



Norwegian University
of Life Sciences

Master's Thesis 2022 60 ECTS

Faculty of Environmental Sciences and Natural Resource Management
(MINA)

Temperature shapes the daily temporal distribution of Neotropical mammals

William Esbjug Gromstad

Master of Science in Ecology

Acknowledgements

This thesis is the final submission of my 60 ECST Master of Science at the University of Life Sciences. Unfortunately, the COVID-19 pandemic made it impossible to carry out my own data collection in the tropics. For a boy who has dreamed about the Amazon his entire life, this became far from the best ending to my five years as a student, but I was ensured there would be other chances. The fact that I was still able to complete my thesis in tropical ecology is only due to the help of several people, who all deserve my gratitude. First and foremost, I am grateful for my main supervisor Torbjørn Haugaasen, who has been incredibly helpful in all aspects of my thesis. He guided me towards an interesting research topic and has helped with all questions I have had during the writing of my thesis. My other supervisors, Elildo Carvalho Jr. and Whaldener Endo, provided me with all the data for my research, as well as guidance along the way, for which I am very grateful. In addition, Andrea Fernanda Vallejo Vargas deserves recognition for helping me with questions I had for my analysis.

The completion of this thesis relied on the support of many people. Friends and family also deserve my gratitude, none more so than my parents, whose support and encouragement mean the world to me. Without them telling me to follow my dreams, the hope of becoming a scientist could have faded a long time ago. This thesis is the result of dedication over a long time, and it hopefully lives up to the high standards I expect of myself. As I am writing this, I feel deeply proud. Not only for finishing my degree, but for knowing that if five-year-old me would have known what he would achieve, he would be just as proud.

Ås 15.12.2022

William Esbjug Gromstad

Abstract

Behavioural adaptations in response to environmental changes is commonly found in wild animals. Such adaptations can be both on the spatial and the temporal scale, with the majority of previous studies focusing on the spatial adaptations. However, temporal activity patterns are also affected by a variety of environmental factors. In this camera trap study, I compare the daily activity budgets of seven mammal species occurring in two vastly different biomes (the Amazon and the Caatinga) to assess whether their activity is influenced by temperature. Animal activity patterns were compared using Kernel density analysis with accompanying coefficients of overlap, while a generalized linear model determined the influence of temperature. For five out of seven study species, activity patterns in the Amazon and in the Caatinga were distinctly different, while all species showed relatively similar patterns within the Amazon. Caatinga animals were much more nocturnal than in the Amazon and appeared to avoid activity during the hottest hours of the day. Temperature had a significant effect on temporal distribution of all species in at least one location, but only on four species in the Caatinga. Jaguars, pumas and ocelots were highly affected by temperature in the Caatinga, but generally not in the Amazon. Results therefore indicate that some species have altered their diel activity patterns to different environments across the Amazon and the Caatinga biomes. This seems to be influenced by the high temperatures in the Caatinga. These results suggest that species may be able to adapt to the increasing temperatures caused by climate change by becoming more nocturnal.

Keywords: temporal distribution, Caatinga, Amazon, thermoregulation, niche partitioning

Table of contents

Acknowledgements	ii
Abstract	iv
Introduction	1
Methods	2
<i>Study sites</i>	<i>2</i>
<i>Camera trap images.....</i>	<i>4</i>
<i>Extraction of temperature data</i>	<i>4</i>
<i>Statistical analysis.....</i>	<i>5</i>
Results	6
<i>Data summary</i>	<i>6</i>
<i>Species activity patterns</i>	<i>8</i>
<i>Effect of temperature.....</i>	<i>15</i>
Discussion	16
References	20
Appendix	v

Introduction

Temporal niche theory or time as an ecological resource may seem abstract in comparison to niches such as food or habitat preferences. The temporal niche can be described in the context of the most relevant environmental cycles, such as the year, the lunar day and month, the solar day, or the tidal cycle (Hut et al., 2012). However, most mammal behaviour and physiology are influenced by the circadian rhythm related to the daily light-dark cycle. Consequently, all wild mammals have a potential to adapt their temporal distribution (Scheibe et al., 2009). A variety of external factors, including temperature, food availability and inter-specific competition can affect an animals' circadian rhythm (Munoz-Delgado et al., 2004). Environmental conditions can be measured on different scales such as seasonal weather events or daily cycles of light and temperature, with the daily cycles often considered as the dominant ecological cause of adaptation (Hut et al., 2012). The daily temporal niche of a species describes what times throughout the day the individuals of said species are active. It is therefore highly related to the circadian rhythm (Attias et al., 2018). Consequently, species can be characterized by what times throughout the 24-hour daily cycle they are active, with diurnal species being active during the day and nocturnal species being active by night. There are also intermediate forms such as crepuscular and cathemeral activity patterns, used when a species is active around dusk or dawn, or during both day and night (Hut et al., 2012). In theory, mammals changing their temporal activity due to heat stress may eventually turn completely nocturnal, allowing them to stay within their current geographical range even with global climate change increasing temperatures (Hut et al., 2012, Levy et al., 2019).

How animals cope with unfavourable conditions is researched at accelerating rates. Most studies are on endotherms' behavioural changes in response to cold temperatures, but because endotherms also react when suffering from heat stress (van Beest et al., 2012), studies of for example larger vertebrates are important as well. Behavioural responses to heat stress have been found in larger mammals such as the black-tailed deer (*Odocoileus hemionus columbianus*), who seek out dense canopy forests on warm days, and the alpine ibex (*Capra ibex*) that climbs to different elevations to escape the summer heat (Bowyer and Kie, 2009, Aublet et al., 2009). Ambient temperature can highly influence animal behaviour, and the physiological stress caused by global climate change can have a direct effect on the species. For this reason, a better understanding of how environmental conditions affect animal behaviour is becoming more important (Harley, 2011, Gunderson and Leal, 2016).

Amazonia is the world's largest tropical rainforest, but its geographical range is rapidly decreasing. Current projections show that intensity and frequency of drought and fire continues to increase in the Amazon (Alencar et al., 2015). This could potentially lead to "savannization" where tropical rainforests are converted into derived savannas (Sales et al., 2020). One of the simulated consequences is that the energetic costs of nocturnality will

decrease, while diurnal species will get higher water demands. This could push diurnal species towards a nocturnal lifestyle in order to survive high temperatures in the future (Kearney et al., 2009, Kearney, 2013, Levy et al., 2019). A global analysis show that most mammals are nocturnal, but that climate has a strong effect on diel activity patterns. Diurnal activity is common in areas with low night temperatures and high energetic costs of nocturnality. Nocturnal species are more abundant in arid, warm regions, and a crepuscular pattern is often seen where climatic conditions are preferable for the species at dusk or dawn (Bennie et al., 2014). Although other factors have been used to explain such temporal changes, it is reasonable to assume that temperature have put evolutionary pressure upon species (Hut et al., 2012, Astete et al., 2016).

Many previous studies have looked at diel activity patterns for large vertebrates in Amazonia (Michalski and Norris, 2011) and other biomes in South America, such as the Caatinga (Penido et al., 2017), the Cerrado (Azevedo et al., 2018) and the Chaco (Romero-Muñoz et al., 2010). Most studies focus on temporal distribution in only one biome. Diel activity patterns of the same mammal species across biomes have not been much studied in the Neotropics, with the exception of one study on jaguars and pumas (Foster et al., 2013). This study focuses on biotic factors as explanations for temporal distribution. However, abiotic explanations are not included. To my knowledge, no previous study has investigated how temperature shapes diel activity patterns of mammals across biomes.

This study analyses camera trap images from Juruena and Terra do Meio in the Brazilian Amazon, and Serra da Capivara in the Caatinga. The two biomes are vastly different, especially when it comes to temperature, humidity, and tree density (Penido et al., 2017). For this reason, the Caatinga can provide valuable insight into how Amazonian species may adapt their temporal distribution when faced with potential “savannization”. In an attempt to fill knowledge gaps regarding temporal niche utilization and switching, the objective of this thesis is divided into two parts: (I) to describe the temporal distribution of species commonly caught by camera traps across the two biomes, and (II) investigate the potential effect of temperature on species temporal distribution patterns. I hypothesise that a distinct difference in temporal distribution is seen between the two biomes, but not between the locations within the Amazon, likely due to the high midday temperatures in the Caatinga.

Methods

Study sites

The study was conducted in two biomes, the Amazon and the Caatinga. In the Amazon, camera traps were placed in Juruena National Park, and in Terra do Meio Ecological Station. The two were chosen due to their relatively pristine rainforest ecosystems. Juruena National Park is

19000 km² and lies mostly within the Tapajós River basin in Mato Grosso. The area is predominantly covered with terra firme forest, a forest type that remains unflooded throughout the year (Dalponte et al., 2016). Terra do Meio Ecological Station covers 33731 km² between the Xingu River and its tributary the Iriri River. It lies within indigenous lands and protected areas, but is faced with an increasing agricultural frontier as well as a variety of other threats by human activities (Ramos et al., 2016). Both Amazonian sites usually have a dry season between June and September (Dalponte et al., 2016, Ramos et al., 2016). In the Caatinga, cameras were placed in Serra da Capivara National Park in the state of Piauí in north-eastern Brazil. Covering 1300 km², the national park is one of the largest in the Caatinga. Temperatures usually vary between 12°C and 45°C, with an annual average of 26°C (Penido et al., 2017). The vegetation in Serra da Capivara mostly consists of shrubs in open, rocky areas, with some patchy high-canopy forests and no permanent water sources (Lemos, 2004, Penido et al., 2017). The rainy season in Serra da Capivara is usually between October and April (Astete et al., 2016).



Figure 1: Map of study area with study sites marked in green (image downloaded from Google Earth).

Camera trap images

All camera trapping was performed within the dry season to minimize the effect of seasonality. In Juruena, there were 220 camera deployments using 138 cameras at 64 different locations between 01.11.2016 and 19.11.2020. The data from Terra do Meio consisted of 113 cameras and camera deployments at 65 locations between 09.06.2016 and 27.08.2017. The available data from the Caatinga was obtained in the Serra da Capivara National Park from 12.06.2016 to 14.06.2017. In some cases, animals roamed the area around the camera, or simply paused in front of it. Sightings of a species were therefore assumed independent if they were separated by at least 30 minutes.

