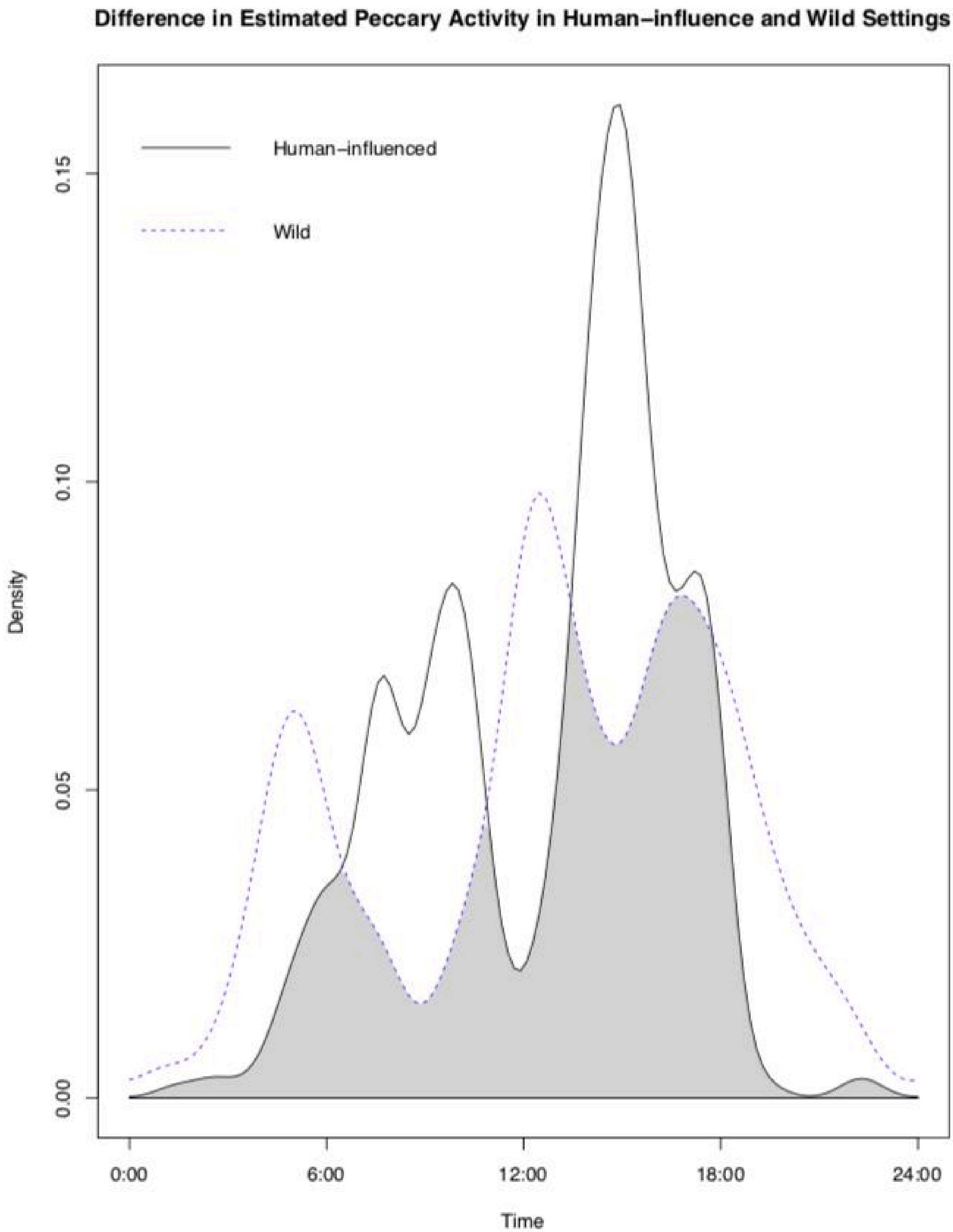

Figure 2: Overlapping density plots of collared peccary detections in human-influenced and wild settings. There were 396 detections of peccary individuals in human-influenced settings and 198 detections of peccary individuals in wild settings.