The Wildlife Insights website provides an automated species identification of the animal on each image. These identifications were spot-checked when manually retrieving the temperature stamp. I only included species if they were present in all locations and had a statistically meaningful number of detections at each site. Some genera are difficult to classify to species level and these were lumped at genus level, in order to avoid misidentification. Considering this, the temporal distribution of seven species were chosen for further analysis: jaguar (*Panthera onca*), puma (*Puma concolor*), ocelot (*Leopardus pardalis*), giant anteater (*Myrmecophaga tridactyla*), *Mazama* spp, *Dasypus* spp, and *Dasyprocta* spp. *Mazama* spp consists of the brown brocket deer (*Mazama nemorivaga*) and red brocket deer (*Mazama americana*). The greater long-nosed armadillo (*Dasypus kappleri*) and the nine-banded armadillo (*Dasypus novemcinctus*) are lumped into *Dasypus* spp. There are other armadillo species not part of the *Dasypus* genus inhabiting the study sites, but these were not included. The assemblage of *Dasypus* spp across the sites varies, and not all species were present at the same sites. *Dasyprocta* spp consists of the black agouti (*Dasyprocta fuliginosa*), and the red-rumped agouti (*Dasyprocta leporine*).

Extraction of temperature data

The temperature data in the Amazon and the Caatinga were retrieved in two different ways. The Cameras were only deployed in the dry season and both extraction methods were standardized to minimize a potential effect of seasonality. The images from Juruena and Terra do Meio included a temperature stamp, but the AI in the Wildlife Insights website was not able to retrieve and include this data in the datasets. Therefore, the temperature had to be retrieved manually. This was done for the datasets of jaguars, pumas, ocelots, and giant anteaters. Due to the time consumption of manually extracting temperature from each independent image for species with very high observation numbers, a different approach was used for representation of *Mazama* spp, *Dasypus* spp, and *Dasyprocta* spp. For these observations, temperature was manually extracted from the first ten images of each week throughout the study period. All obtained temperatures within the same hour were then pooled. The final temperature data consists of the average temperature for each hour

throughout the day (0-23) (Figure 2), which was used for the generalized linear model. However, there was no temperature stamp available in Serra da Capivara, and temperatures were retrieved from NASA satellite data. These data have been tested and proven reliable when compared to ground level monitoring stations in open environments (Shamkhi et al., 2019), meaning this was not an option for the dense forested areas of Juruena and Terra do Meio. Satellite data was obtained directly with the R package “nasapower” (Sparks, 2018). The package yields hourly temperatures for the entire period each camera trap has been in the field if provided with the coordinates of the camera. Temperature data for each of the 60 cameras was then pooled into a singular dataset, with the average temperatures for each hour throughout the study period (Figure 2).

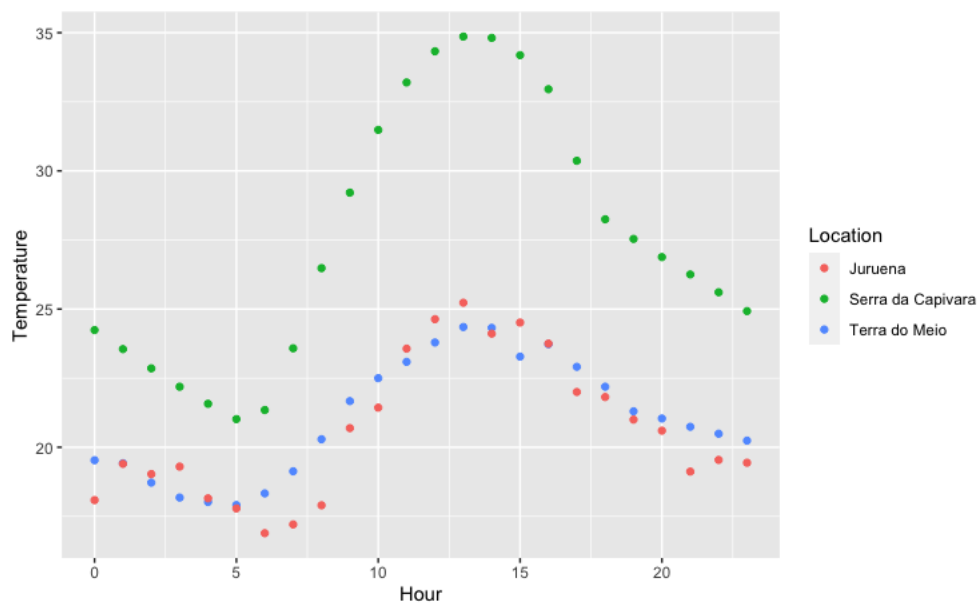


Figure 2: Mean hourly temperatures at the three study sites during the study period.

Statistical analysis

RStudio (version 2021.09.2) was used for all statistical analysis. Temporal patterns were estimated with kernel density estimation (Ridout and Linkie, 2009), and a coefficient of overlap (Δ). The estimator used was Dhat1 and Dhat4, depending on whether sample sizes were below or above 75. Standard errors were obtained from the estimated confidence intervals from 10000 bootstrap samples (Ridout and Linkie, 2009). A Kernel concentration of $k = 3$ with smoothness parameter of $c = 1$ was used for the analysis, as recommended by Ridout and Linkie (2009). The analyses were performed in R using the “overlap” package (Ridout and Linkie, 2009). Temporal activity patterns were divided into three categories, diurnal, nocturnal, and crepuscular. The Kernel density analysis is useful when population density does not fit a parametric description. It is a non-parametric statistical method used to

estimate probability density functions from random samples. After the activity patterns for all focal species were estimated, the study sites were compared pairwise in overlap plots. These plots are the basis of coefficient of overlap calculated from two activity patterns, meaning that a total of three coefficients of overlap was calculated for each species. This coefficient ranges from 0, indicating no overlap, and 1, indicating complete overlap and identical temporal distribution. The coefficient of overlap does not have a distinct threshold value below which two activity curves are significantly different. It is therefore a descriptive value (Lashley et al., 2018).

A generalized linear model was used to evaluate the potential effect of temperature on animal activity, with frequency of observations as the response variable and temperature as the predictor variable. Because temperature represent a predictor variable of continuous count data, a Poisson regression was the best fit. The analysis yields an estimate as well as a standard error, and a p-value. The estimate can be both positive and negative and describes the average change in the logarithmic odds for activity when temperature changes by one degree.

Results

Data summary

In total, the 311 cameras deployed in either Juruena, Terra do Meio and Serra da Capivara captured 26374 independent images of wildlife in total (Appendix 1). Of these, 9806 were of the focal species (Appendix 1). *Dasypus* spp, *Dasyprocta* spp, the giant anteater, and *Mazama* spp portrayed a higher number of detections at one of the Amazonian sites compared to the Caatinga site, while the three felids were more commonly detected in the Caatinga (Table 1). Overall, *Dasyprocta* spp was the most abundantly registered focal animal, whereas the giant anteater had the fewest number of detections across the sites (Table 1).

Table 1: List of independent camera trap detections of the focal species in Juruena, Terra do Meio and Serra da Capivara. The columns after each site indicate the percentage of each species' detections out of the total number of detections at the site.

Species	English name	Juruena	% of detections	Terra do Meio	% of detections	Serra da Capivara	% of detections
<i>Felidae</i>							
<i>Panthera onca</i>	Jaguar	34	0.51	20	0.11	58	2.70
<i>Puma concolor</i>	Puma	32	0.48	38	0.22	59	2.75
<i>Leopardus pardalis</i>	Ocelot	90	1.34	176	1.01	255	11.88
<i>Cervidae</i>							
<i>Mazama species</i>	<i>Mazama species</i>	535	7.96	502	2.87	108	5.03
<i>Mazama americana</i>	Red brocket	297	4.42	549	3.14	0	0.00
<i>Mazama gouazoupira</i>	Amazonian brown brocket	91	1.35	65	0.37	0	0.00
<i>Myrmecophagidae</i>							
<i>Myrmecophaga tridactyla</i>	Giant anteater	37	0.55	36	0.21	17	0.79
<i>Dasyodidae</i>							
<i>Dasypus species</i>	<i>Dasypus species</i>	439	6.53	387	2.21	0	0.00
<i>Dasypus novemcinctus</i>	Nine-banded armadillo	222	3.30	0	0.00	51	2.38
<i>Dasypus kepplei</i>	Greater long-nosed armadillo	3	0.04	10	0.06	0	0.00
<i>Dasyproctidae</i>							
<i>Dasyprocta species</i>	<i>Dasyprocta species</i>	1398	20.79	4255	24.31	25	1.16
<i>Dasyprocta fuliginosa</i>	Black agouti	9	0.13	0	0.00	0	0.00
<i>Dasyprocta leporina</i>	Red-rumped agouti	8	0.12	0	0.00	0	0.00
Total		3195	47.52	6038	34.49	573	26.70

Species activity patterns

The coefficients of overlap show that the diel activity patterns between the two sites in Amazonia were more similar to each other than they were to Serra da Capivara (Table 2). This pattern was apparent for the three felids, the giant anteater and to some degree in the *Mazama* spp and *Dasyprocta* spp (Figure 3; Table 2).

The jaguars of Juruena and Terra do Meio show a mostly diurnal, somewhat bimodal activity pattern (Figure 3). They have long activity periods including two distinct peaks both before and after noon. Contrastingly, these cats were largely nocturnal at Serra da Capivara (Figure 3). The highest coefficient of overlap was between Juruena and Terra do Meio (0.74), while the lowest was at 0.5 between Juruena and Serra da Capivara.

Puma was largely diurnal at the Amazonian sites, whereas it was mostly nocturnal in Serra da Capivara (Figure 3). Activity peaks in the Amazon were varied. There was a bimodal pattern in Terra do Meio, with activity peaks at dawn and after noon (Figure 3). In Juruena there was high activity levels shortly after dawn and most other activity during the day (Figure 3). The coefficient of overlap for pumas showed a high overlap between Juruena and Terra do Meio (0.77). Both the Amazonian locations produced low coefficients of overlap when compared to Serra da Capivara (Table 2).

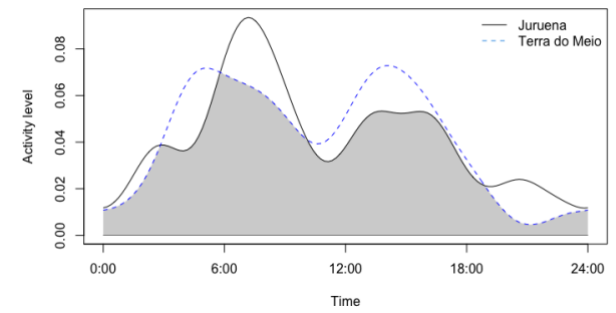
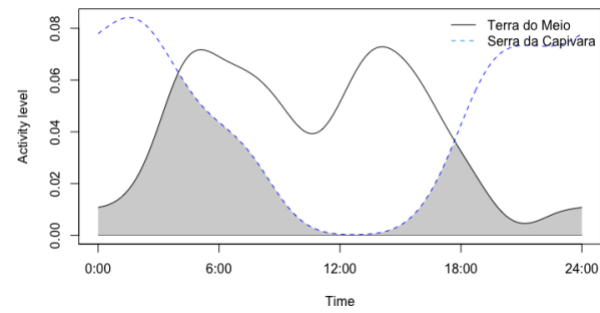
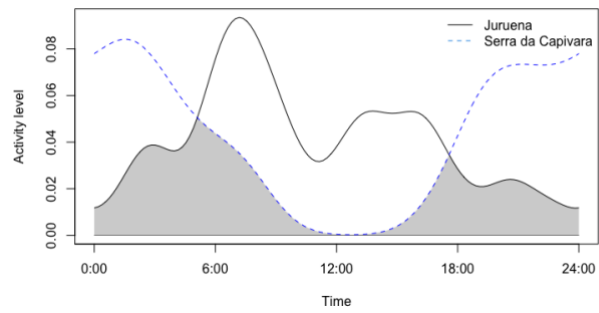
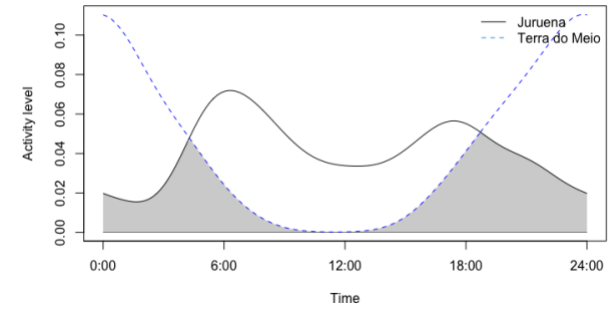
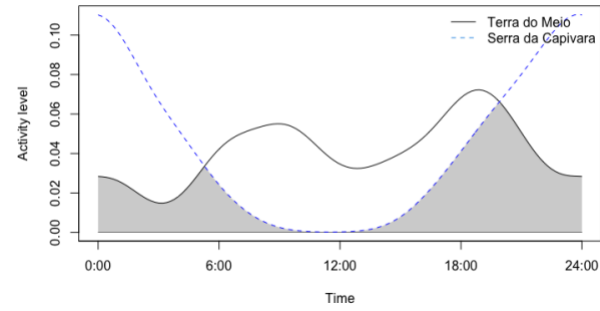
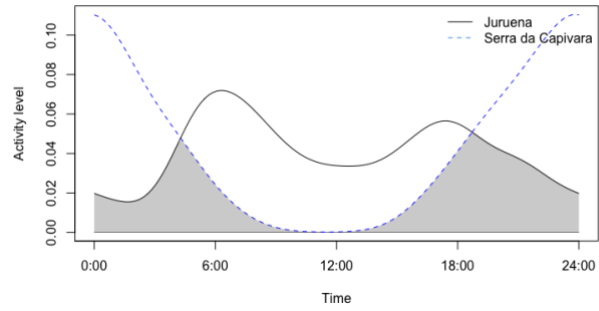
Ocelots portrayed a mostly nocturnal lifestyle at all three study sites (Figure 3). This pattern was especially strong in Serra da Capivara, where activity levels peaked just after dusk and remained high until dawn (Figure 3). At the Amazonian sites, ocelot activity was very similar for both Juruena and Terra do Meio. They were most active during the night but maintained some activity throughout the day. In general, the coefficients of overlap between all combinations of sites were high (Table 2).

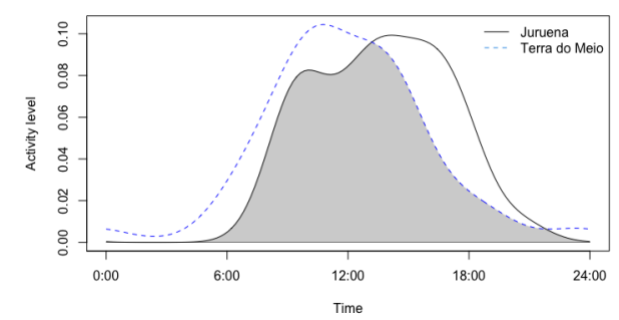
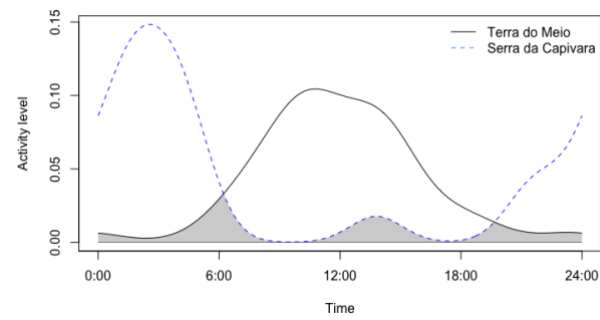
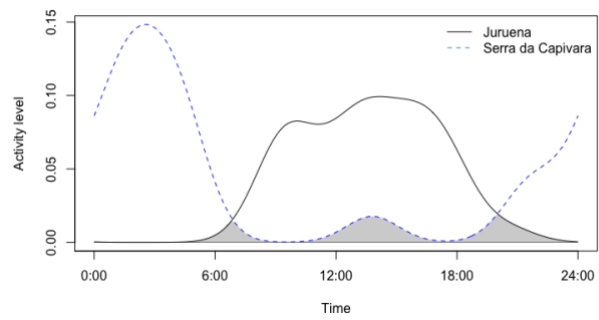
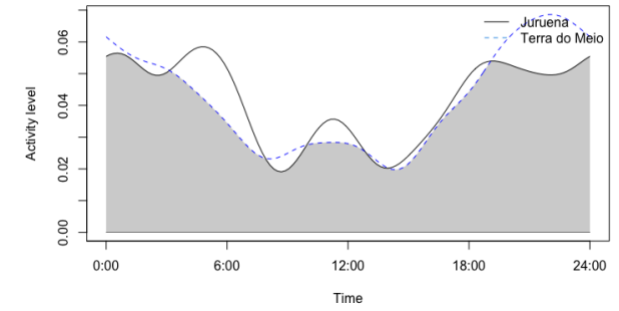
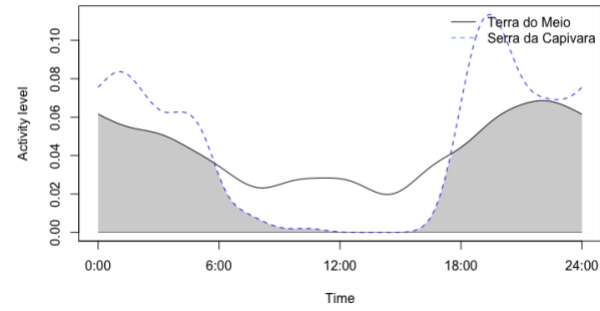
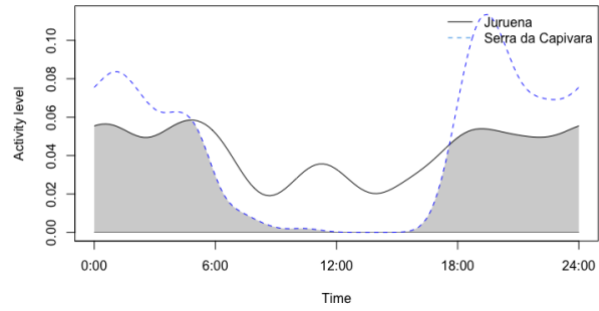
In the Amazon, giant anteaters were strictly diurnal, with peak activity at noon in Terra do Meio, and around 14:00h in Juruena (Figure 3). However, the 17 observations of giant anteater in Serra da Capivara portray a largely nocturnal lifestyle, with peak activity in the middle of the night at around 03:00h (Figure 3). The coefficients of overlap reflected this, with low overlaps between the two Amazonian sites and Serra da Capivara (Table 2).

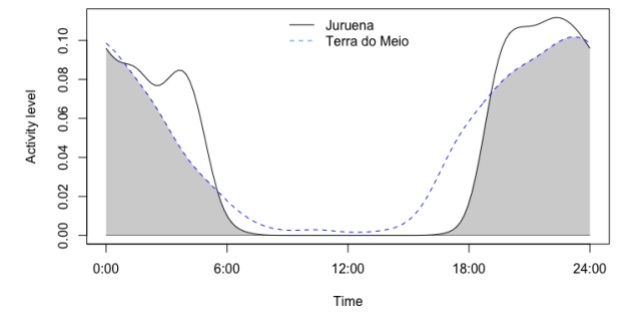
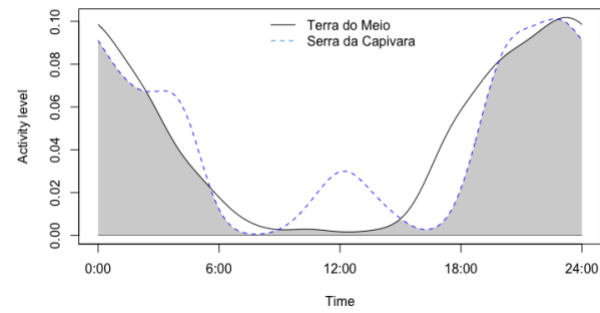
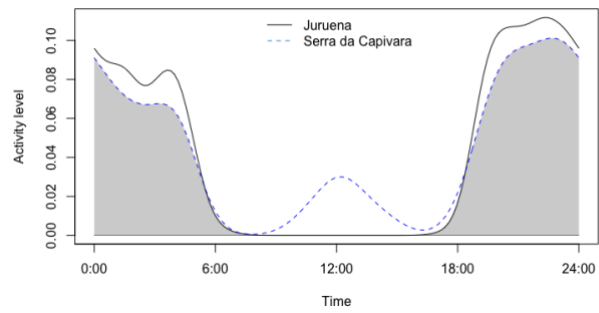
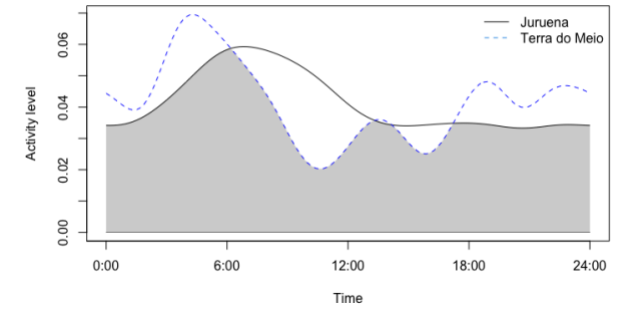
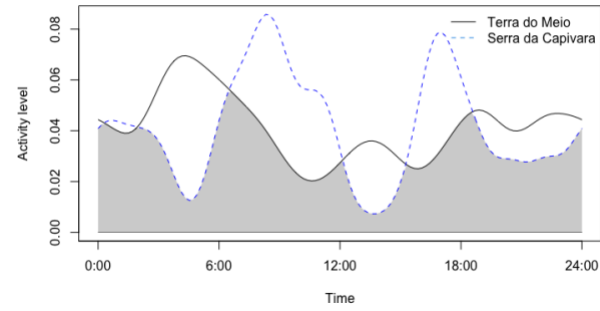
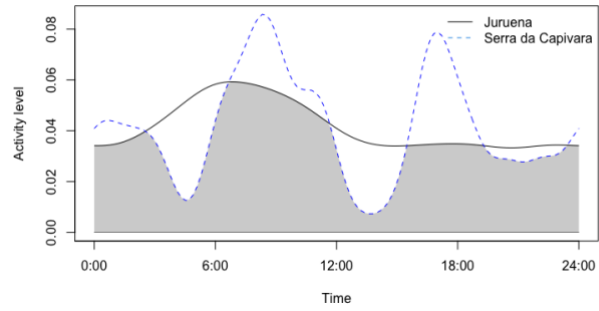
The *Mazama* spp in Serra da Capivara showed high activity levels from dawn until noon, as well as another activity peak at dusk, in addition to some nocturnal activity. In Juruena, activity levels were roughly the same throughout the day, except for a small peak during the first half of the day (Figure 3). A similar pattern was found in Terra do Meio, but activity levels showed some more variation, and were at its highest before dawn (Figure 3). Activity patterns were similar at all three locations (Figure 3), and all the coefficients of overlap were relatively high (Table 2).