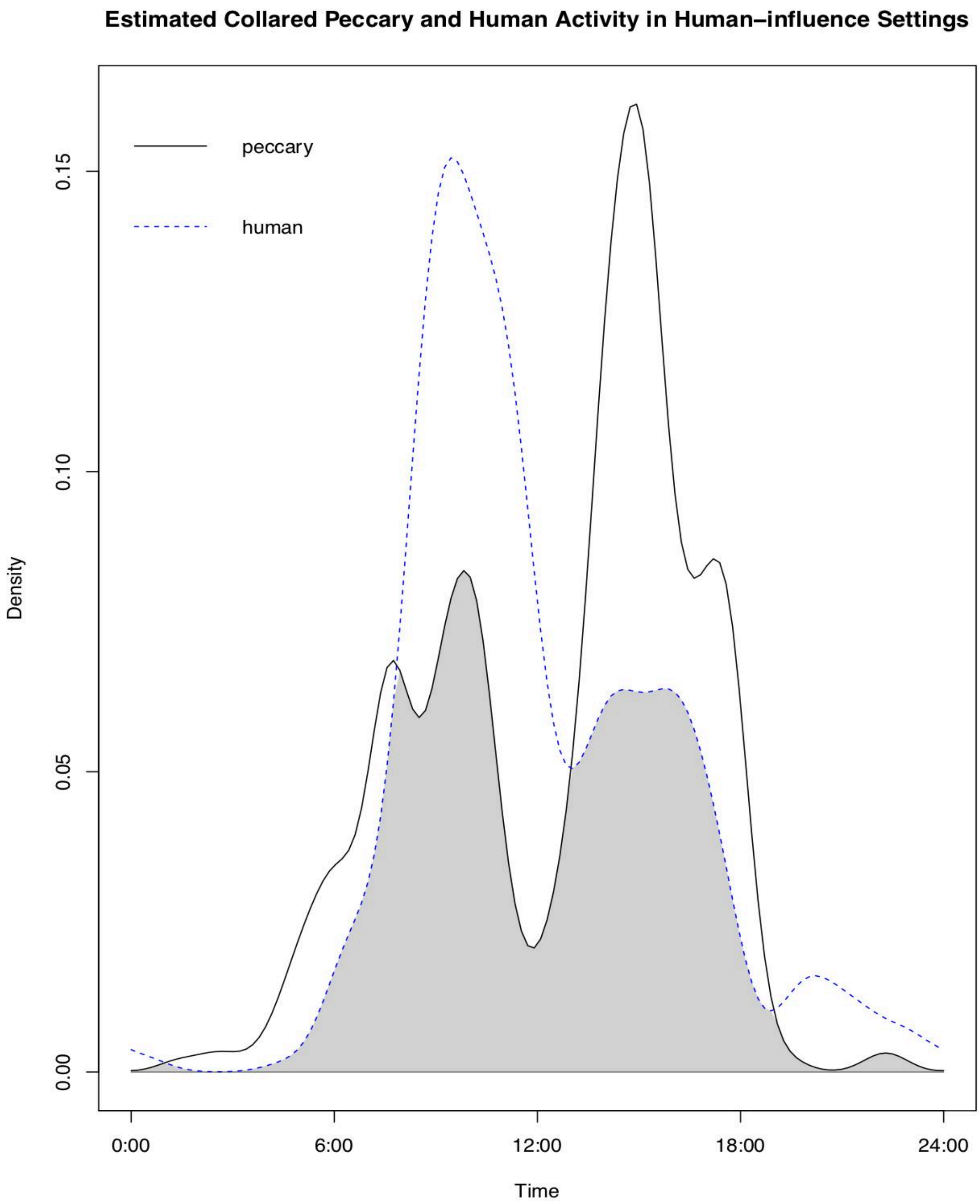

Figure 3: Overlapping density plots of collared peccary and human detections in human-influenced settings. There were 396 detections of peccary individuals and 482 detections of human individuals in human-influenced settings.