Activity levels for the agoutis were quite similar within the Amazon (Figure 3; Table 2), and they portrayed a mostly diurnal lifestyle, although there were activity peaks at dusk and dawn in Juruena. The agoutis in Serra da Capivara showed a clear crepuscular pattern, with two very distinct activity peaks around dusk and dawn (Figure 3). During the warmest hours of the day after noon, there was no agouti activity in Serra da Capivara. The coefficients of overlap show higher overlap within the Amazon than when comparing Juruena or Terra do Meio to Serra da Capivara (Table 2).

The genus *Dasypus* portrayed a nocturnal lifestyle, and only the armadillos in Serra da Capivara were active to some degree around noon. Their activity period in Terra do Meio is slightly shorter in Juruena than at the two other sites (Figure 3). The coefficients of overlap were high between all combinations of the sites (Table 2).







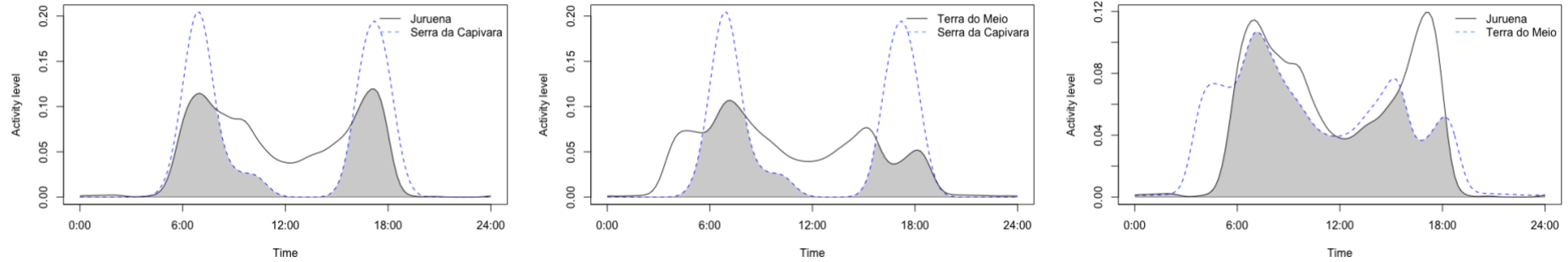


Figure 3: Temporal distribution of jaguar, puma, ocelot, giant anteater, *Mazama* spp, *Dasybus* spp and *Dasyprocta* spp in the Amazon and Caatinga biomes. The graphs show animal activity throughout a 24h-cycle based on the number of observations in the camera trap images. The image above each row of temporal distributions indicate what animal is represented in the graphs. The grey area beneath the graphs shows overlap between the two temporal distributions.

Table 2: The coefficient of overlap for the three combinations of sites for the seven study species. The table includes coefficients derived from 10000 bootstrap samples, with the 95% confidence intervals in the parenthesis after each coefficient. The coefficient of overlap correlates to the grey areas in Figure 3.

Jaguar	Juruena	Terra do Meio
Serra da Capivara	0.51 (0.32 - 0.62)	0.50 (0.32 - 0.69)
Juruena		0.74 (0.69 - 0.99)
Puma	Juruena	Terra do Meio
Serra da Capivara	0.51 (0.31 - 0.64)	0.48 (0.30 - 0.58)
Juruena		0.77 (0.70 - 0.96)
Ocelot	Juruena	Terra do Meio
Serra da Capivara	0.71 (0.62 - 0.80)	0.75 (0.68 - 0.81)
Juruena		0.87 (0.83 - 0.98)
Giant Anteater	Juruena	Terra do Meio
Serra da Capivara	0.16 (0.03 - 0.25)	0.22 (0.03 - 0.33)
Juruena		0.76 (0.64 - 0.93)
Mazama spp	Juruena	Terra do Meio
Serra da Capivara	0.81 (0.74 - 0.89)	0.74 (0.62 - 0.80)
Juruena		0.87 (0.81 - 0.91)
Dasypus spp	Juruena	Terra do Meio
Serra da Capivara	0.83 (0.78 - 0.95)	0.82 (0.74 - 0.93)
Juruena		0.85 (0.81 - 0.89)
Dasypsecta spp	Juruena	Terra do Meio
Serra da Capivara	0.68 (0.52 - 0.78)	0.58 (0.37 - 0.63)
Juruena		0.81 (0.77 - 0.82)

Effect of temperature

Temperature had a significant effect on activity in at least one location for all seven focal species (Table 3). Where this effect was present, most species (jaguar, puma, ocelot, *Mazama* spp, and *Dasypus* spp) showed less activity with increasing temperature. Contrastingly, the giant anteater and *Dasyprocta* spp displayed greater activity levels with increasing temperatures. Temperature had a strong significant effect on all three felids at Serra da Capivara. Ocelot activity was significantly affected by temperature in Terra do Meio as well, but no effect was seen in Juruena. The giant anteater, *Mazama* spp, and *Dasyprocta* spp were only significantly affected by temperature at the Amazonian sites. Activity levels of *Dasypus* spp were highly influenced by temperature in all locations, in both biomes.

Table 3: The effect of temperature on the study species' temporal distribution. The estimate indicates the average change in the logarithmic odds for activity when temperature increases by one degree. P-value show the level of significance (***P < 0.001, **P < 0,01, *P < 0,05).

Species	Location	Estimate	Standard error	p-value
Jaguar	Juruena	-0.01	0.08	0.39
Jaguar	Terra do Meio	0.05	0.12	0.64
Jaguar	Serra da Capivara	-0.2	0.05	<0.001***
Puma	Juruena	0.01	0.08	0.92
Puma	Terra do Meio	0.14	0.1	0.15
Puma	Serra da Capivara	-0.21	0.05	<0.001***
Ocelot	Juruena	-0.07	0.05	0.13
Ocelot	Terra do Meio	-0.15	0.05	<0.001***
Ocelot	Serra da Capivara	-0.2	0.02	<0.001***
Giant anteater	Juruena	0.35	0.07	<0.001***
Giant anteater	Terra do Meio	0.47	0.1	<0.001***
Giant anteater	Serra da Capivara	-0.11	0.09	0.20
<i>Mazama</i> spp.	Juruena	-0.05	0.2	0.008**
<i>Mazama</i> spp.	Terra do Meio	-0.16	0.03	<0.001***
<i>Mazama</i> spp.	Serra da Capivara	-0.01	0.02	0.81
<i>Dasypus</i> spp.	Juruena	-0.3	0.02	<0.001***
<i>Dasypus</i> spp.	Terra do Meio	-0.34	0.03	<0.001***
<i>Dasypus</i> spp.	Serra da Capivara	-0.14	0.02	<0.001***
<i>Dasyprocta</i> spp.	Juruena	0.08	0.01	<0.001***
<i>Dasyprocta</i> spp.	Terra do Meio	0.09	0.01	<0.001***
<i>Dasyprocta</i> spp.	Serra da Capivara	-0.02	0.05	0.68

Discussion

In general, the major difference in temporal distribution between the Caatinga and the Amazonian sites was the close to complete absence of activity during the hottest hours around noon in Serra da Capivara (Figure 2). All study species displayed different temporal distribution between the two biomes, with the exception of the mainly nocturnal *Dasypus* genus. In addition, all species were significantly affected by temperature in at least one study site, but only four in Serra da Capivara. This was unexpected as the high temperatures would suggest this to be a major influence on the temporal distribution of the wildlife in the area. Only two species, the giant anteater and *Dasyprocta* spp, were positively affected by increasing temperatures (Table 3). This could be because giant anteaters are imperfect homeotherms, meaning that they are able to generate heat as other placental mammals, but they have limited ability to regulate it (McNab, 1980). Giant anteaters have a wide region of thermoneutrality, but seem to thrive in temperatures between 15°C and 36°C (McNab, 2009). Despite this, they inhabit areas where temperatures can go well outside this range, such as the Pantanal and the Caatinga, indicating that giant anteaters are able of behavioural changes in response to unfavourable climatic conditions. For example, days with high temperatures seem to be counteracted by more nocturnal activity (Camilo-Alves and Mourao, 2005), which is consistent with results in this study. The positive effect of temperature on *Dasyprocta* spp activity supports numerous studies (Gómez et al., 2005, Suselbeek et al., 2014, García-Restrepo et al., 2019, Mendoza et al., 2019), but could also be linked to predator avoidance (Romero et al., 2016).

Both the jaguar and the puma had a mostly diurnal lifestyle at the Amazonian sites, while they displayed a nocturnal temporal distribution in Serra da Capivara (Figure 3). This supports previous research suggesting these species can be active throughout the diel cycle (Sunquist and Sunquist, 2002, Scognamillo et al., 2006, Romero-Muñoz et al., 2010), even though some studies find them to be predominately nocturnal (Astete et al., 2016). A significant effect of temperature on jaguar and puma activity was only observed in the Caatinga. Both species were less likely to be active with increasing temperatures. Several factors have been used to explain how suitable a habitat is for jaguars and pumas, but for jaguars, arid habitats have relatively low suitability (Rodríguez-Soto et al., 2011). Jaguars in Serra da Capivara tend to be drawn towards areas of higher elevation and their mobility is highly influenced by proximity to water (Morato et al., 2014). Distance to human settlements and more favourable vegetation may explain this pattern, whereas others have suggested thermoregulation as an alternative theory (Morato et al., 2014, Astete et al., 2016). The higher elevations of the Caatinga have the highest concentration of canyons, rock formations and caves in the area. Although temperatures may reach 50°C outside such refuges, the temperature inside will usually not exceed 30°C (Astete et al., 2016). This indicates that the extreme temperatures in the area are affecting jaguar activity patterns, as the results presented here suggest. Because felids are unable to thermoregulate by panting (West, 2005), they probably have to change

their behaviour in order to survive in such a harsh environment. This could explain why both jaguars and pumas have a mostly nocturnal lifestyle in Serra da Capivara, and a more diurnal lifestyle in Juruena and Terra do Meio, where the temperatures are lower (Astete, 2008, Foster et al., 2013).

The temporal distribution of ocelots suggests it is a mostly nocturnal species in all locations, although the degree of its nocturnality is different between the two biomes (Figure 3). This correlates with previous research on ocelot activity patterns (Penido et al., 2017). Even though ocelots are predominantly nocturnal, or in some cases a mix of nocturnal and crepuscular, they usually show some diurnal activity in most environments (Di Bitetti et al., 2006, Di Bitetti et al., 2010, Martínez-Hernández et al., 2015). This can be seen in both Juruena and Terra do Meio, where there is some activity throughout the diel cycle. The ocelot probably alters its temporal distribution to adapt to the environment. Researchers have found more nocturnal activity during the dry season than the wet season (Pérez-Irineo and Santos-Moreno, 2014), and the variation in activity during the day seem to be linked with the high temperatures in Serra da Capivara. Rodents are common prey for ocelots in Serra da Capivara. However, high temperatures and low humidity may be more plausible explanations for their activity patterns, as the temporal distribution of ocelot and their prey is significantly different in the Caatinga (Penido et al., 2017). Temperature had a significant negative effect on ocelot activity in both Terra do Meio and Serra da Capivara (Table 3). Other factors, such as competition from larger felids, are probably also influencing the temporal distribution of ocelots in these environments (Goulart et al., 2009). This would be consistent with the results in my study, as the ocelots are more active when jaguar and puma activity is at its lowest (Figure 3). These factors may be especially important in Juruena, where activity patterns were not influenced by temperature.

Temporal distribution of the giant anteater in the Amazon and in the Caatinga was completely different, as it has the lowest coefficient of overlap between the Caatinga and the two Amazonian sites of any of the study species (Table 2). While diurnal in both Juruena and Terra do Meio, the giant anteaters in Serra da Capivara show a nocturnal activity pattern. Temperature positively influenced activity patterns of giant anteaters at both Amazonian sites. As previous studies show more nocturnal activity in high temperature (Camilo-Alves and Mourao, 2005, Mourão and Medri, 2006), I expected the giant anteaters in Serra da Capivara to be nocturnal. However, no significance was found. This is likely due to the low number of detections, as only 17 detections of giant anteaters were made during the study period. Therefore, the resulting activity budgets should be considered as indicative rather than conclusive. In the Caatinga, both jaguars and pumas mostly prey upon mammals such as armadillos and giant anteaters (Astete et al., 2016). Predators may influence the temporal distribution of these species, but giant anteaters and its predators are all nocturnal in Serra da Capivara. This suggests predators are not the reason for the giant anteaters' activity patterns.

The brocket deer (*Mazama* spp) was active during both day and night at all three sites, with a somewhat cathemeral temporal distribution at Serra da Capivara (Figure 3). Although there was activity throughout the day at the Amazonian sites, animals at both sites had an activity peak around dawn (Figure 3). The findings may reflect the lumping of brown and red brocket deer in the analysis, as the former is predominantly diurnal and the latter is mainly nocturnal (Tobler et al., 2009, Ferregueti et al., 2015). This temporal niche partitioning may enable these two closely related species to coexist in the same environment. However, their activity patterns seem to vary among habitats, especially for the brown brocket deer. It is more active around dawn in some areas (Rivero et al., 2005), a pattern to some degree reflected in both Juruena and Terra do Meio (Figure 3). Even though the temporal partitioning between the two species is lost when both red and brown brocket deer are pooled together, the data should still be useful for comparisons between the different sites. The brocket deer in Serra da Capivara show a different temporal distribution than those in the Amazon, with two distinct activity peaks during the day (Figure 3). The dip in activity during the warmest hours of the day may suggest a link with temperature. Despite this, the statistical analysis shows that temperature has a significant effect on brocket deer activity only at the Amazonian sites, where it was negatively affected by increasing temperatures (Table 3). Other factors, such as avoidance of predators, may be shaping the temporal distribution at Serra da Capivara (Astete et al., 2016). Results suggest this may be part of the explanation. Both jaguars and pumas were strictly nocturnal at the Caatinga site (Figure 3), which could explain the activity peaks of the brocket deer.

The *Dasypus* genus mostly consists of nocturnal species in the tropics (Trolle, 2003). This is consistent with results presented here (Figure 3). I found almost no activity during daylight hours at the Amazonian sites. Yet, *Dasypus* spp have a small activity peak at midday at Serra da Capivara, in addition to their largely nocturnal habits. This contrasts with most other focal species at the Caatinga site, but supports previous research on nine-banded armadillos in the Pantanal, where short periods of diurnal activity were observed (Maccarini et al., 2015). However, the diurnal activity consists of only 6 observations between 10:00 and 14:00, and the majority of observations underlines a nocturnal lifestyle. The members of the genus are imperfect homeotherms (McNab, 1980), and it is well established that some armadillo species are entering or leaving their burrows in response to ambient temperature (McNab, 1980, Breece and Dusi, 1985, Superina and Boily, 2007, Maccarini et al., 2015). This is likely the case at all my study sites as well, as temperature was found to significantly decrease *Dasypus* spp activity (Table 3).

The agoutis (*Dasyprocta* spp) in Juruena and Terra do Meio showed a diurnal temporal distribution, with activity peaks concentrated around dusk and dawn. The temporal distribution was especially clear in Juruena, but temperature had a significant positive effect on activity at both sites. Similar patterns have been seen in tropical rainforests in Mexico, Brazil, Panama, and Colombia (Gómez et al., 2005, Suselbeek et al., 2014, García-Restrepo et

al., 2019, Mendoza et al., 2019). This diurnal behaviour is possibly linked with avoidance of its main predator, the mostly nocturnal ocelot (Romero et al., 2016). This may explain their temporal distribution in the Amazon (Figure 3). However, in Serra da Capivara they displayed a crepuscular activity pattern to a much higher degree than at the Amazonian sites. Such changes in temporal activity patterns could be explained by the high temperatures found in Serra da Capivara compared to Amazonia. Previous studies have also found agouti activity to decrease with increasing ambient temperatures (Romero et al., 2016). Although no significance was found when testing for the effect of temperature (Table 3), this could be influenced by the low sampling number in Serra da Capivara, as only 25 agouti detections were made. The highly crepuscular activity pattern likely increases the risk of predation as the temporal overlap with ocelots increase (Figure 3). Both fruit availability and mean daily temperature have been found to significantly explain agouti activity, and could explain why they increase exposure to predators in the Caatinga (Lambert et al., 2009).

The statistical framework used in this thesis is based on some assumptions that may influence the results. The kernel density analysis assumes that the temporal distribution of each animal is consistent throughout the year, even though temporal distribution changes with the seasons for some species and among individuals (Weller and Bennett, 2001, Oliveira-Santos et al., 2010). The data for this thesis was mostly collected during the same months, but there may have been yearly differences in seasonality that affects the results, as some of the data was collected in different years. In addition, the probability of capturing an individual on camera is likely not the same at all times, as both animal activity type and the sensitivity of the camera trigger can vary (Rowcliffe et al., 2014, Meek et al., 2015). However, using camera traps for data collections have major advantages, as it is a non-invasive, relatively cheap method that provides data on a wide range of animals, including those too elusive for other methods (Rowcliffe et al., 2014). The generalized linear model provides some evidence for the effect of temperature on animal diel activity patterns. However, there are no other variables tested. Activity budgets may be influenced by a number of factors (Penido et al., 2017, Mendoza et al., 2019), either individually or combined. Testing with only one predictor variable is therefore perhaps the biggest limitation of this study. Yet, the results provide valuable information, as the world's temperatures continue to increase.

Results presented here indicate that some species have adapted to different environments across the Amazon and Caatinga biomes. Except for *Mazama* spp and *Dasypus* spp, the comparisons between the two biomes resulted in relatively different activity patterns (Figure 3). Since the distinct difference in diel activity patterns seen for some species between the two biomes were highly influenced by temperature, the high temperatures in the Caatinga seem to have turned the mammals in the area more nocturnal. Should the environment in the Amazon become more like the Caatinga, due to deforestation, climate change and fires, the seven focal species may have potential to change their temporal distribution as a response. The results therefore indicate that this suite of species have great plasticity and high resilience.

The giant anteater, for example, was able to almost alter its temporal distribution completely between the two biomes. However, it is likely that the evident temporal adaptation in the Amazon and the Caatinga have evolved over a long time period. The results do not answer how quickly the animals are able to adapt their activity patterns. This should be in focus in future studies on the subject.

References

- ALENCAR, A., BRANDO, P., ASNER, G. & PUTZ, F. E. 2015. Landscape fragmentation, severe drought and the new Amazon forest fire regime. *Ecological Applications*, 25, 1493-1505.
- ASTETE, S. 2008. Comparative Ecology of Jaguars in Brazil. *CAT News Special Issue 4*.
- ASTETE, S., MARINHO-FILHO, J., MACHADO, R. B., ZIMBRES, B., JÁCOMO, A. T. A., SOLLMANN, R., TÔRRES, N. M. & SILVEIRA, L. 2016. Living in extreme environments: modeling habitat suitability for jaguars, pumas, and their prey in a semiarid habitat. *Journal of Mammalogy*, 98, 464-474.
- ATTIAS, N., OLIVEIRA-SANTOS, L. G. R., FAGAN, W. F. & MOURÃO, G. 2018. Effects of air temperature on habitat selection and activity patterns of two tropical imperfect homeotherms. *Animal Behaviour*, 140, 129-140.
- AUBLET, J. F., FESTA-BIANCHET, M., BERGERO, D. & BASSANO, B. 2009. Temperature constraints on foraging behaviour of male Alpine ibex (*Capra ibex*) in summer. *Oecologia*, 159, 237-47.
- AZEVEDO, F. C., LEMOS, F. G., FREITAS-JUNIOR, M. C., ROCHA, D. G. & AZEVEDO, F. C. C. 2018. Puma activity patterns and temporal overlap with prey in a human-modified landscape at Southeastern Brazil. *Journal of Zoology*, 305, 246-255.
- BENNIE, J., DUFFY, J., INGER, R. & GASTON, K. 2014. Biogeography of time partitioning in mammals. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 13727-13732.
- BOWYER, R. & KIE, J. 2009. Thermal landscapes and resource selection by black-tailed deer: Implications for large herbivores. *California Fish and Game*, 95, 128-139.
- BREECE, G. A. & DUSI, J. L. Food habits and home ranges of the common long nosed armadillo *Dasypus novemcinctus* in Alabama, USA. 1985.
- CAMILO-ALVES, C. D. S. E. P. & MOURAO, G. D. M. 2005. Responses of a specialized insectivorous mammal (*Myrmecophaga tridactyla*) to variation in ambient temperature. *Biotropica*, 38, 52-56.
- DALPONTE, J. C., GREGORIN, R., ESTEVES-COSTA, V. A., ROCHA, E. C. & MARCELINO, R. 2016. Bat survey of the lower Juruena River and five new records for the state of Mato Grosso, Brazil. *Acta Amazonica*, 46, 227-232.
- DI BITETTI, M. S., DE ANGELO, C. D., DI BLANCO, Y. E. & PAVIOLO, A. 2010. Niche partitioning and species coexistence in a Neotropical felid assemblage. *Acta Oecologica*, 36, 403-412.
- DI BITETTI, M. S., PAVIOLO, A. & DE ANGELO, C. 2006. Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic Forest of Misiones, Argentina. *Journal of Zoology*, 270, 153-163.