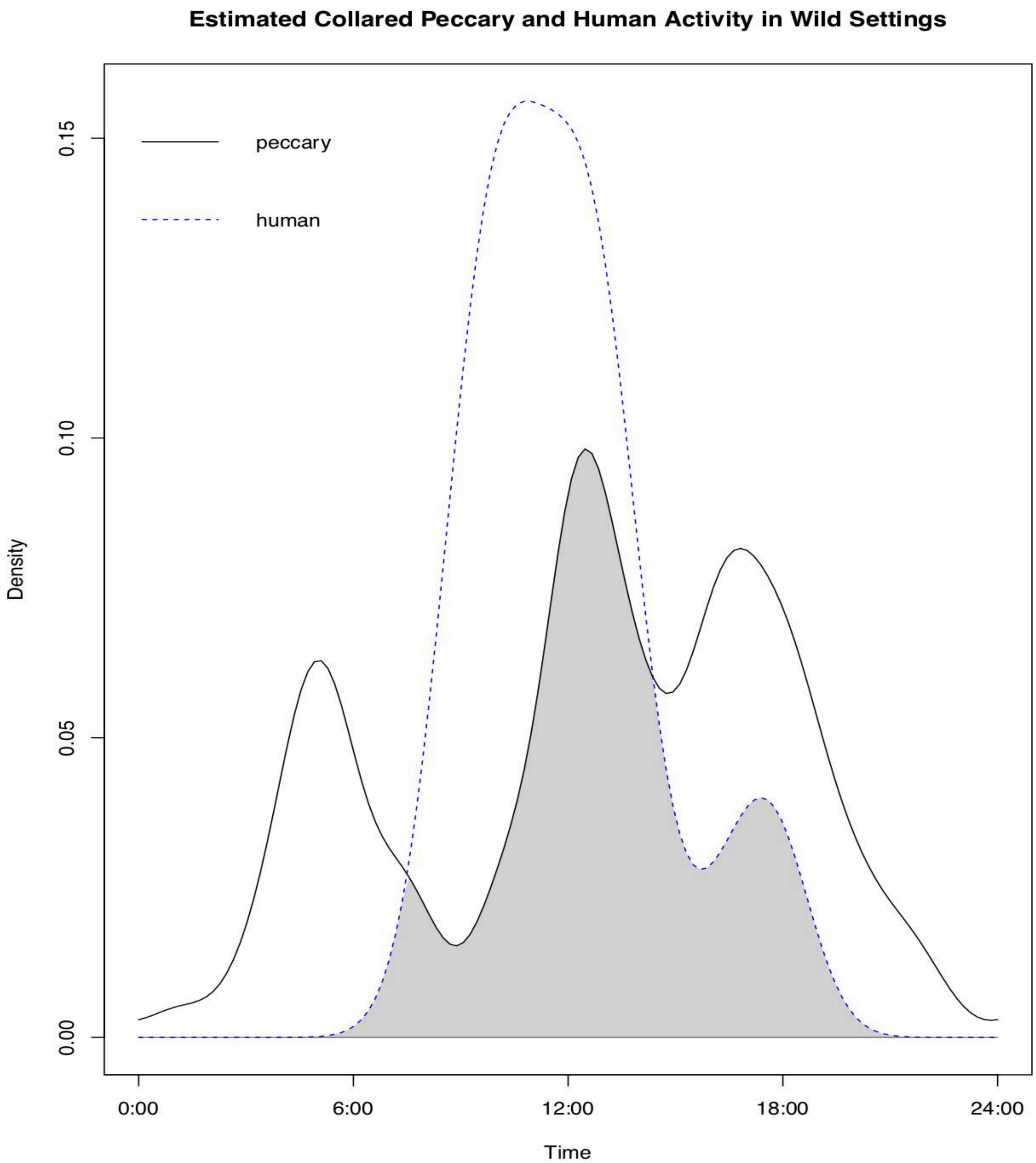

Figure 4: Overlapping density plots of collared peccary and human detections in wild settings. There were 198 detections of peccary individuals and 21 detections of human individuals in wild settings.