- FERREGUETTI, Á. C., TOMÁS, W. M. & BERGALLO, H. G. 2015. Density, occupancy, and activity pattern of two sympatric deer (*Mazama*) in the Atlantic Forest, Brazil. *Journal of Mammalogy*, 96, 1245-1254.
- FOSTER, V. C., SARMENTO, P., SOLLMANN, R., TÔRRES, N., JÁCOMO, A. T. A., NEGRÕES, N., FONSECA, C. & SILVEIRA, L. 2013. Jaguar and puma activity patterns and predator-prey interactions in four Brazilian biomes. *Biotropica*, 45, 373-379.
- GARCÍA-RESTREPO, S., BOTERO-CAÑOLA, S., SÁNCHEZ-GIRALDO, C. & SOLARI, S. 2019. Habitat use and activity patterns of *Leopardus pardalis* (Felidae) in the Northern Andes, Antioquia, Colombia. *Biodiversity*, 20, 5-19.
- GÓMEZ, H., WALLACE, R. B., AYALA, G. & TEJADA, R. 2005. Dry season activity periods of some Amazonian mammals. *Studies on Neotropical Fauna and Environment*, 40, 91-95.
- GOULART, F., GRAIPEL, M. E., TORTATO, M., GHIZONI-JR, I., OLIVEIRA-SANTOS, L. G. & CÁCERES, N. 2009. Ecology of the ocelot (*Leopardus pardalis*) in the Atlantic Forest of Southern Brazil. *Neotropical Biology and Conservation*, 4, 137-143.
- GUNDERSON, A. R. & LEAL, M. 2016. A conceptual framework for understanding thermal constraints on ectotherm activity with implications for predicting responses to global change. *Ecology Letters*, 19, 111-120.
- HARLEY, C. D. G. 2011. Climate change, keystone predation, and biodiversity loss. *Science*, 334, 1124-1127.
- HUT, R. A., KRONFELD-SCHOR, N., VAN DER VINNE, V. & DE LA IGLESIA, H. 2012. In search of a temporal niche: environmental factors. *Progress in Brain Research*, 199, 281-304.
- KEARNEY, M. 2013. Activity restriction and the mechanistic basis for extinctions under climate warming. *Ecology letters*, 16.
- KEARNEY, M., SHINE, R. & PORTER, W. 2009. The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 3835-3840.
- LAMBERT, T. D., KAYS, R. W., JANSEN, P. A., ALIAGA-ROSSEL, E. & WIKELSKI, M. 2009. Nocturnal activity by the primarily diurnal Central American agouti (*Dasyprocta punctata*) in relation to environmental conditions, resource abundance and predation risk. *Journal of Tropical Ecology*, 25, 211-215.
- LASHLEY, M. A., COVE, M. V., CHITWOOD, M. C., PENIDO, G., GARDNER, B., DEPERNO, C. S. & MOORMAN, C. E. 2018. Estimating wildlife activity curves: comparison of methods and sample size. *Scientific Reports*, 8, 41-73.
- LEMONS, J. 2004. Composição florística do Parque Nacional Serra da Capivara, Piauí, Brasil. *Rodriguésia*, 55, 55-66.
- LEVY, O., DAYAN, T., PORTER, W. P. & KRONFELD-SCHOR, N. 2019. Time and ecological resilience: can diurnal animals compensate for climate change by shifting to nocturnal activity? *Ecological Monographs*, 89, 1-21.
- MACCARINI, T. B., ATTÍAS, N., MEDRI, Í. M., MARINHO-FILHO, J. & MOURÃO, G. 2015. Temperature influences the activity patterns of armadillo species in a large neotropical wetland. *Mammal Research*, 60, 403-409.
- MARTÍNEZ-HERNÁNDEZ, A., ROSAS-ROSAS, O. C., CLEMENTE-SÁNCHEZ, F., TARANGO-ARÁMBULA, L. A., PALACIO-NÚÑEZ, J., BENDER, L. C. & HERRERA-HARO, J. G. 2015. Density of threatened ocelot *Leopardus pardalis* in the Sierra Abra-Tanchipa Biosphere Reserve, San Luis Potosí, Mexico. *Oryx*, 49, 619-625.

- MCNAB, B. 2009. Physiological convergence among ant- and termite-eating mammals. *Journal of Zoology*, 203, 485-510.
- MCNAB, B. K. 1980. Energetics and the Limits to a Temperate Distribution in Armadillos. *Journal of Mammalogy*, 61, 606-627.
- MEEK, P. D., BALLARD, G.-A. & FLEMING, P. J. S. 2015. The pitfalls of wildlife camera trapping as a survey tool in Australia. *Australian Mammalogy*, 37.
- MENDOZA, E., CAMARGO-SANABRIA, A. A. & BASURTO-GODOY, J. 2019. Activity patterns of terrestrial frugivorous mammals in a Mexican Neotropical forest. *Therya*, 10, 371-380.
- MICHALSKI, F. & NORRIS, D. 2011. Activity pattern of *Cuniculus paca* (Rodentia: Cuniculidae) in relation to lunar illumination and other abiotic variables in the southern Brazilian Amazon. *Zoologia (Curitiba)*, 28, 701-708.
- MORATO, R. G., FERRAZ, K. M., DE PAULA, R. C. & DE CAMPOS, C. B. 2014. Identification of priority conservation areas and potential corridors for jaguars in the Caatinga biome, Brazil. *PLoS One*, 9, e92950.
- MOURÃO, G. & MEDRI, Í. 2006. Activity of a specialized insectivorous mammal (*Myrmecophaga tridactyla*) in the Pantanal of Brazil. *Journal of Zoology*, 271, 187-192.
- MUNOZ-DELGADO, J., CORSI-CABRERA, M., CANALES-ESPINOSA, D., SANTILLAN-DOHERTY, A. M. & ERKERT, H. G. 2004. Astronomical and meteorological parameters and rest-activity rhythm in the spider monkey *Ateles geoffroyi*. *Physiology & Behavior*, 83, 107-117.
- OLIVEIRA-SANTOS, L., MACHADO-FILHO, L., TORTATO, M. & BRUSIUS, L. 2010. Influence of extrinsic variables on activity and habitat selection of lowland tapirs (*Tapirus terrestris*) in the coastal sand plain shrub, southern Brazil. *Mammalian Biology* 75, 219-226.
- PENIDO, G., ASTETE, S., JÁCOMO, A. T. A., SOLLMANN, R., TÔRRES, N., SILVEIRA, L. & MARINHO FILHO, J. 2017. Mesocarnivore activity patterns in the semiarid Caatinga: limited by the harsh environment or affected by interspecific interactions? *Journal of Mammalogy*, 98, 1732-1740.
- PÉREZ-IRINEO, G. & SANTOS-MORENO, A. 2014. Density, distribution, and activity of the ocelot *Leopardus pardalis* (Carnivora: Felidae) in Southeast Mexican rainforests. *Revista de biología tropical*, 62, 1421-32.
- RAMOS, R. M., PEZZUTI, J. C. B. & VIEIRA, E. M. 2016. Age structure of the Vulnerable white-lipped peccary *Tayassu pecari* in areas under different levels of hunting pressure in the Amazon Forest. *ORYX*, 50, 56-62.
- RIDOUT, M. S. & LINKIE, M. 2009. Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, 14, 322-337.
- RIVERO, K., RUMIZ, D. & TABER, A. 2005. Differential habitat use by two sympatric brocket deer species (*Mazama americana* and *M. gouazoubira*) in a seasonal Chiquitano forest of Bolivia. *Mammalia*, 69, 169-183.
- RODRÍGUEZ-SOTO, C., MONROY-VILCHIS, O., MAIORANO, L., BOITANI, L., FALLER, J., BRIONES, M., NUÑEZ, R., ROSAS ROSAS, O., CEBALLOS, G. & FALCUCCI, A. 2011. Predicting potential distribution of the jaguar (*Panthera onca*) in Mexico: Identification of priority areas for conservation. *Diversity and Distributions*, 17, 350-361.

- ROMERO, A., MCCLEARN, D., GEROW, K. G. & TIMM, R. M. 2016. Nonvolant mammalian populations in primary and secondary Central American rainforests as revealed by transect surveys. *Journal of Mammalogy*, 97, 331-346.
- ROMERO-MUÑOZ, A., MAFFEI, L., CUÉLLAR, E. & NOSS, A. J. 2010. Temporal separation between jaguar and puma in the dry forests of southern Bolivia. *Journal of Tropical Ecology*, 26, 303-311.
- ROWCLIFFE, J. M., KAYS, R., KRANSTAUBER, B., CARBONE, C., JANSEN, P. A. & FISHER, D. 2014. Quantifying levels of animal activity using camera trap data. *Methods in Ecology and Evolution*, 5, 1170-1179.
- SALES, L. P., GALETTI, M. & PIRES, M. M. 2020. Climate and land-use change will lead to a faunal "savannization" on tropical rainforests. *Global Change Biology*, 26, 7036-7044.
- SCHEIBE, K. M., ROBINSON, T. L., SCHEIBE, A. & BERGER, A. 2009. Variation of the phase of the 24-h activity period in different large herbivore species under European and African conditions. *Biological Rhythm Research*, 40, 169-179.
- SCOGNAMILLO, D., MAXIT, I. E., SUNQUIST, M. & POLISAR, J. 2006. Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. *Journal of Zoology*, 259, 269-279.
- SHAMKHI, M., JAWAD, A. & JAMEEL, T. Comparison between satellite rainfall data and rain gauge stations in Galal-Badra Watershed, Iraq. 2019 12th International Conference on Developments in eSystems Engineering (DeSE), 7-10 Oct. 2019. 340-344.
- SPARKS, A., H. 2018. nasapower: A NASA POWER Global Meteorology, Surface Solar Energy and Climatology Data Client for R. *The Journal of Open Source Software*, 3.
- SUNQUIST, M. & SUNQUIST, F. 2002. Wild cats of the world. *University of Chicago Press*, 452 pp.
- SUPERINA, M. & BOILY, P. 2007. Hibernation and daily torpor in an armadillo, the pichi (*Zaedyus pichiy*). *Comparative Biochemistry and Physiology - Part A Molecular & Integrative Physiology*, 148, 893-8.
- SUSELBEEK, L., ESENS, W.-J., HIRSCH, B. T., KAYS, R., ROWCLIFFE, J. M., ZAMORA-GUTIERREZ, V. & JANSEN, P. A. 2014. Food acquisition and predator avoidance in a Neotropical rodent. *Animal Behaviour*, 88, 41-48.
- TOBLER, M. W., CARRILLO-PERCASTEGUI, S. E. & POWELL, G. 2009. Habitat use, activity patterns and use of mineral licks by five species of ungulate in south-eastern Peru. *Journal of Tropical Ecology*, 25, 261-270.
- TROLLE, M. 2003. Mammal survey in the southeastern Pantanal, Brazil. *Biodiversity and Conservation*, 12, 823-836.
- VAN BEEST, F. M., VAN MOORTER, B. & MILNER, J. M. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Animal Behaviour*, 84, 723-735.
- WELLER, S. H. & BENNETT, C. L. 2001. Twenty-four hour activity budgets and patterns of behavior in captive ocelots (*Leopardus pardalis*). *Appl Anim Behav Sci*, 71, 67-79.
- WEST, P. M. 2005. The lion's mane: neither a token of royalty nor a shield for fighting, the mane is a signal of quality to mates and rivals, but one that comes with consequences. *American Scientist*, 93, 226+.

Appendix

Appendix 1: Complete list of independent camera trap detections of mammals in Juruena, Terra do Meio and Serra da Capivara. The columns after each site indicate how many percent the detections of each species are out of the total number of detections.

Species	English name	Juruena	% of detections	Terra do Meio	% of detections	Serra da Capivara	% of detections
MAMMALIA							
<i>Carnivora</i>							
<i>Felidae</i>							
<i>Panthera onca</i>	Jaguar	34	0.51	20	0.11	58	2.70
<i>Puma concolor</i>	Puma	32	0.48	38	0.22	59	2.75
<i>Puma yagouaroundi</i>	Jaguarundi	4	0.06	12	0.07	30	1.40
<i>Leopardus species</i>	Leopardus species	1	0.01	3	0.02	14	0.65
<i>Leopardus pardalis</i>	Ocelot	90	1.34	176	1.01	255	11.88
<i>Leopardus tigrinis</i>	Oncilla	0	0.00	0	0.00	80	3.73
<i>Leopardus wiedii</i>	Margay	9	0.13	21	0.12	0	0.00
<i>Procyonidae</i>							
<i>Procyon cancrivorus</i>	Crab-eating raccoon	7	0.10	10	0.06	5	0.23
<i>Nasua nasua</i>	South American coati	31	0.46	135	0.77	0	0.00
<i>Mustelidae</i>							
<i>Eira barbara</i>	Tayra	28	0.42	26	0.15	2	0.09
<i>Lontra longicaudis</i>	Neotropical otter	1	0.01	0	0.00	0	0.00
<i>Galictis vittata</i>	Greater grison	2	0.03	1	0.01	0	0.00
<i>Mephitidae</i>							

<i>Conepatus semistriatus</i>	Striped hog-nosed skunk	0	0.00	0	0.00	45	2.10
<i>Canidae</i>							
<i>Speothos venaticus</i>	Bush Dog	0	0.00	3	0.02	0	0.00
<i>Cerdocyon thous</i>	Crab-eating fox	3	0.04	1	0.01	194	9.04
<i>Atelocynus microtis</i>	Short-eared dog	14	0.21	0	0.00	0	0.00
<i>Canis familiaris</i>	Domestic dog	0	0.00	0	0.00	12	0.56
<i>Artiodactyla</i>							
<i>Cervidae</i>							
<i>Mazama species</i>	<i>Mazama species</i>	535	7.96	502	2.87	108	5.03
<i>Mazama americana</i>	Red brocket	297	4.42	549	3.14	0	0.00
<i>Mazama gouazoupira</i>	Amazonian brown brocket	91	1.35	65	0.37	0	0.00
<i>Perissodactyla</i>							
<i>Tapiridae</i>							
<i>Tapirus terrestris</i>	Lowland tapir	271	4.03	358	2.05	0	0.00
<i>Equidae</i>							
<i>Equus ferus</i>	Horse	0	0.00	0	0.00	6	0.28
<i>Equus asinus</i>	Donkey	0	0.00	0	0.00	11	0.51
<i>Artiodactyla</i>							
<i>Tayassuidae</i>							
<i>Pecari species</i>	<i>Pecari species</i>	6	0.09	0	0.00	0	0.00
<i>Pecari tajacu</i>	Collared peccary	428	6.37	0	0.00	8	0.37
<i>Tayassu pecari</i>	White-lipped peccary	74	1.10	213	1.22	0	0.00
<i>Bos taurus</i>	Cattle	0	0.00	0	0.00	49	2.28
<i>Bovidae</i>							
<i>Capra hircus</i>	Goat	0	0.00	0	0.00	43	2.00
<i>Xenarthra</i>							
<i>Myrmecophagidae</i>							

<i>Myrmecophaga tridactyla</i>	Giant anteater	37	0.55	36	0.21	17	0.79
<i>Tamandua tetradactyla</i>	Southern tamandua	34	0.51	17	0.10	9	0.42
<i>Dasyodidae</i>							
<i>Dasypus</i> species	<i>Dasypus</i> species	439	6.53	387	2.21	0	0.00
<i>Dasypus novemcinctus</i>	Nine-banded armadillo	222	3.30	0	0.00	51	2.38
<i>Dasypus kepplei</i>	Greater long-nosed armadillo	3	0.04	10	0.06	0	0.00
<i>Chlamyphoridae</i>							
<i>Cabassous unicinctus</i>	Southern naked-tailed armadillo	12	0.18	1	0.01	0	0.00
<i>Tolypeutes tricinctus</i>	Brazilian three-banded armadillo	0	0.00	0	0.00	45	2.10
<i>Euphractus sexcinctus</i>	Six-banded armadillo	2	0.03	0	0.00	4	0.19
<i>Priodontes maximus</i>	Giant armadillo	53	0.79	51	0.29	0	0.00
<i>Choloepodidae</i>							
<i>Choloepus didactylus</i>	Linné's two-toed sloth	0	0.00	1	0.01	0	0.00
<i>Rodentia</i>							
<i>Dasyproctidae</i>							
<i>Dasyprocta</i> species	<i>Dasyprocta</i> species	1398	20.79	4255	24.31	25	1.16
<i>Dasyprocta fuliginosa</i>	Black agouti	9	0.13	0	0.00	0	0.00
<i>Dasyprocta leporina</i>	Red-rumped agouti	8	0.12	0	0.00	0	0.00
<i>Caviidae</i>							
<i>Cavia</i> species	Cavia	0	0.00	0	0.00	186	8.67
<i>Hydrochoerus hydrochaeris</i>	Capybara	5	0.07	0	0.00	0	0.00
<i>Kerodon rupestris</i>	Rock cavy	0	0.00	0	0.00	37	1.72
<i>Cricetidae</i> species	<i>Cricetidae</i> species	1	0.01	0	0.00	0	0.00
<i>Erethizontidae</i>							
<i>Coendou prehensilis</i>	Brazilian porcupine	1	0.01	0	0.00	1	0.05
<i>Echimyidae</i>							
<i>Dactylomys</i> species	<i>Dactylomys</i> species	0	0.00	1	0.01	0	0.00

<i>Proechimys</i> species	<i>Proechimys</i> species	0	0.00	51	0.29	0	0.00
<i>Thrichomys apereoides</i>	Common punaré	0	0.00	0	0.00	54	2.52
<i>Sciuridae</i>							
<i>Sciurus</i> species	<i>Sciurus</i> species	12	0.18	157	0.90	0	0.00
<i>Sciurus aestuans</i>	Guianan squirrel	2	0.03	0	0.00	0	0.00
<i>Sciurus spadiceus</i>	Southern Amazon red squirrel	17	0.25	0	0.00	0	0.00
<i>Cuniculidae</i>							
<i>Cuniculus paca</i>	Spotted paca	492	7.32	764	4.36	0	0.00
<i>Chiroptera</i>							
<i>Chiroptera</i> species	Unknown bat	0	0.00	0	0.00	4	0.19
<i>Lagomorpha</i>							
<i>Leporidae</i>							
<i>Sylvilagus brasiliensis</i>	Common tapeti	0	0.00	0	0.00	1	0.05
<i>Primates</i>							
<i>Cebidae</i>							
<i>Cebus</i> species	<i>Cebus</i> speices	2	0.03	0	0.00	0	0.00
<i>Cebidae</i> species	<i>Cebidae</i> species	0	0.00	46	0.26	0	0.00
<i>Saimiri</i> species	<i>Saimiri</i> species	1	0.01	3	0.02	0	0.00
<i>Sapajus libidinosus</i>	Black-striped capuchin	0	0.00	0	0.00	5	0.23
<i>Cebus albifrons</i>	Humboldt's white-fronted capuchin	4	0.06	0	0.00	0	0.00
<i>Callitrichidae</i>							
<i>Mico melanurus</i>	Black-tailed marmoset	1	0.01	0	0.00	0	0.00
<i>Didelphimorphia</i>							
<i>Didelphidae</i>							
<i>Didelphidae</i> species	Unknown opossum	0	0.00	0	0.00	1	0.05
<i>Didelphis marsupialis</i>	Common opossum	90	1.34	14	0.08	6	0.28
<i>Metachirini nudicaudatus</i>	Brown four-eyed opossum	113	1.68	0	0.00	0	0.00

<i>Philander opossum</i>	Gray four-eyed opossum	19	0.28	0	0.00	0	0.00
<i>Monodelphis brevicaudata</i>	Northern red-sided opossum	2	0.03	0	0.00	0	0.00
AVES							
<i>Aves</i>	Unknown bird	0	0.00	0	0.00	134	6.24
<i>Tinamiformes</i>							
<i>Tinamidae</i>							
<i>Crypturellus species</i>	<i>Crypturellus species</i>	53	0.79	275	1.57	0	0.00
<i>Tinamus species</i>	<i>Tinamus species</i>	128	1.90	305	1.74	0	0.00
<i>Crypturellus undulatus</i>	Undulated tinamou	8	0.12	30	0.17	0	0.00
<i>Crypturellus variegatus</i>	Variegated tinamou	0	0.00	109	0.62	0	0.00
<i>Crypturellus noctivagus</i>	Yellow-legged tinamou	0	0.00	0	0.00	6	0.28
<i>Crypturellus strigulosos</i>	Brazilian tinamou	0	0.00	2	0.01	0	0.00
<i>Crypturellus cinereus</i>	Cinereous Tinamou	2	0.03	33	0.19	0	0.00
<i>Crypturellus soui</i>	Little tinamou	0	0.00	3	0.02	0	0.00
<i>Rhynchotus rufescens</i>	Red-winged tinamou	0	0.00	1	0.01	0	0.00
<i>Tinamus guttatus</i>	White-throated tinamou	3	0.04	8	0.05	0	0.00
<i>Tinamus major</i>	Great tinamou	37	0.55	154	0.88	0	0.00
<i>Tinamus tao</i>	Grey tinamou	106	1.58	153	0.87	0	0.00
<i>Falconiformes</i>							
<i>Falconidae</i>							
<i>Falco femoralis</i>	Aplomado falcon	0	0.00	0	0.00	1	0.05
<i>Herpetotheres cachinnans</i>	Laughing falcon	0	0.00	0	0.00	1	0.05
<i>Micrastur mintoni</i>	Cryptic forest-falcon	0	0.00	1	0.01	0	0.00
<i>Accipitriformes</i>							
<i>Accipitridae</i>							
<i>Leptodon species</i>	<i>Leptodon species</i>	1	0.01	0	0.00	0	0.00
<i>Accipitridae species</i>	Unknown hawk	1	0.01	0	0.00	18	0.84

<i>Buteogallus urubitinga</i>	Great black hawk	1	0.01	0	0.00	0	0.00
<i>Buteo Brachyurus</i>	Short-tailed hawk	0	0.00	0	0.00	1	0.05
<i>Harpia harpyja</i>	Harpy eagle	1	0.01	0	0.00	0	0.00
<i>Cathartidae</i>							
<i>Cathartes species</i>	<i>Cathartes species</i>	0	0.00	3	0.02	34	1.58
<i>Cathartes burrovianus</i>	Lesser yellow-headed vulture	1	0.01	0	0.00	0	0.00
<i>Coragyps atratus</i>	Black vulture	0	0.00	0	0.00	19	0.89
<i>Strigiformes</i>							
<i>Strigidae</i>							
<i>Strix species</i>	Unknown owl	0	0.00	1	0.01	10	0.47
<i>Strix virgata</i>	Mottled owl	1	0.01	0	0.00	0	0.00
<i>Galliformes</i>							
<i>Cracidae</i>							
<i>Penelope species</i>	<i>Penelope species</i>	42	0.62	50	0.29	128	5.96
<i>Pipile species</i>	<i>Pipile species</i>	4	0.06	0	0.00	0	0.00
<i>Aburria aburri</i>	Aburria	1	0.01	1	0.01	0	0.00
<i>Ortalis guttata</i>	Speckled Chakalaca	1	0.01	0	0.00	0	0.00
<i>Penelope jacquacu</i>	Spix's guan	22	0.33	0	0.00	0	0.00
<i>Penelope pileata</i>	White-crested guan	0	0.00	55	0.31	0	0.00
<i>Penelope superciliaris</i>	Rusty-margined guan	2	0.03	184	1.05	0	0.00
<i>Crax fasciolata</i>	Bare-faced curassow	45	0.67	0	0.00	0	0.00
<i>Nothocrax urumutum</i>	Nocturnal curassow	2	0.03	0	0.00	0	0.00
<i>Mitu tuberosum</i>	Razor-billed curassow	674	10.02	6225	35.56	0	0.00
<i>Pipile cubuji</i>	Red-throated piping guan	2	0.03	0	0.00	0	0.00
<i>Odontophoridae</i>							
<i>Odontophorus species</i>	<i>Odontophorus species</i>	1	0.01	0	0.00	0	0.00
<i>Odontophorus gujanensis</i>	Marbled wood-quail	0	0.00	129	0.74	0	0.00

Gruiformes

Psophiidae

<i>Psophia</i> species	<i>Psophia</i> species	223	3.32	0	0.00	0	0.00
<i>Psophia viridis</i>	Dark-winged trumpeter	161	2.39	912	5.21	0	0.00
<i>Aramides cajaenus</i>	Grey-necked wood-rail	5	0.07	32	0.18	0	0.00

Passeriformes

Passerellidae

<i>Cyanocompsa</i> species	<i>Cyanocompsa</i> species	0	0.00	0	0.00	1	0.05
<i>Arremon</i> species	<i>Arremon</i> species	0	0.00	3	0.02	0	0.00

Thraupidae

<i>Coereba flaveola</i>	Bananaquit	0	0.00	1	0.01	0	0.00
-------------------------	------------	---	------	---	------	---	------

Momotidae

<i>Momotus</i> species	<i>Momotus</i> species	0	0.00	1	0.01	0	0.00
<i>Momotus momota</i>	Amazonian motmot	1	0.01	22	0.13	0	0.00

Thamnophilidae

<i>Rhegmatorhina</i> species	<i>Rhegmatorhina</i> species	0	0.00	1	0.01	0	0.00
<i>Myrmoborus</i> species	<i>Myrmoborus</i> species	0	0.00	1	0.01	0	0.00
<i>Myrmoborus myotherinus</i>	Black-faced antbird	0	0.00	1	0.01	0	0.00

Formicariidae

<i>Formicarius</i> species	<i>Formicarius</i> species	0	0.00	24	0.14	0	0.00
<i>Chamaeza</i> species	<i>Chamaeza</i> species	0	0.00	1	0.01	0	0.00
<i>Chamaeza nobilis</i>	Striated antthrush	0	0.00	141	0.81	0	0.00
<i>Formicarius analis</i>	Black-faced antthrush	0	0.00	1	0.01	0	0.00
<i>Formicarius colma</i>	Rufous-capped antthrush	3	0.04	58	0.33	0	0.00

Grallariidae

<i>Myrmothera campanisona</i>	Thrush-like antpitta	0	0.00	1	0.01	0	0.00
-------------------------------	----------------------	---	------	---	------	---	------

<i>Icteridae</i>							
<i>Cacicus solitarius</i>	Solitary Cacique	1	0.01	0	0.00	0	0.00
<i>Corvidae</i>							
<i>Cyanocorax species</i>	<i>Cyanocorax species</i>	0	0.00	0	0.00	9	0.42
<i>Cuculiformes</i>							
<i>Cuculidae</i>							
<i>Neomorphus species</i>	<i>Neomorphus species</i>	0	0.00	1	0.01	0	0.00
<i>Ani species</i>	<i>Ani species</i>	0	0.00	0	0.00	1	0.05
<i>Neomorphus squamiger</i>	Scaled ground-cuckoo	0	0.00	10	0.06	0	0.00
<i>Columbiformes</i>							
<i>Columbidae</i>							
<i>Leptotila species</i>	<i>Leptotila species</i>	59	0.88	345	1.97	221	10.30
<i>Leptotila verreauxi</i>	White-lipped dove	104	1.55	6	0.03	0	0.00
<i>Leptotila rufaxilla</i>	Grey-fronted dove	0	0.00	128	0.73	0	0.00
<i>Columbina squammata</i>	Scaled dove	0	0.00	0	0.00	37	1.72
<i>Geotrygon montana</i>	Ruddy quail dove	50	0.74	46	0.26	0	0.00
<i>Piciformes</i>							
<i>Picidae</i>							
<i>Celeus species</i>	<i>Celeus species</i>	1	0.01	0	0.00	0	0.00
<i>Campephilus species</i>	<i>Campephilus species</i>	0	0.00	4	0.02	0	0.00
<i>Bucconidae</i>							
<i>Monasa species</i>	<i>Monasa species</i>	1	0.01	3	0.02	0	0.00
<i>Monasa nigrifrons</i>	Black-fronted nunbird	3	0.04	0	0.00	0	0.00
<i>Monasa morphoeus</i>	White-fronted nunbird	0	0.00	86	0.49	0	0.00
<i>Pelecaniformes</i>							
<i>Ardeidae</i>							
<i>Tigrisoma species</i>	<i>Tigrisoma species</i>	0	0.00	1	0.01	0	0.00

<i>Cochlearius cochlearius</i>	Boat-billed heron	0	0.00	2	0.01	0	0.00
<i>Pilherodus pileatus</i>	Capped heron	18	0.27	0	0.00	0	0.00
<i>Tigrisoma lineatum</i>	Rufescent tiger-heron	15	0.22	0	0.00	0	0.00
<i>Threskiornithidae</i>							
<i>Mesembrinibis cayennensis</i>	Green ibis	1	0.01	10	0.06	0	0.00
<i>Eurypygiiformes</i>							
<i>Eurypygidae</i>							
<i>Eurypyga helias</i>	Sunbittern	0	0.00	13	0.07	0	0.00
<i>Cariamiformes</i>							
<i>Cariamidae</i>							
<i>Cariama cristata</i>	Red-legged seriama	0	0.00	0	0.00	47	2.19
<i>Caprimulgiformes</i>							
<i>Caprimilgidae</i>							
<i>Caprimilgidae</i> species	<i>Caprimilgidae</i> species	0	0.00	0	0.00	6	0.28
<i>Nyctidromus albicollis</i>	Pauraque	2	0.03	0	0.00	0	0.00
REPTILIA							
<i>Squamata</i>							
<i>Iguanidae</i>							
<i>Iguana</i> species	<i>Iguana</i> species	0	0.00	0	0.00	8	0.37
<i>Lacertoidea</i>							
<i>Lacertoidea</i> species	Unknown lizard	0	0.00	0	0.00	25	1.16
<i>Alethinophidia</i>							
<i>Alethinophidia</i> species	Unknown snake	0	0.00	0	0.00	1	0.05
INSECTA							
<i>Insecta</i> species	Unknown insect	0	0.00	0	0.00	1	0.05
<i>Coleoptera</i>							
<i>Coleoptera</i> species	Unknown beetle	0	0.00	0	0.00	4	0.19

Lepidoptera

<i>Lepidoptera</i> species	Unknown butterfly	0	0.00	0	0.00	8	0.37
Total detections		6724		17504		2146	



Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitenskapelige universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway