Niche partitioning in felids of the cloud forest of Costa Rica

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by

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Cover image: Ben Luke

Preface

This report serves as a study for my bachelor thesis. My motivation for this research stems from a desire to make a meaningful and scientific contribution to the field of wildlife conservation, with a specific focus on the feline species inhabiting Costa Rica's cloud forests. By investigating the behaviour and spatial distribution of these elusive cats, I hope to provide valuable insights that can inform future conservation strategies. This work reflects my commitment to understanding the complexities of wildlife coexistence and contributing to the preservation of biodiversity.

The primary objective of this research is to explore how different feline species coexist within the same ecological landscape. By analysing camera trap data, I aim to better understand the interactions between these felids, their habitat preferences, and their activity patterns. I hope this knowledge could offer new insights into the mechanisms that allow these species to share resources and space, thereby helping to shape future conservation efforts aimed at protecting these felid species.

Acknowledgements

I would like to express my gratitude to Greilin Fallas Rodríguez, Madelyn Peterson, and Maximilian King for their support in helping me get started at Cloudbridge and for their valuable feedback on this report. I also want to thank my professor, Daphne Vink, for her valuable assistance and insightful feedback. A special thanks goes to Ben Luke for generously sharing his data with me and doing fieldwork together. Finally, I want to thank everyone who joined me in the field for data collection. All help was greatly appreciated!

Abstract

This study investigates the coexistence strategies of six wild felid species—jaguar (*Panthera onca*), puma (*Puma concolor*), ocelot (*Leopardus pardalis*), margay (*Leopardus wiedii*), oncilla (*Leopardus pardinoides*), and jaguarundi (*Herpailurus yagouaroundi*)—in the Cloudbridge Nature Reserve, a tropical montane cloud forest in Costa Rica. The aim of this study was to identify differences in their spatial and temporal distribution in relation to time, space, and diet. The following research question is asked:

What is the difference in the spatial and temporal distribution, considering the available resources (time, space and diet), of the six felid species (jaguar, jaguarundi, puma, oncilla, margay and ocelot) present in the Cloudbridge Nature Reserve?

To answer this research question, four sub questions are asked:

- *What are the diets of the six felid species and is there any overlap?*
- *At which times are the felid species active and is there temporal overlap within this felid guild?*
- *At which places are the felid species active and is there any spatial overlap within this felid guild?*
- *What are the main competitors (primary and secondary) for each felid within the felid guild?*

This study hypothesizes that the six felid species in the Cloudbridge Reserve exhibit niche partitioning across dietary, temporal, and spatial dimensions to reduce competition and enable coexistence.

To address this, camera trap data collected over a ten-year period were analysed using species-specific prey base assessments and activity pattern comparisons. Overlap analyses were conducted using statistical analyses including RAI, the Watson U^2 and Wr tests, and activity overlap estimates.

The results show that while some species, such as the jaguarundi, exhibit strong niche partitioning through diurnal activity and dietary separation, others, especially the smaller *Leopardus* species, demonstrate high temporal and dietary overlap. Jaguars and pumas also share prey but likely avoid direct competition through spatial or prey selection differences.

The conclusion is that niche partitioning is only partially present, and coexistence likely relies on a complex interplay of behavioural and ecological mechanisms beyond time, space or diet alone. These findings contribute to understanding interspecific interactions within predator guilds and offer valuable input for local conservation strategies.

Abstract in Dutch

Deze studie onderzoekt de manieren waarop zes wilde katachtigen—jaguar (*Panthera onca*), poema (*Puma concolor*), ocelot (*Leopardus pardalis*), margay (*Leopardus wiedii*), oncilla (*Leopardus pardinoides*) en jaguarundi (*Herpailurus yagouaroundi*)—samenleven in het nevelwoud van het Cloudbridge Nature Reserve in Costa Rica. Het doel van dit onderzoek was om verschillen in ruimtelijke en temporele verspreiding te identificeren in relatie tot tijd, ruimte en voedsel. De volgende onderzoeksvraag gesteld:

Wat is het verschil in de ruimtelijke en temporele verspreiding, kijkend naar de beschikbare hulpbronnen (tijd, ruimte en dieet), van de zes katachtigen (jaguar, jaguarundi, poema, tijgerkat, margay en ocelot) die voorkomen in het Cloudbridge Nature Reserve?

Om deze onderzoeksvraag te beantwoorden, zijn vier deelvragen opgesteld:

- *Wat zijn de diëten van de zes katachtige soorten en is er sprake van overlap?*
- *Op welke tijdstippen zijn de katachtigen actie en is er sprake van temporele overlap binnen deze soortengroep?*
- *Op welke locaties zijn de katachtigen actief en is er sprake van ruimtelijke overlap binnen deze soortengroep?*
- *Wat zijn belangrijkste concurrenten (primaire en secundaire) voor elke katachtige binnen deze soortengroep?*

Deze studie stelt als hypothese dat de zes katachtigen in het Cloudbridge Nature Reserve gebruikmaken van nicheverdeling op het gebied van dieet, tijd en ruimte om concurrentie te verminderen en co-existentie mogelijk te maken.

Om dit te onderzoeken werden cameravaldata uit een periode van tien jaar geanalyseerd in combinatie met prooiprofielen en activiteitspatronen per soort. Overlap tussen soorten werd bepaald met statistische analyses, waaronder RAI, de Watson U^2- en Wr-toetsen, en activiteitsoverlap analyses.

Uit de resultaten blijkt dat sommige soorten, zoals de jaguarundi, duidelijke nichescheiding tonen in activiteit en dieet. Andere soorten, vooral de kleinere *Leopardus*-soorten, overlappen sterk in zowel activiteit als dieet. Jaguars en poema's jagen op vergelijkbare prooisoorten, maar vermijden waarschijnlijk directe competitie door verschillen in ruimtelijke verspreiding of door het selecteren van andere prooisoorten binnen hetzelfde prooispectrum.

De conclusie is dat nichescheiding slechts gedeeltelijk optreedt en dat co-existentie vermoedelijk afhankelijk is van een complex samenspel van gedrags- en ecologische strategieën. De bevindingen leveren waardevolle inzichten op voor het begrijpen van interacties tussen roofdieren en bieden aanknopingspunten voor gerichte natuurbescherming.

Index

1. Introduction

Felids are integral to the health of ecosystems, functioning as apex predators that influence prey populations and, by extension, impact plant communities (Wang, 2002). In the rich biodiversity of tropical (montane) forests, such as those found in Costa Rica, these predators play a critical role in maintaining ecological balance.

Recent scientific research on wild cat species in Central America and South America highlights several trends. Conservation efforts are increasingly focusing on lesser-known small felines like oncilla (*Leopardus spp.*), also known as tiger cats, alongside more iconic species such as jaguars (*Panthera onca*) (Ramírez-Fernández et al., 2021). New taxonomic updates, such as the recognition of *Leopardus pardinoides oncilla* as a separate species in 2024, are reshaping conservation priorities, particularly in countries like Costa Rica, where the oncilla is now considered one of the most endangered cats (Trigo et al., 2013; Ramírez-Fernández et al., 2024).

Habitat loss, especially due to agriculture and urban development, remains a significant threat to wild cats (Arroyo-Arce et al., 2014; Salom-Pérez et al., 2021; Ramírez-Fernández et al., 2021). This underscores the importance of habitat preservation as the primary conservation strategy for wild cat species. In Costa Rica, there is a growing recognition of the need for habitat conservation, particularly in light of the threats posed by agriculture and urban development. Efforts include sustainable land-use practices to balance economic development with wildlife protection (Sierra & Russman, 2005; Miller et al., 2023). Moreover, tropical montane ecosystems are widely recognised as being highly vulnerable to climate change impacts (Laurance et al., 2010; González-Zeas et al., 2018). This poses also a threat for cat species inhabiting these areas.

Within the Cloudbridge reserve, part of the tropical montane cloud forest in Costa Rica, all of the six Costa Rican felines can be found: jaguar (*Panthera onca*), puma (*Puma concolor*), ocelot (*Leopardus pardalis*), jaguarundi (*Herpailurus yagouaroundi*), margay (*Leopardus wiedii*), and oncilla (*Leopardus pardinoides*) (Cloudbridge Nature Reserve, n.d.). In this carnivore community the felids have dietary overlap and compete partially for the same resources (Wang, 2002; Botts et al., 2020). Intense competition for prey can lead to competitive exclusion unless these species employ strategies to partition their activities in time or space (Foster et al., 2013; Valeix et al., 2007). Therefore, they might use a strategy called temporal niche partitioning. Temporal niche partitioning, which refer to the changes in timing, placing and dietary preferences of an animal, are particularly important for understanding how different species with overlapping resources can coexist (Lear et al., 2021).

Competition among carnivores may be influenced not only by predation on the prey species of the felids, but also by the perceived or actual threat of intraguild killing (Santos et al., 2019). Numerous studies provide evidence of interspecific killing between various pairs of sympatric carnivore species, especially felids, can strongly influence the composition and dynamics of carnivore communities. (Palomares & Caro, 1999; Fedriani et al., 2000; Donadio & Buskirk, 2006; De Oliveira & Pereira, 2013; Santos et al., 2019).

Behavioural variation over the three primary niche dimensions (habitat, food, and time) may promote resource partitioning (Hearn et al., 2018) and thereby reducing competition. Diet partitioning is an ecological concept where different species within the same habitat reduce competition for food by specialising in different types of prey or food sources (Kent & Sherry, 2020). In the case of predators, diet partitioning involves hunting different prey species. Spatial partitioning occurs when organisms live in different areas within the same habitat. Temporal partitioning is when multiple species use the same resources but at different times of the day or year, which reduces direct competition (Albrecht, 2001; Frey et al., 2017; Mugerwa et al., 2017; Botts et al., 2020). For instance, predators might alter their hunting times to avoid overlap with other predators. These three strategies allow predators to coexist by minimising direct competition for the same resources. These forms of resource partitioning help to maintain biodiversity by allowing multiple species to thrive in the same environment.

Diet overlap

Research has been conducted in Costa Rica on forms of resource partitioning. It is important to know if there is any overlap between the felid species within their diet. The study by Botts et al. (2020) investigated how mammalian predators and their prey divide their activity times, using data collected from twelve long-term camera trap studies carried out in the Pacific slope and Talamanca Cordillera regions of Costa Rica. This study provided a dietary list for eight predators, including the six feline species of Costa Rica (Appendix I). A study conducted by Wang (2002) explored the diets of three small cat species (*L. pardalis*, *L. wiedii*, and *L. tigrinus*) by analysing scat and regurgitation samples collected over a year in southeastern Brazil.

Temporal overlap

Previous studies have demonstrated that different felid species exhibit distinct activity patterns to minimize competition (Di Bitetti et al., 2010; Monterrosso et al., 2013; Herrera et al., 2018; Botts et al., 2020). For example, in Costa Rica, smaller felids like ocelots, margays, and oncillas are often primarily nocturnal, while larger felids like jaguars and pumas are active at various times throughout the day and night (Botts et al., 2020).

Analysis by Botts et al. (2020) findings confirmed that the eight predator species displayed distinct activity patterns, indicating temporal separation in their niches. (jaguar, puma, ocelot, coyote, jaguarundi, tayra, margay, oncilla) in Costa Rica. Within the carnivore community, activity patterns varied notably by species. Smaller Leopardus species (ocelot, margay, and oncilla) were primarily nocturnal. In contrast, the bigger carnivores, jaguar, puma, and coyote, were frequently active across both daylight and nighttime hours, indicating a cathemeral activity patterns. Meanwhile, jaguarundi and tayra restricted their activity almost entirely to daytime, showing a diurnal rhythm. Table 1 shows the expected temporal overlap for the six felid species in Cloudbridge according to Botts et al. (2020).

Table 1 Temporal overlap according to Botts et al. (2020)

Felid sp.	Nocturnal	Cathemeral	Diurnal
Jaguar		X	
Puma		X	
Ocelot	X		
Oncilla	X		
Margay	X		
Jaguarundi			X

Di Bitetti et al. (2010) found that felid species with similar physical traits in Argentina exhibited distinctly different activity patterns. The margay showed a strictly nocturnal rythm, while the jaguarundi was active during the day (Table 2). Other species, including the jaguar, puma, ocelot, and oncilla, were cathemeral but showed activity peaks that corresponded to the relative sequence of their body weight.

Table 2 Temporal overlap according to Di Bitetti et al. (2010)

Felid sp.	Nocturnal	Cathemeral	Diurnal
Jaguar		X	
Puma		X	
Ocelot		X	
Jaguarundi			X
Margay	X		
Oncilla		X	

Foster et al. (2013) investigated the activity patterns and predator-prey interactions in Brazil, finding minimal partition in time among jaguars and pumas, as their activity patterns showed considerable overlap. They suggested that differences in habitat use and food resources could play a more significant role in facilitating coexistence between these top predators.

Herrera et al. (2018) studied time partitioning among jaguars, pumas and ocelots in Costa Rica and found a strong temporal overlap among these three felids. Jaguar and puma exhibited significant overlap in time with prey species of medium and large size, while the time of activity of ocelots coincided more with smaller prey species. The high overlap in activity patterns among these felids suggests that temporal segregation alone is unlikely to be the primary factor driving their coexistence. Instead, fine-scale spatial and temporal differences in their behaviour might play a more important role in allowing these species to coexist in the same habitat.

Spatial overlap

A study conducted by Santos et al. (2019) examined the spatiotemporal composition of six different cat species (jaguar, puma, ocelot, jaguarundi, margay, and oncilla) based on data collected from eight neotropical forest locations situated across six different countries in South and Central America. The researchers found that prey abundance played a more significant role in determining the local presence and spatial distribution of these felids than species interactions. In particular, the habitat use patterns of jaguar, puma, and ocelot were primarily explained by the availability of prey.

1.1 Importance of research

Studying felids is difficult because they are elusive and found in low abundance (Linkie & Ridout, 2011). Moreover, conservation efforts have mostly focused on larger, and more recognizable feline species, while smaller felids have often been ignored (Ramírez-Fernández et al., 2021). This gap is significant because these smaller species also have important ecological roles and face their own conservation challenges (Ramírez-Fernández et al., 2021). To effectively conserve all felid species, it is essential to understand their spatial and temporal distribution within their habitats.

However, temporal niche partitioning varies between different environments. This study will take place in the tropical montane cloud forest within the Cloudbridge reserve in Costa Rica, so it might be different in the Cloudbridge reserve. What is missing is specific information about how these activity patterns work in Cloudbridge. More details are needed to understand how these felid species interact within the same area and how their activity patterns can guide better conservation strategies. Using camera traps and analysing the data with advanced tools can help provide a clearer picture of how these felids live and interact with each other in the reserve.

Given this context, the scope of the research is to explore the spatial and temporal distribution of six felid species in the Cloudbridge reserve. By investigating their activity patterns and how these patterns relate to their prey, this study aims to reveal how these felids coordinate their behaviours to coexist within the same habitat. Understanding these dynamics will provide valuable insights for developing effective conservation strategies, ensuring that all felid species can thrive and contribute to the overall health of the ecosystem.

1.2 Research questions

To research this subject, the following research question is asked:

What is the difference in the spatial and temporal distribution, considering the available resources (time, space and diet), of the six felid species (jaguar, jaguarundi, puma, oncilla, margay and ocelot) present in the Cloudbridge Nature Reserve?

To answer this research question, four sub questions are asked.

-What are the diets of the six felid species and is there any overlap?

-At which times are the felid species active and is there temporal overlap within this felid guild?

-At which places are the felid species active and is there any spatial overlap within this felid guild?

-What are the main competitors (primary and secondary) for each felid within the felid guild?

This study hypothesizes that the six felid species in the Cloudbridge Reserve exhibit niche partitioning across dietary, temporal, and spatial dimensions to reduce competition and enable coexistence.

Answering the research questions will help to get better information about which variables (time, space and diet) contribute to the coexistence of certain felid species in an area. This helps to improve conservation efforts of nature reserves like Cloudbridge, who can use the information for effective monitoring and conservation purposes. This can help to support the overall health of tropical montane forests.

2. Methodology

2.1 Study Area

Data collection was done in 2024 from August 12th until October 20th in the Cloudbridge reserve (9.472325502733705, -83.57734885467406), located in Pérez Zeledón, Costa Rica (Figure 1). Cloudbridge is a private reserve in the Talamanca Mountains cloud forest, ranging from 1550 to 2600 meters above sea level (Cloudbridge Nature Reserve, n.d.). The size of the study area amounts to 220 hectares. This reserve was created to protect and restore a vital section of the cloud forest adjacent to the Chirripó Pacifico River, situated on the slopes of Mount Chirripó (Cloudbridge Nature Reserve, n.d.).

Figure 1 Location of Cloudbridge Nature Reserve

A cloud forest is a type of tropical rainforest located at high elevations, where it is characterized by nearly constant humidity throughout the year. This unique ecosystem is often shrouded in clouds that drift through the valleys and canopy. Water is collected in the forest through a process called evapotranspiration, where moisture from the atmosphere accumulates on the forest floor and on epiphytes—plants that grow on the surface of trees and absorb water directly from the air (Cloudbridge Nature Reserve, n.d.).

The study area knows two seasons: the dry and wet season. The dry season is generally between late December and April. The wet season lasts from May through November. The average temperature is fairly constant all year round and varies from 15 degrees Celsius at night to 25 degrees Celsius during the day (Cloudbridge Nature Reserve, n.d.).

2.2 Methods

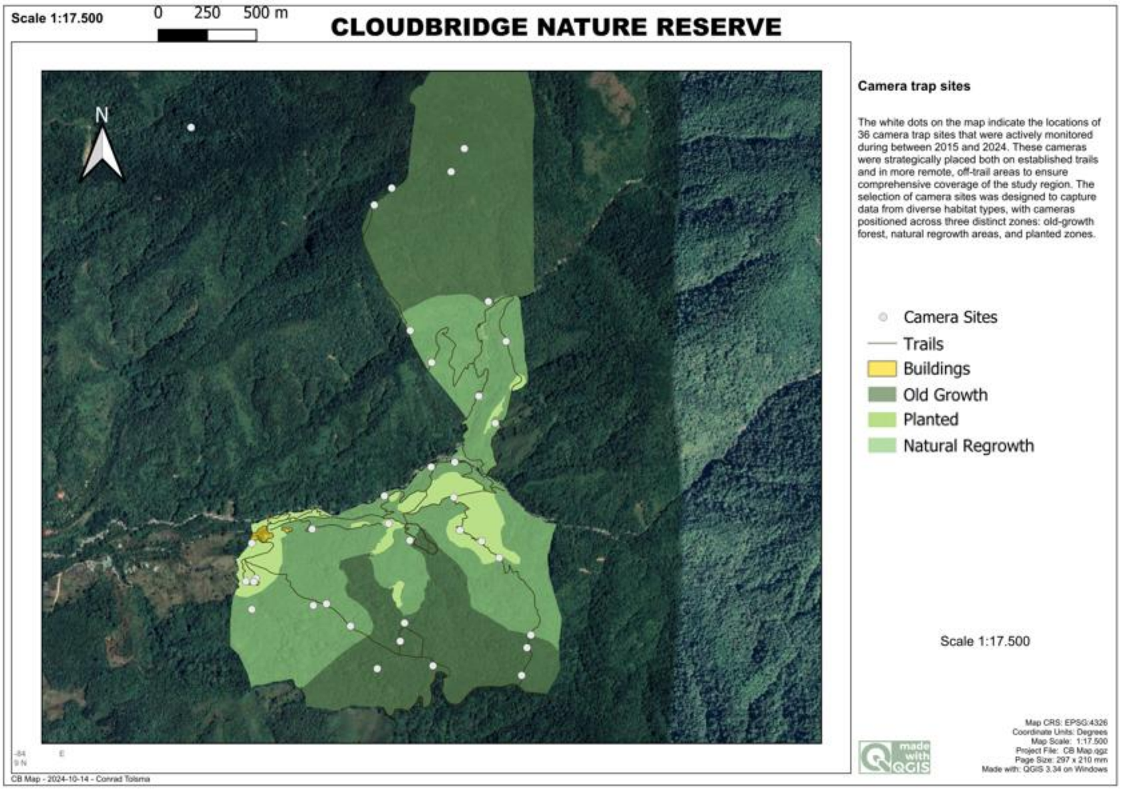
This study utilises a quantitative method using statistical analysis for objective measurement and hypothesis testing. Data collection was done by combining data attained during the research period with historical data from previous studies in the reserve. The historical databases contained similar variables as this study. In total this study used 37 camera trap sites for 10 trails within the reserve (Figure 2).

2.2.1 Camera traps

For data collection this study used the camera trapping method. Camera traps are an effective and non-invasive tool for wildlife research, capturing continuous data on animal presence and behaviour without disturbing their natural activities. They are especially useful for monitoring nocturnal or elusive species like wild cats. Camera traps are capable of functioning continuously over extended durations in remote locations, providing valuable data on species distribution, habitat use, and behaviour while being cost-effective and requiring minimal maintenance. These benefits make them a key method in modern wildlife research and conservation efforts (Caravaggi et al., 2017).

In total there were 37 camera traps deployed in the study area (see Figure 2 and Table 3). Each individual trail camera was checked at intervals of two weeks to retrieve data from the SD cards and ensure proper functionality throughout the research period.

Figure 2 Locations of camera traps in Cloudbridge reserve



The white dots on the map indicate the locations of 36 camera trap sites that were actively monitored during between 2015 and 2024. These cameras were strategically placed both on established trails and in more remote, off-trail areas to ensure comprehensive coverage of the study region. The selection of camera sites was designed to capture data from diverse habitat types, with cameras positioned across three distinct zones: old-growth forest, natural regrowth areas, and planted zones.

Map CRS: EPSG:4326
Coordinate Units: Degrees
Map Scale: 1:17.500
Project File: CB Map.qgz
Page Size: 297 x 210 mm
Made with: QGIS 3.34 on Windows

CB Map - 2024-10-14 - Conrad Tolsma

Table 3 Location, elevation and active days of camera traps

Location ID	Location Name	Habitat Type	GPS Longitude	GPS Latitude	Elevation	Active camera days
D1	Don Victor Trail	Old Growth Forest	N 09°28.6930	W 083°34.0796	1746m	670
D2	Don Victor Trail	Old Growth Forest	N 09°28.9433	W 083°34.0429	1808m	591
E0	Jilguero Loop	Planted Forest	N 09°28.1733	W 083°34.7155	1616m	254
E1	Jilguero Trail	Naturally Regenerated Forest	N 09°28.1203	W 083°34.4954	1818m	1164
E11	Jilguero Trail	Naturally Regenerated Forest	N 09°28.105	W 083°34.704	1671m	291
E2	Jilguero Loop	Planted Forest	N 09°28.1769	W 083°34.7039	1687m	55
E7	Jilguero Trail	Planted Forest	N 09°28.289	W 083°34.704	1576m	1
E9	Jilguero Trail	Old Growth Forest	N 09°27.940	W 083°34.355	1960m	223
G1	Gavilan Trail	Naturally Regenerated Forest	N 09°28.3438	W 083°34.3235	1707m	648
G2	Gavilan Trail	Planted Forest	N 09°28.305	W 083°34.338	1726m	417
G4	Gavilan Trail	Old Growth Forest	N 09°28.0664	W 083°34.2772	1869m	1288
H1	Heliconia Trail	Naturally Regenerated Forest	N 09°28.328	W 083°34.537	1606m	390
K1	Skutch Trail	Old Growth Forest	N 09°29.447	W 083°34.873	2092m	39
K2	Skutch Trail	Old Growth Forest	N 09°29.323	W 083°34.150	2401m	116
K3	Skutch Trail	Old Growth Forest	N 09°29.388	W 083°34.113	2426m	141
M1	Montaña Trail	Planted Forest	N 09°28.3318	W 083°34.1323	1829m	111
M2	Montaña Trail	Planted Forest	N 09°28.4174	W 083°34.1398	1743m	160
M3	Montaña Trail	Old Growth Forest	N 09°27.9246	W 083°33.9551	2144m	15
M4	Montaña Trail	Natural Regrowth	N 09°28.2488	W 083°34.0155	1898m	234
M5	Montana	Planted Forest	N 09°28.2947	W 083°34.0647	1860m	1
M9	Montana	Old Growth Forest	N 09°27.9984	W 083°33.9384	2124m	349
Q1	Los Quetzales Trail	Naturally Regenerated Forest	N 09°28.8565	W 083°34.0001	1825m	518
Q2	Los Quetzales Trail	Naturally Regenerated Forest	N 09°28.6257	W 083°34.0300	1787m	82
R3	Rio Trail	Naturally Regenerated Forest	N 09°28.5016	W 083°34.2040	1668m	318
R4	Rio Trail	Planted Forest	N 09°28.4169	W 083°34.3373	1680m	657
R5	Rio Trail	Naturally Regenerated Forest	N 09°28.5188	W 083°34.1332	1671m	136
S1	Sentinel Trail	Naturally Regenerated Forest	N 09°28.2912	W 083°34.2740	1740m	652
S2	Sentinel Trail	Naturally Regenerated Forest	N 09°28.280	W 083°34.215	1755m	33
Sk1	Skutch Trail	Old Growth Forest	N 09°28.7924	W 083°34.2019	1947m	58
Sk1 Ben	Skutch Trail	Old Growth Forest	N 09°29.113	W 083°34.393	2273m	20
Sk2	Skutch Trail	Old Growth Forest	N 09°28.8812	W 083°34.2632	2032m	55
Sk2 Ben	Skutch Trail	Old Growth Forest	N 09°29.292	W 083°34.295	2421m	51
Sk3	Skutch Trail	Old Growth Forest	N 09°29.2333	W 083°34.3634	2417m	23
E7	El Jilgeuro Trail	Naturally Regenerated Forest	N 09°28.132	W 083°34.478	1799m	3
G5	Gavilan Trail	Old Growth Forest	N 09°28.0580	W 083°34.2820	1929m	5
M7	Montaña Trail	Natural Regrowth	N 09°28.308	W 083°34.018	1853m	1
M8	Montaña Trail	Natural Regrowth	N 09°28.192	W 083°33.963	1972m	214
						Total = 9985

For this study, a range of trail cameras from six different brands were utilised: Gamekeeper, Bushnell, Wosoda, Ceyomur, Apeman, and Campark. All cameras employed motion-triggered sensors to capture wildlife activity, ensuring that footage was recorded only when movement was detected within the camera's field of view. Each camera was equipped with infrared sensors, allowing for nocturnal monitoring without emitting visible light that could disturb wildlife behaviour.

For the setup of trail cameras, several settings were configured to ensure consistency and accuracy in data collection. First, the internal clock of each camera was synchronized to the correct date and time to allow for precise timestamping of the footage. The cameras were set to video mode, with the video quality adjusted to the highest available setting, and the format selected as full screen to maximize resolution and field of view. The LED control was set to high to enhance night-time illumination, while the camera name was updated to reflect the specific deployment location for ease of data management.

The recording time was set to 10 seconds. The interval between consecutive video recordings was set to the minimum allowable by each camera model, which was either 0.6, 1 or 3 seconds depending on the model. The sensor sensitivity was adjusted according to environmental conditions, with auto, mid, or high sensitivity selected depending on the expected activity level at each site. Additionally, the night vision (NV) shutter was configured to auto, allowing the camera to adjust automatically based on lighting conditions. All cameras were set to operate continuously in 24-hour mode to ensure uninterrupted recording throughout the study period.

Prior to each deployment, the SD card was formatted to prevent data corruption and ensure sufficient storage capacity. The time-stamp function was enabled on all cameras to record the exact time of each event. The field scan feature, which captures images at pre-set intervals regardless of motion, was deactivated to focus solely on motion-triggered events. Lastly, the coordinate input function was disabled because it was not required for this study. However, GPS tagging of all the camera sites was done using a GPS tracker. These standardised settings ensured the collection of high-quality, consistent video data for analysis.

Every animal video captured by the trail cameras was organised into a shared database. The variables from the footage were added to another database in Excel. The database contains a dataset which documents the camera id, location, common name, scientific name, date of capture, time of observation and number of individuals. In this research the camera trap footage from 37 camera sites were analysed from 9985 camera trap days. Independent records were defined as observations separated by a minimum of 60 minutes at the same camera site, reducing temporal autocorrelation.

This study also relied on the historical data that was collected prior to the current data collection. Multiple databases, including the data that was collected during the fieldwork of this thesis, were combined in order to create one big dataset containing ten years' worth of observation records recorded.

2.2.2 Prey base

A potential prey base, compiled from scientific literature, was estimated to determine a selection of prey for each felid since there was no option to gather dietary data from scats or killings to analyse for this study. The prey selection in this potential prey base functioned as a starting point for further statistical analyses to investigate the overlap in activity times of predator and prey, using both historical from Cloudbridge and collected data from this study, in order to determine the overlap in the diet of the six wild felids. This was necessary because only abundance of the potential prey will not exactly tell the chance of them becoming actual prey since activity times of both parties (predator and prey) need to overlap in time as well. Search terms such as: “*Panthera onca*”, “*Puma concolor*”, “*Leopardus pardalis*”, “*Herpailurus yagouaroundi*”, “*Leopardus wiedii*”, “*Leopardus pardinoides*”, “diet”, “prey” and “food niche overlap” were used for each of the six felids in Google Scholar to get the correct information. Comparing the prey base of each felid species provides insight into the competition for food resources.

2.2.3 Activity times

To evaluate potential temporal niche partitioning, the observed activity patterns of the six felid species were compared with expected baseline activity times. These baselines were derived from descriptions in the field guide *Mamíferos de Costa Rica* (Carrillo et al., 2002), which classifies each species as diurnal, nocturnal, or crepuscular. These categories were visualised in a 24-hour timetable (starting and ending at midnight) and compared to the hourly detection data obtained from the camera trap dataset. This comparison enabled an assessment of whether the species' observed circadian activity in the Cloudbridge reserve aligns with general expectations from the literature. In Appendix II, these times are visualised in a table.

2.3 Data analysis

The analysis and tests used in this research were done according to the research of Botts et al. (2020), with some minor adjustments. Overlap is calculated using the Relative Abundance Index (RAI) and three measures of significance (Watson’s U2, Wr and Fisher’s Exact Test).

2.3.1 Activity patterns

To account for day and night activity patterns, sunrise and sunset times for San José, Costa Rica, were collected from two sources (Worlddata.info, n.d.; Sunrise and sunset.com, n.d.) for each month of the study period. When data about time was missing in the dataset, sunrise and sunset times were imputed using the monthly averages to ensure completeness. Each observation was classified as day or night based on its timing relative to the daily sunrise and sunset. Observations recorded between sunrise and sunset were classified as day, while those recorded before sunrise or after sunset were classified as night. For each species, the total number of independent records was calculated separately for day and night periods. The results were summarised in a table. The numbers of day and night observations for each species were then converted to percentages in order to classify the species as nocturnal (≥90% of records at night), mostly nocturnal (70–89% of records at night), cathemeral (30–69% of records at night), mostly diurnal (10–29% of records at night) and diurnal (<10% of records at night). This classification system was adapted from Gómez et al. (2005), Azevedo et al. (2018) and Botts et al. (2020).

For each felid species, the number of independent detections per trail was extracted from the dataset. To allow comparisons across trails, these raw counts were converted into percentages. The percentage for each species on a given trail was calculated by dividing the number of observations of a species on that trail by the total number of observations for that species across all trails, then multiplying by 100.

Each camera trap location was associated with both a habitat type and an elevation value. Elevation was determined using GPS measurements taken during camera placement. Habitat classifications were provided by Cloudbridge Nature Reserve and linked to each camera site. The number of detections per felid species was aggregated per habitat type, allowing visual comparisons across habitats. Similarly, the number of observations per species was plotted against the elevation to visualise vertical distribution patterns.

2.3.2 Relative Abundance Index

In the research of Botts et al. (2020), the RAI was determined by the number of independent records divided by the number of days the cameras were active times 1000. However, since there was no data available of the number of active camera days, this research compensated this by estimating the active camera days using the dates from the main database which contained the dates of all observations. First, the earliest and latest observation dates for each camera were identified. Second, the difference between these dates was calculated.

To counter the problem that cameras were not always consistently active between the start and end dates, an estimate effort was made based on known deployment schedules. If a camera did not have any continued observations over a period more than one month, the period with no observations were subtracted till the next observation in order to rectify the number of camera days. This was done because it seemed likely that very long periods without observations probably reflect inactive cameras rather than true absence of wildlife. By excluding these periods, the camera effort (number of active days) better reflects the actual time cameras were functioning, leading to more accurate RAI calculations.

To implement this into the analyses the difference in days between consecutive observations for each camera were calculated. The formula used to calculate the Relative Abundance Index was:

$$RAI = \frac{number\ of\ observations\ of\ a\ species}{Total\ camera\ days} * 1000$$

2.3.3 Overlap analysis

The overlap analysis was conducted to estimate the overlap coefficient (Δ) between the activity patterns of the six cat species (Jaguar, Puma, Ocelot, Jaguarundi, Margay, and Oncilla) and all selected prey species and the other cats in the dataset. The analysis was performed using the methodology from Ridout and Linkie (2009) as described in Botts et al. (2020), which estimates overlap from two sets of circular data.

To ensure accurate calculations, the observation times for each species were first converted to radians. This transformation was necessary for the proper computation of the overlap coefficient, as it allows for the handling of circular data. The observation times were converted to radians using the following formula: $radians = \left(\frac{Time}{24}\right) \times 2\pi$

Additionally, missing time data (represented by empty cells in the time column) were handled by calculating circular average times, ensuring that gaps in the dataset did not affect the analysis. The mean direction is computed by averaging the sine and cosine components of the angles. Specifically, the average cosine component $\bar{x}$ is calculated as: $\bar{x} = \frac{1}{n}\sum_{i=1}^{n} cos\ (\theta_i)$ and the average sine component $\bar{y}$ is calculated as: $\bar{y} = \frac{1}{n}\sum_{i=1}^{n} sin\ (\theta_i)$, where θ_i are the angles (in radians) of the time points, and n is the number of observations.

The circular mean was then determined by finding the angle of the resultant vector using the formula: $\bar{\theta} = atan2(\bar{y}, \bar{x})$. The function $atan2(\bar{y}, \bar{x})$ was used to ensure the angle is in the correct quadrant.

Finally, if the resulting mean angle $\bar{\theta}$ was negative, it was adjusted to lie within the range of $[0,2\pi]$ by adding 2π if necessary ($\bar{\theta} = \bar{\theta} + 2\pi$ if $\bar{\theta} < 0$). If the average time in hours was desired, the circular mean could be converted back to the original scale using the formula: $\bar{t} = T \times \frac{\bar{\theta}}{2\pi}$ where $\bar{t}$ is the average time in hours, and T is the total duration of the cycle (e.g., 24 hours).

For the overlap analysis, the minimum number of observations required for each species was set to 5, which was a reduction from the original threshold of 15 as done in Botts et al. (2020). This adjustment allowed the inclusion of the Jaguarundi, which had fewer than 15 observations but more than 5, and thus made it possible to analyse its overlap with other species.

The overlap coefficient was calculated for each pair of species that both had at least 5 observations. The overlap coefficient and its confidence intervals were computed using bootstrapping, with 10,000 bootstrap trials. The resulting estimates provided a measure of the temporal overlap in activity patterns between the species, which is essential for understanding potential competition and prey interactions.

The Watson U^2 test

The Watson U^2 test is used to measure the overlap between two sets of circular data, like activity patterns measured over time (Landler et al., 2021). It operates by converting the time data into radians, calculating cumulative frequency distributions for each species, and then determining the difference between the distributions of the two species (Alsultany, 2025). The U^2 statistic is then calculated to represent the degree of overlap between their activity patterns. A p-value is derived using bootstrapping, which assesses the statistical significance of the overlap.

In this research, the Watson U^2 test was essential for analysing the temporal overlap between cat species and their competitors or prey. This test allowed for a more accurate assessment of how these species interact, helping to understand their competitive dynamics, resource partitioning, and ecological relationships. Given that the data is circular (activity times), the Watson U^2 test is a fitting statistical tool to analyse this type of data.

Watson-Williams test

The Wr test, also known as the Watson-Williams test, is a statistical test used to compare the mean directions of two sets of circular data. It is designed to determine whether two groups have significantly different activity patterns in terms of their circular mean. The test is particularly useful when interested in comparing the central tendency of circular data between two groups, such as activity times or movement patterns (Berens, 2009). The null hypothesis of the test is that the two groups have the same mean direction, while the alternative hypothesis suggests that they differ significantly.

In this research, the Wr test was valuable to compare the central activity times of different species. The test could be used to test whether the peak activity times of a particular cat species significantly differ from the peak activity times of their competitors or prey species. This comparison provides insights into whether the species have distinct activity windows, which could have ecological implications for competition or prey-predator interactions.

Fisher’s Exact Test

The Fisher's Exact Test is useful to assess whether two species exhibit significantly different activity distributions (Mooring et al., 2020). For example, a comparison could be made for the activity patterns of a Jaguar and a Puma to see if their activity times are distributed differently across a 24-hour period. If the activity patterns are significantly different, it could indicate that they avoid each other in time, which may suggest spatial or temporal partitioning of resources.

Since activity times are circular (in radians), they were binned into discrete time intervals, creating a contingency table of species detections per bin. Fisher’s Exact Test was then used instead of a Chi-square test because some bins contained low observation counts, making the latter unreliable. Fisher’s test calculated exact probabilities and remained valid even when expected values were below five. This approach facilitated the identification of potential avoidance patterns or competition in activity timing, providing insight into niche partitioning within the felid community.

2.3.4 Primary and secondary competitors

For each felid species, the primary prey was identified based on predictions about potential competition among the felids (Botts et al., 2020). This identification relied on the assumption that these predators are opportunistic hunters, typically targeting prey species they encounter most frequently and that are within their suitable prey range. The frequency of such encounters was determined by considering both the prey's relative abundance and the degree of spatial and temporal overlap between the predator and prey. As a result, prey encounter rates were estimated using a combination of relative abundance and activity overlap metrics (Botts et al., 2020).

To determine the main competitor (primary and secondary) within the felid-guild it was assumed that cats will hunt prey with similar body masses. By comparing the body mass and the prey preferences (see prey base in Appendix I), the potential overlap for competition could be identified when incorporated within the competition overlap analyses.

To calculate the overlap in diet, the body mass similarity of two species was calculated with the following formula: $Body\ mass\ similarity = \frac{|M_1 - M_2|}{Max(M_1, M_2)}$. This formula calculates the similarity of the body masses of two species, using a scale from 0 to 1. M_1 and M_2 are the body masses of two species. If M_1 and M_2 are identical, the score will be 1, indicating a high similarity.

The diet similarity was calculated by comparing the overlap in prey species between two cats. The Jaccard Index was used to calculate the diet similarity using the following formula: $Diet\ similarity = \frac{|P_1 \cap P_2|}{|P_1 \cup P_2|}$. P_1 and P_2 are the prey species from the prey base (Appendix I). The numerator is the count of prey species shared by both species and the denominator is the total number of distinct prey species combined.

To measure the competition overlap, the four overlap metrics (Overall RAI, Overlap Estimate, Watson U² and Wr) were combined. To standardise these, a weighted sum approach was used. Different weights were assigned to each of these overlap measures based on an estimated importance. The formula to calculate the competition overlap is: $Competiton\ overlap = w_1 \times Overall\ RAI + w_2 \times Overlap\ Estimate + w_3 \times Watson\ U^2 + w_4 \times Wr$. The w_1, w_2, w_3 and $w_4$are weights for the overlap estimates, which sum up to 1. The following numbers were applied to each weight: w1=0.1 (Overall RAI); w2=0.4 (Overlap Estimate); w3=0.2 (Watson U^2); w4=0.3 (Wr).

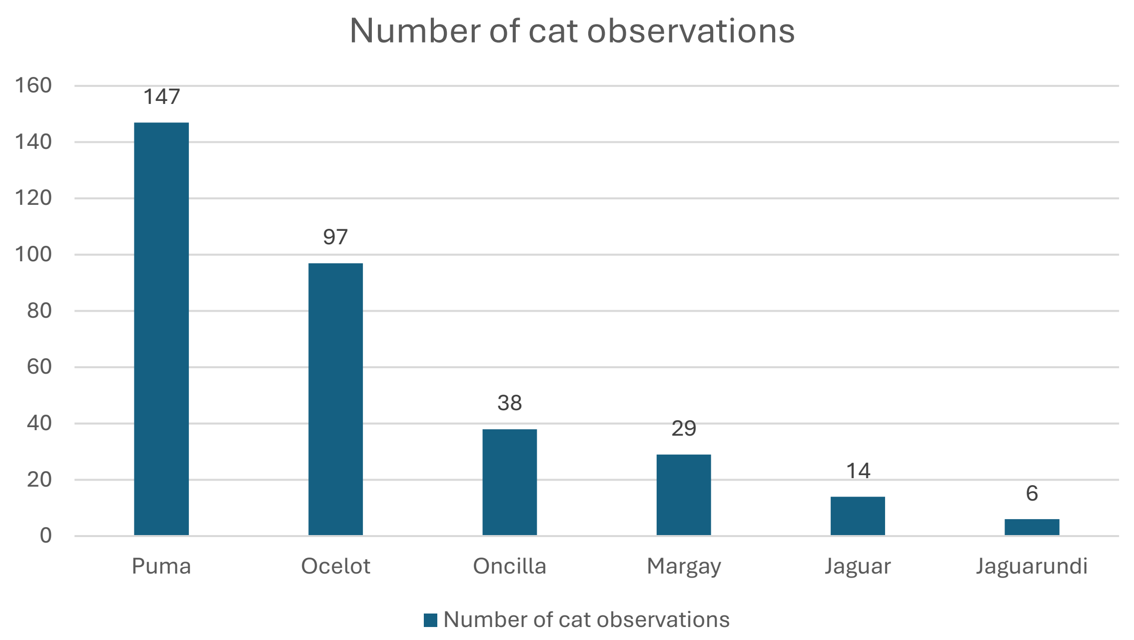
With all these variables combined the final competitor score was calculated using the following formula: $Final\ competition\ score = \alpha \times BMS + \beta \times DS + \gamma \times CO.$ α, β and γ are the weights for respectively body mass similarity (BMS), diet similarity (DS), and competition overlap (CO). These weights were evenly distributed (α = 1/3, $\beta = 1/3$, γ = 1/3).

3. Results

Most common cat species

Overall, the most commonly recorded cat species in the Cloudbridge reserve were the puma (N=147) and ocelot (N=97), less common cat species were oncilla (N=38), margay (N=29) and jaguar (N=14), and the most uncommon cat species was the jaguarundi (N=6) (Figure 3).

Figure 3 Number of cat observations in Cloudbridge reserve



3.1 Temporal overlap

Circadian activity patterns

This research examined the circadian activity for each cat species and prey species from all camera trap sites in the Cloudbridge reserve using the classification system as per Gómez et al. (2005), Azevedo et al. (2018) and Botts et al. (2020). The activity patterns of the cat species varied, with the smaller *Leopardus* species (ocelot, margay, and oncilla) being primarily nocturnal (≥90% of records at night) or mostly nocturnal (70–89% of records at night) within the reserve and showed less activity during the day compared with jaguar, puma and margay. The bigger felid species, jaguar and puma, were observed to be mostly nocturnal (70–89% of records at night). The jaguarundi is the only cat species that stands out as diurnal (<10% of records at night). Most prey species had the tendency to show nocturnal or mostly nocturnal behaviour. Although with a few prey species being cathemeral and (mostly) diurnal. In Table 4, the circadian activity patterns of all cat and prey species are shown.

Table 4 Circadian activity patterns of cat and prey species

Common name	Scientific name	N	%Day	%Night	Classification
Alston's Mouse Opossum	*Marmosa alstoni*	44	2%	98%	Nocturnal
Cacomistle	*Bassariscus sumichrasti*	12	17%	83%	Mostly Nocturnal
Central American Agouti	*Dasyprocta punctata*	17	88%	12%	Mostly Diurnal
Collared Peccary**	*Pecari tajacu*	1887	73%	27%	Mostly Diurnal
Common Opossum	*Didelphis marsupialis*	389	10%	90%	Nocturnal
Dice's Cottontail ***	*Sylvilagus dicei*	688	15%	85%	Mostly Nocturnal
Gray Four-Eyed Opossum	*Philander opossum*	135	1%	99%	Nocturnal
Jaguar	*Panthera onca*	14	29%	71%	Mostly Nocturnal
Jaguarundi	*Herpailurus yagouaroundi*	6	100%	0%	Diurnal
Kinkajou	*Potos flavus*	17	0%	100%	Nocturnal
Long-Tailed Weasel	*Mustela frenata*	26	52%	48%	Cathemeral
Margay	*Leopardus wiedii*	29	7%	93%	Nocturnal
Mexican Hairy Dwarf Porcupine	*Sphiggurus mexicanus*	13	0%	100%	Nocturnal
Mexican Mouse Opossum	*Marmosa mexicana*	28	0%	100%	Nocturnal
Nine-Banded Armadillo	*Dasypus novemcinctus*	21	50%	50%	Cathemeral
Northern Olingo	*Bassaricyon gabbii*	1	0%	100%	Nocturnal
Northern Raccoon	*Procyon lotor*	3	33%	67%	Cathemeral
Northern Tamandua	*Tamandua mexicana*	24	17%	83%	Mostly Nocturnal
Ocelot	*Leopardus pardalis*	97	9%	91%	Nocturnal
Oncilla	*Leopardus tigrinus*	38	11%	89%	Mostly Nocturnal
other (small) Rodent	*Rodentia sp.*	309	3%	97%	Nocturnal
Paca	*Cuniculus paca*	320	4%	96%	Nocturnal
Puma	*Puma concolor*	147	26%	74%	Mostly Nocturnal
Red-Tailed Squirrel	*Sciurus granatensis*	1427	94%	6%	Diurnal
Striped Hog-Nosed Skunk	*Conepatus semistriatus*	15	7%	93%	Nocturnal
Tayra	*Eira barbara*	110	92%	8%	Diurnal
White-Nosed Coati	*Nasua narica*	906	88%	12%	Mostly Diurnal

Activity overlap in time

Table 5 presents the number of individual felids recorded per hour across a 24-hour period. The table includes six felid species: jaguar, puma, ocelot, jaguarundi, margay, and oncilla. Each hour is represented as a time interval (e.g., 00:00-00:59).

Across the entire dataset, the puma was the most frequently recorded species (151 individuals), followed by the ocelot (98 individuals), oncilla (38 individuals), margay (30 individuals), jaguar (14 individuals), and jaguarundi (6 individuals). The data indicates that activity is distributed unevenly throughout the day, with the highest number of observations occurring at night and early morning hours for most species.

The jaguar is observed much less frequently than other species, with only 14 recorded sightings. Its presence is scattered across both night and day, though most occurrences are during nocturnal hours. Peak observations occur at 03:00-03:59 and 20:00-20:59, each with three individuals recorded.

The puma exhibits a peak in activity between 18:00 and 01:00, with the highest single-hour count (17 individuals) recorded at 18:00-18:59. Its activity remains relatively high until the early morning hours before declining after 06:00.

The ocelot also displays predominantly nocturnal activity, with notable peaks at 20:00-20:59 (12 individuals) and 03:00-03:59 (10 individuals), before decreasing in frequency after 06:00.

The jaguarundi, with the lowest number of recorded individuals (6), is observed sporadically throughout the dataset, with no distinct peak in activity. However, the table shows it is that the jaguarundi is only observed during the day.

The margay shows a moderate level of activity at night, with a peak of six individuals at both 03:00-03:59 and 04:00-04:59, and relatively few detections at other times.

The oncilla follows a similar nocturnal pattern to the ocelot, with peak activity at 19:00-19:59 (8 individuals) and 21:00-21:59 (5 individuals), suggesting a preference for night-time movement.

Table 5 Number of individual felids recorded in the dataset per hour across a 24-hour period

Time	**Jaguar**	**Puma**	**Ocelot**	**Jaguarundi**	**Margay**	**Oncilla**
00:00-00:59	1	16	9		1	2
01:00-01:59		5	5		1	4
02:00-02:59		5	6		1	2
03:00-03:59	2	6	10		6	2
04:00-04:59	1	3	9		6	2
05:00-05:59	1	8	10		2	2
06:00-06:59		2	1	1		
07:00-07:59		1		1		1
09:00-09:59	1	2				
10:00-10:59		3		1		
11:00-11:59	1	2				1
12:00-12:59		5	2			
13:00-13:59		2				
14:00-14:59		3				
15:00-15:59		2	1	1	1	
16:00-16:59		4	1	1	1	2
17:00-17:59	2	10	2	1		1
18:00-18:59	1	17	4		2	1
19:00-19:59		8	7		4	8
20:00-20:59	3	15	12		1	2
21:00-21:59	1	13	6		1	5
22:00-22:59		6	8		3	
23:00-23:59		13	5			3
Total	**14**	**151**	**98**	**6**	**30**	**38**

Overall, for the majority of species, the most activity occurred between 18:00 and 06:00. Very few observations are recorded during the late morning and early afternoon. The data in Table 5 was used to generate a timetable illustrating the number of individuals observed per hour, which also includes expected activity times from the literature (Carillo et al., 1999; Henderson, 2002) for comparative analysis.

The timetable (Table 6) provides a direct comparison between expected and observed activity patterns for each species. For the jaguar, the literature indicates continuous activity throughout the 24-hour period, which is also shown in this research. The puma is described in the literature as active throughout the day and night. Observations show high nocturnal activity, but also some activity during the day. The ocelot is classified as nocturnal in the literature, which aligns with the data from this research. The jaguarundi is expected to be diurnal according to the literature. The data from this research confirms this, as all recorded occurrences are within daylight hours. The margay is classified as nocturnal, which is reflected in the data of this research. The activity of the oncilla also peaks during the night, which aligns well with the expected pattern from the literature. The absence of recorded activity during most daytime hours supports its classification as a night-active species.

Table 6 Timetable with comparison between expected and observed activity patterns for each cat species

Jaguar

Time	00:00	01:00	02:00	03:00	04:00	05:00	06:00	07:00	08:00	09:00	10:00	11:00	12:00	13:00	14:00	15:00	16:00	17:00	18:00	19:00	20:00	21:00	22:00	23:00
Active	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
N	1			2	1	1				1		1						2	1		3	1		

Puma

Time	00:00	01:00	02:00	03:00	04:00	05:00	06:00	07:00	08:00	09:00	10:00	11:00	12:00	13:00	14:00	15:00	16:00	17:00	18:00	19:00	20:00	21:00	22:00	23:00
Active	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
N	16	5	5	6	3	8	2	1		2	3	2	5	2	3	2	4	10	17	8	15	13	6	13

Ocelot

Time	00:00	01:00	02:00	03:00	04:00	05:00	06:00	07:00	08:00	09:00	10:00	11:00	12:00	13:00	14:00	15:00	16:00	17:00	18:00	19:00	20:00	21:00	22:00	23:00
Active	■	■	■	■	■														■	■	■	■	■	■
N	9	5	6	10	9	10	1						2			1	1	2	4	7	12	6	8	5

Jaguarundi

Time	00:00	01:00	02:00	03:00	04:00	05:00	06:00	07:00	08:00	09:00	10:00	11:00	12:00	13:00	14:00	15:00	16:00	17:00	18:00	19:00	20:00	21:00	22:00	23:00
Active						■	■	■	■	■	■	■	■	■	■	■	■	■	■					
N							1	1			1					1	1	1						

Margay

Time	00:00	01:00	02:00	03:00	04:00	05:00	06:00	07:00	08:00	09:00	10:00	11:00	12:00	13:00	14:00	15:00	16:00	17:00	18:00	19:00	20:00	21:00	22:00	23:00
Active	■	■	■	■	■															■	■	■	■	■
N	1	1	1	6	6	2										1	1		2	4	1	1	3	

Oncilla

Time	00:00	01:00	02:00	03:00	04:00	05:00	06:00	07:00	08:00	09:00	10:00	11:00	12:00	13:00	14:00	15:00	16:00	17:00	18:00	19:00	20:00	21:00	22:00	23:00
Active	■	■	■	■	■															■	■	■	■	■
N	2	4	2	2	2	2		1				1					2	1	1	8	2	5		3

To assess the significance of the findings, the 24-hour activity patterns of each of the six felid species were compared to those of other species recorded by the camera traps, employing various overlap metrics. These included the Relative Abundance Index (RAI), overlap estimates (Δ) with accompanying 95% confidence intervals, and three statistical tests: Watson's U^2, the Watson-Williams test (Wr), and Fisher's Exact Test. The results for each felid species across all camera sites are presented in Tables 7 to 12.

The data indicates that the larger felids, jaguar and puma, had a coefficient of overlap (Δ = 0.75) (Tables 7 and 8). The smaller felids show varying degrees of overlap with one another. The ocelot has a notable coefficient of overlap with all other felids except the jaguarundi (Table 9). The highest overlap for the ocelot is with the puma (Δ = 0.77) and oncilla (Δ = 0.83), followed by the jaguar (Δ = 0.72) and margay (Δ = 0.77). The jaguarundi shows a low overlap with all other felids (Table 10), with the highest overlap for the jaguar (Δ = 0.36) and puma (Δ = 0.31), which is consistent with the figures showing that these two species are more active during the day. The margay has a moderate overlap with all other felids (Table 11), except with the jaguarundi, with the highest overlap with the ocelot (Δ = 0.77) and oncilla (Δ = 0.72). The oncilla exhibits relatively high overlap with all other cats (Table 12), except for the jaguarundi, with the highest overlap with the puma (Δ = 0.85) and ocelot (Δ = 0.83).

Table 7 Results of overlap statistics jaguar

Species-1	N1	Species-2	N2	Overall RAI	Overlap Estimate	95% Lower	95% Upper	Watson U²	P-U²	Wr	P-Wr	Fisher's Exact
Jaguar	14	Puma	147	17,22	0.7523	0,5618	0,9152	0,0571	0,6464	0,7337	0,0000	0,7186
Jaguar	14	Ocelot	97	11,93	0.7187	0,5243	0,8911	0,1376	0,1286	4,5157	0,0000	0,1584
Jaguar	14	Margay	29	6,55	0.7043	0,5015	0,8759	0,0646	0,5718	1,0710	0,0000	0,2464
Jaguar	14	Jaguarundi	6	2,58	0.3579	0,1191	0,6082	0,2339	0,0155	8,4457	0,0000	0,1410
Jaguar	14	Oncilla	38	13,38	0.7663	0,5776	0,9261	0,0809	0,4136	1,7833	0,0000	0,6721

Table 8 Results of overlap statistics puma

Species-1	N1	Species-2	N2	Overall RAI	Overlap Estimate	95% Lower	95% Upper	Watson U²	P-U²	Wr	P-Wr	Fisher's Exact
Puma	147	Jaguar	14	5,58	0.7523	0,5638	0,9167	0,0571	0,6453	0,7337	0,0000	0,7177
Puma	147	Ocelot	97	11,93	0.7684	0,6688	0,8582	0,3552	0,0017	10,0214	0,0000	0,0118
Puma	147	Margay	29	6,55	0.6692	0,5077	0,8162	0,2322	0,0196	4,1932	0,0000	0,0672
Puma	147	Jaguarundi	6	2,58	0.3098	0,1338	0,4947	0,2952	0,0019	9,8061	0,0000	0,0028
Puma	147	Oncilla	38	13,38	0.8521	0,7397	0,9464	0,0689	0,5149	0,4395	0,0001	0,9431

Table 9 Results of overlap statistics ocelot

Species-1	N1	Species-2	N2	Overall RAI	Overlap Estimate	95% Lower	95% Upper	Watson U²	P-U²	Wr	P-Wr	Fisher's Exact
Ocelot	97	Puma	147	17,22	0.7684	0,6700	0,8575	0,3552	0,0020	10,0214	0,0000	0,0130
Ocelot	97	Jaguar	14	5,58	0.7187	0,5200	0,8929	0,1376	0,1243	4,5157	0,0000	0,1606
Ocelot	97	Margay	29	6,55	0.7703	0,6249	0,8950	0,1314	0,1533	3,9109	0,0000	0,4657
Ocelot	97	Jaguarundi	6	2,58	0.1786	0,0252	0,3586	0,4322	0,0000	12,3154	0,0000	0,0000
Ocelot	97	Oncilla	38	13,38	0.8300	0,6989	0,9348	0,0783	0,4192	1,9553	0,0000	0,4081

Table 10 Results of overlap statistics jaguarundi

Species-1	N1	Species-2	N2	Overall RAI	Overlap Estimate	95% Lower	95% Upper	Watson U^2	P-U^2	Wr	P-Wr	Fisher's Exact
Jaguarundi	6	Puma	147	17,22	0.3098	0,1322	0,4982	0,2952	0,0028	9,8061	0,0000	0,0026
Jaguarundi	6	Ocelot	97	11,93	0.1786	0,0259	0,3623	0,4322	0,0000	12,3154	0,0000	0,0000
Jaguarundi	6	Margay	29	6,55	0.2051	0,0168	0,4246	0,3473	0,0006	11,6525	0,0000	0,0006
Jaguarundi	6	Jaguar	14	5,58	0.3579	0,1210	0,6173	0,2339	0,0126	8,4457	0,0000	0,1411
Jaguarundi	6	Oncilla	38	13,38	0.2296	0,0606	0,4284	0,3513	0,0004	11,6573	0,0000	0,0020

Table 11 Results of overlap statistics margay

Species-1	N1	Species-2	N2	Overall RAI	Overlap Estimate	95% Lower	95% Upper	Watson U^2	P-U^2	Wr	P-Wr	Fisher's Exact
Margay	29	Puma	147	17,22	0.6692	0,5074	0,8148	0,2322	0,0206	4,1932	0,0000	0,0671
Margay	29	Ocelot	97	11,93	0.7703	0,6245	0,8923	0,1314	0,1468	3,9109	0,0000	0,4633
Margay	29	Jaguar	14	5,58	0.7043	0,4971	0,8783	0,0646	0,5682	1,0710	0,0000	0,2474
Margay	29	Jaguarundi	6	2,58	0.2051	0,0186	0,4224	0,3473	0,0006	11,6525	0,0000	0,0005
Margay	29	Oncilla	38	13,38	0.719	0,5457	0,8650	0,1691	0,0689	5,0060	0,0000	0,3456

Table 12 Results of overlap statistics oncilla

Species-1	N1	Species-2	N2	Overall RAI	Overlap Estimate	95% Lower	95% Upper	Watson U^2	P-U^2	Wr	P-Wr	Fisher's Exact
Oncilla	38	Puma	147	17,22	0.8521	0,7412	0,9473	0,0689	0,5186	0,4395	0,0002	0,9430
Oncilla	38	Ocelot	97	11,93	0.83	0,6992	0,9356	0,0783	0,4295	1,9553	0,0000	0,4059
Oncilla	38	Margay	29	6,55	0.719	0,5476	0,8651	0,1691	0,0686	5,0060	0,0000	0,3480
Oncilla	38	Jaguarundi	6	2,58	0.2296	0,0597	0,4272	0,3513	0,0004	11,6573	0,0000	0,0022
Oncilla	38	Jaguar	14	5,58	0.7663	0,5751	0,9230	0,0809	0,4215	1,7833	0,0000	0,6699

In Figures 4 to 9, the activity patterns of each felid species after conducting the overlap analyses are shown. The jaguar peaks in the nightly hours but also shows activity during the day between 6:00 and 12:00 in the morning (Figure 4). Although the figure of the jaguar shows some diurnal activity the main activity was recorded at night. The activity patterns of the puma were mostly nocturnal, with a high peak early in the night (Figure 5). The ocelot shows a clear nocturnal activity pattern where activity was recorded during most parts of the night (Figure 6). The jaguarundi was only recorded during the day, with a high peak during the late afternoon (Figure 7). The figure of the jaguarundi also shows a low activity pattern for the early afternoon. The margay shows nocturnal activity times, with a high peak around late night (Figure 8). The figure for the oncilla shows also clear nocturnal activity patterns, with a high peak for the early night (Figure 9).

The figures show that the smaller *Leopardus* felids (ocelot, margay and oncilla) have overlapping activity patterns. This does also count for the bigger felids (jaguar and puma) whose activities patterns can be seen during the day and night but with a preference for the nocturnal hours and therefore also overlapping the smaller cats, including jaguarundi.

Figure 4 Activity pattern (after conducting the overlap analyses) of jaguar

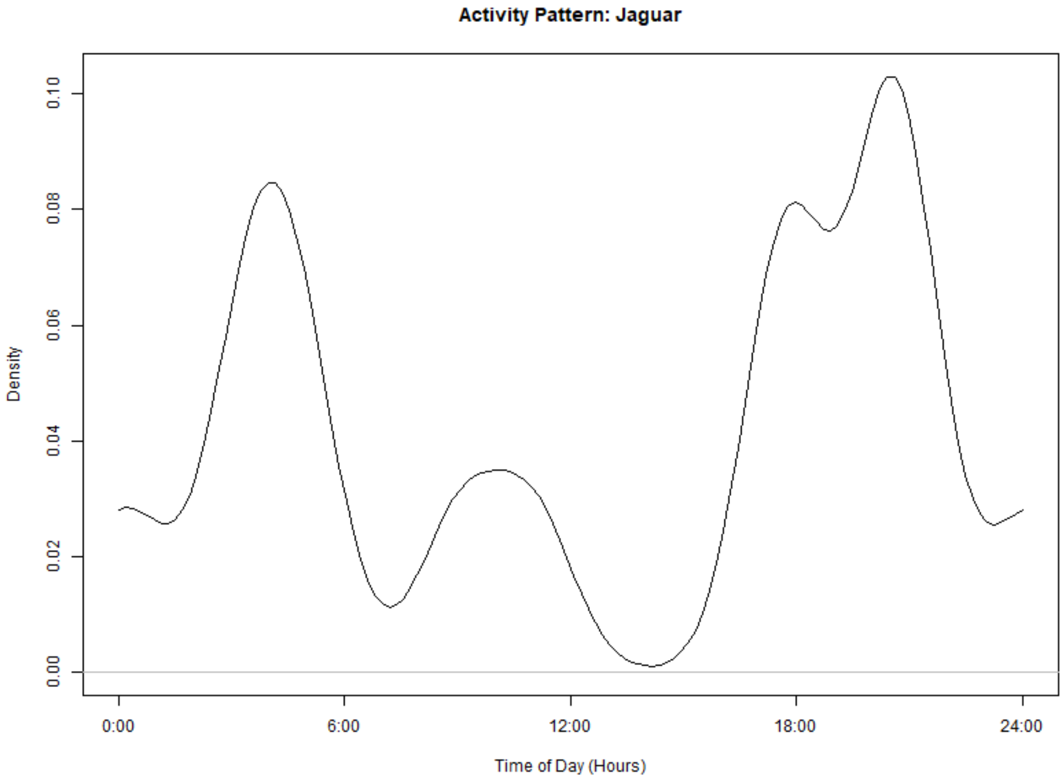


Figure 5 Activity pattern (after conducting the overlap analyses) of puma

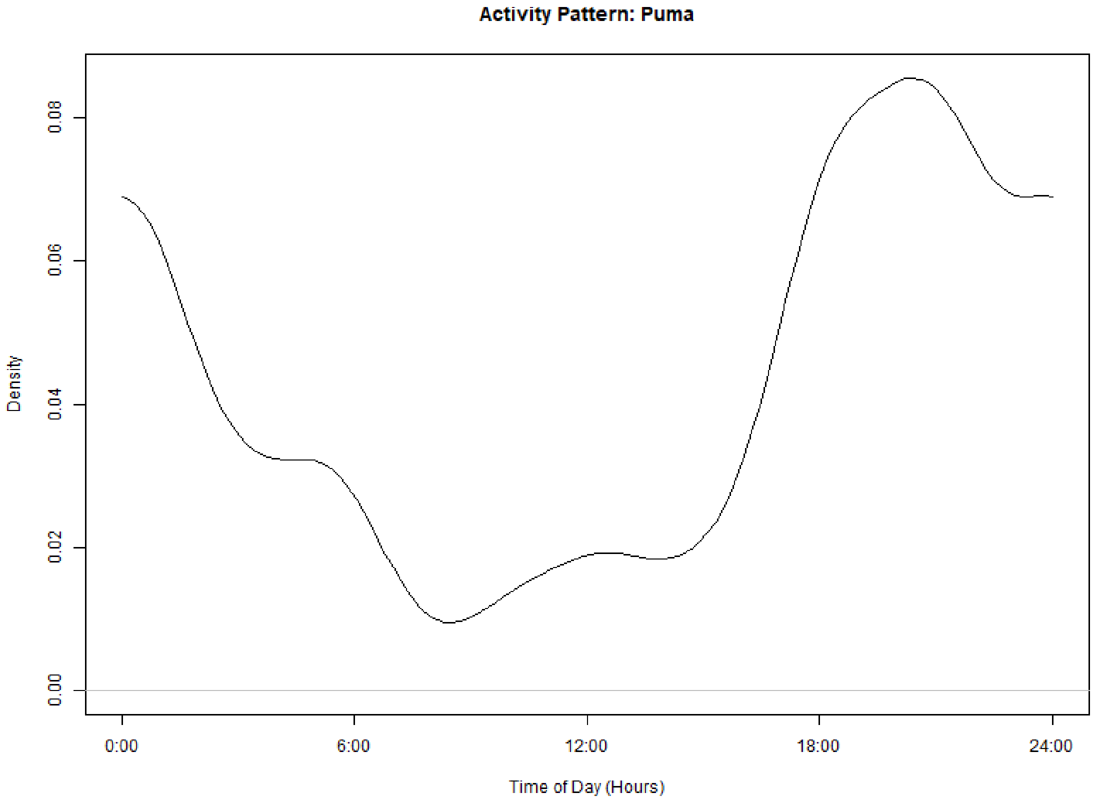


Figure 6 Activity pattern (after conducting the overlap analyses) of ocelot

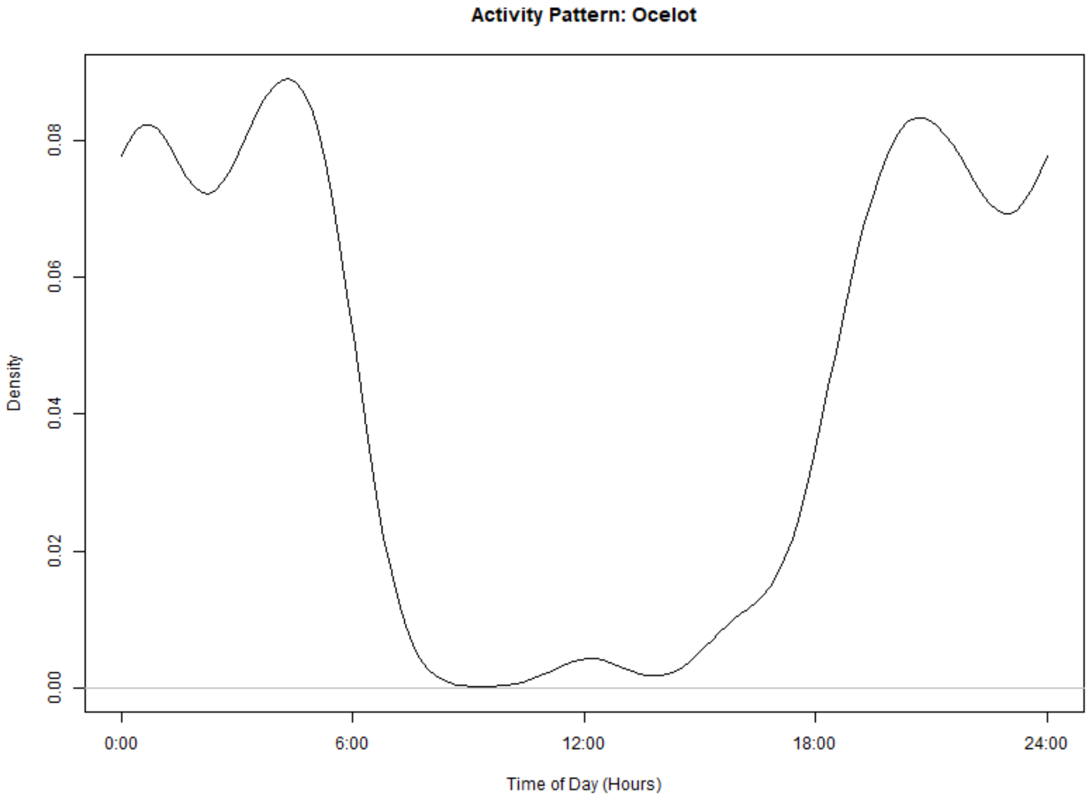


Figure 7 Activity pattern (after conducting the overlap analyses) of jaguarundi

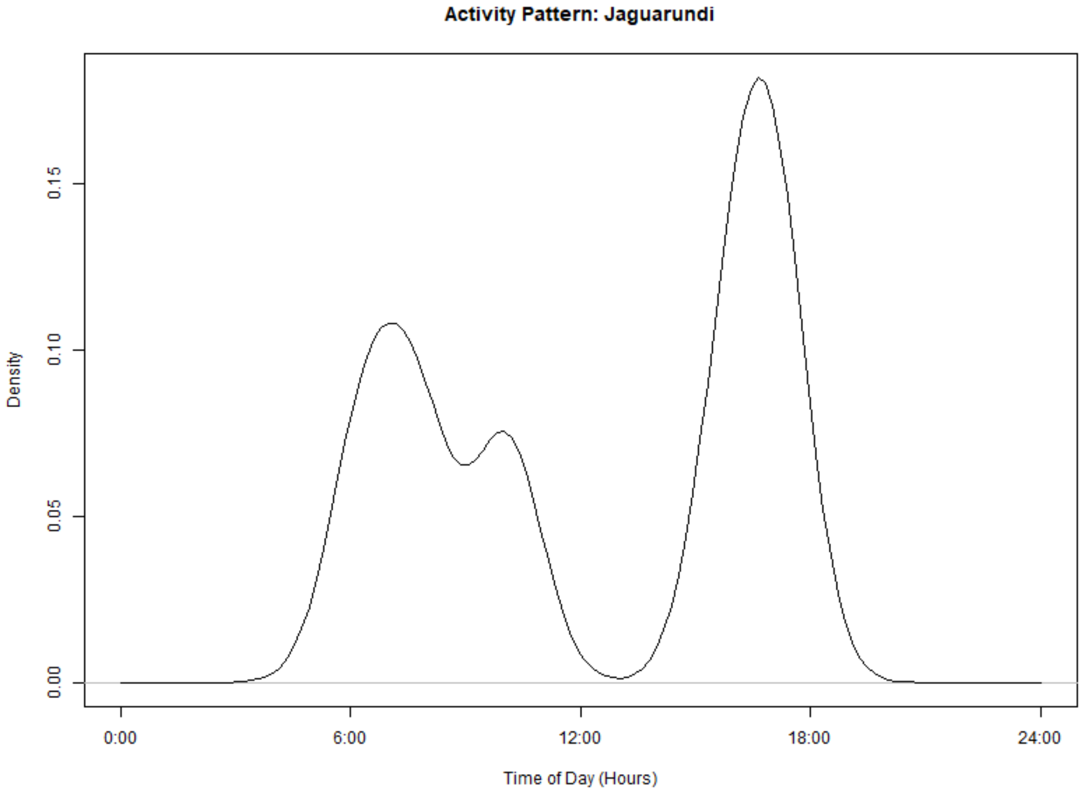


Figure 8 Activity pattern (after conducting the overlap analyses) of margay

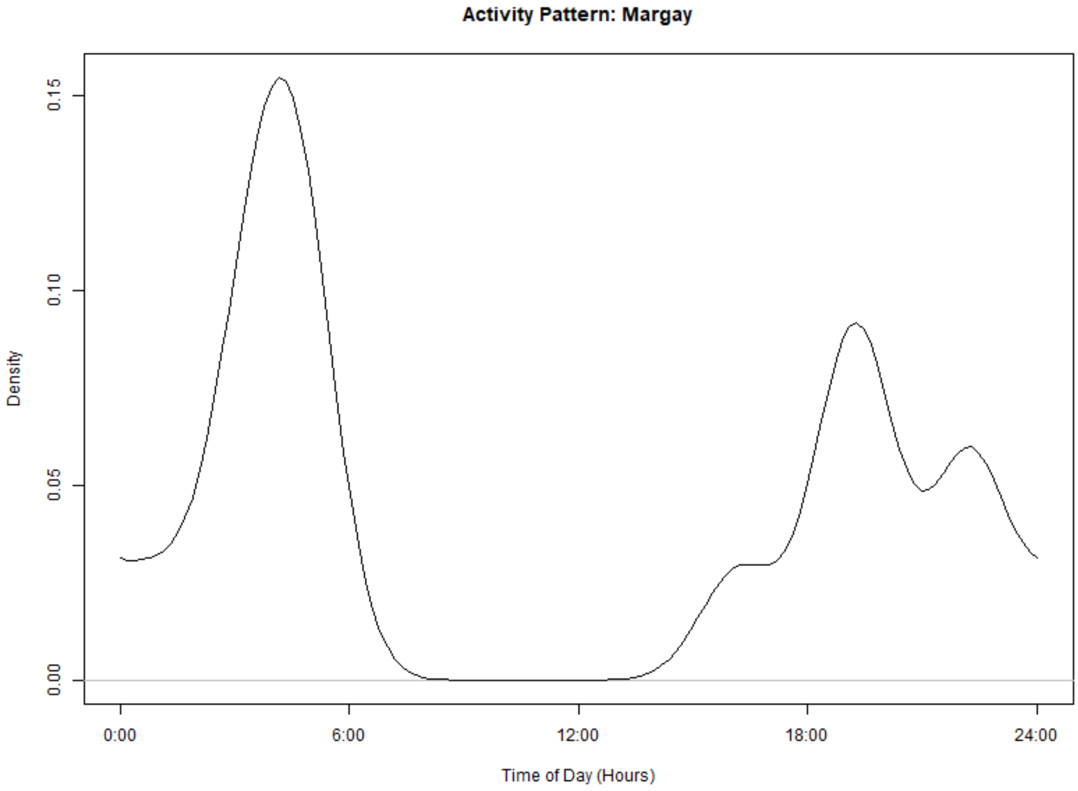
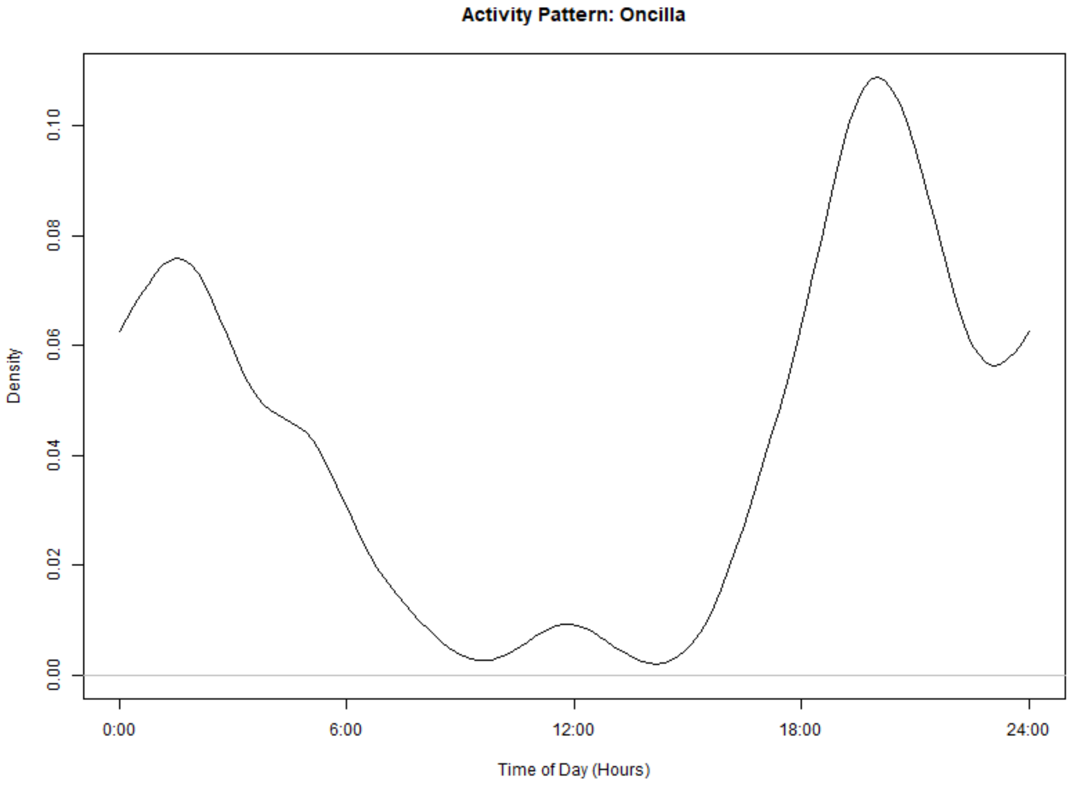


Figure 9 Activity pattern (after conducting the overlap analyses) of oncilla

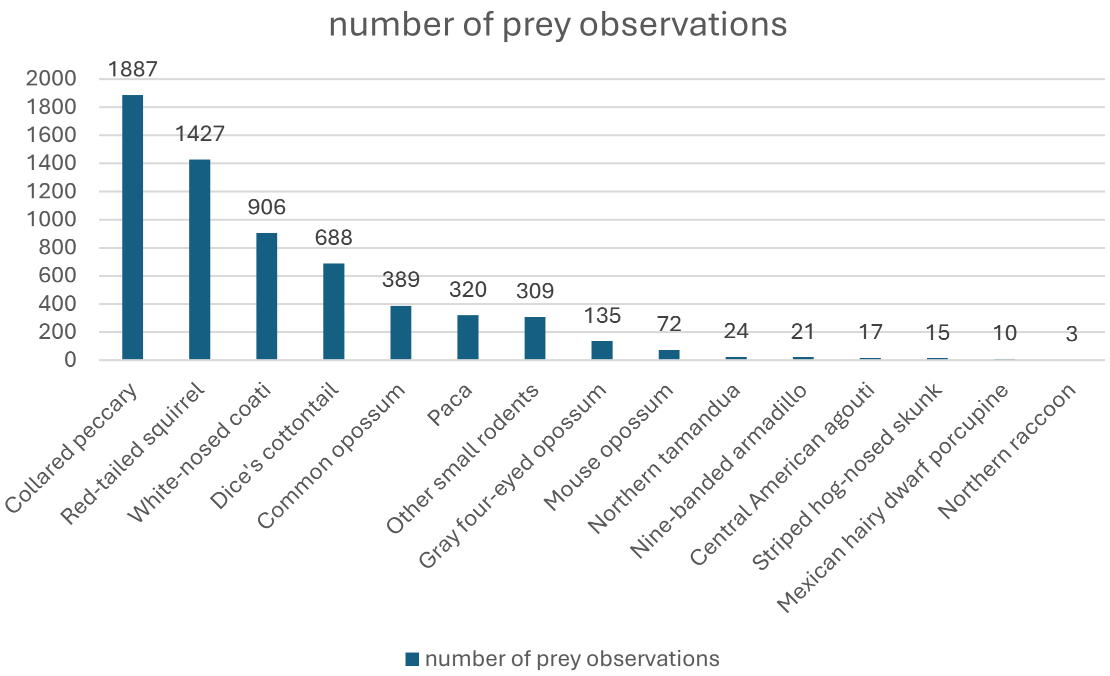


3.2 Dietary overlap

Most common prey species

The most abundant prey species were collared peccary (N=1.887), Red-tailed squirrel (N=1.427), white-nosed coati (N=906), and dice’s cottontail (N=688). Other common prey species were the common opossum (N=389), paca (N=320), other small rodents (N=309), gray four-eyed opossum (N=135), and mouse opossums (N=72). The less common preys were northern tamandua (N=24), nine-banded armadillo (N=21), central American agouti (N=17), striped hog-nosed skunk (N=15), mexican hairy dwarf porcupine (N=10) and the northern raccoon (N=3) (Figure 10).

Figure 10 Number of prey observations in Cloudbridge reserve



Diet jaguar

When looking at the RAI and overlap estimate (Table 13), the main prey for the jaguar are collared peccary (Δ = 0,54; Overall = RAI 205,62), gray four-eyed opossum (Δ = 0,66; Overall RAI = 29,30), paca (Δ = 0,58; Overall RAI = 42,65), common opossum (Δ = 0,70; Overall RAI = 55,11), and dice’s cottontail (Δ = 0,69; Overall RAI = 84,00).

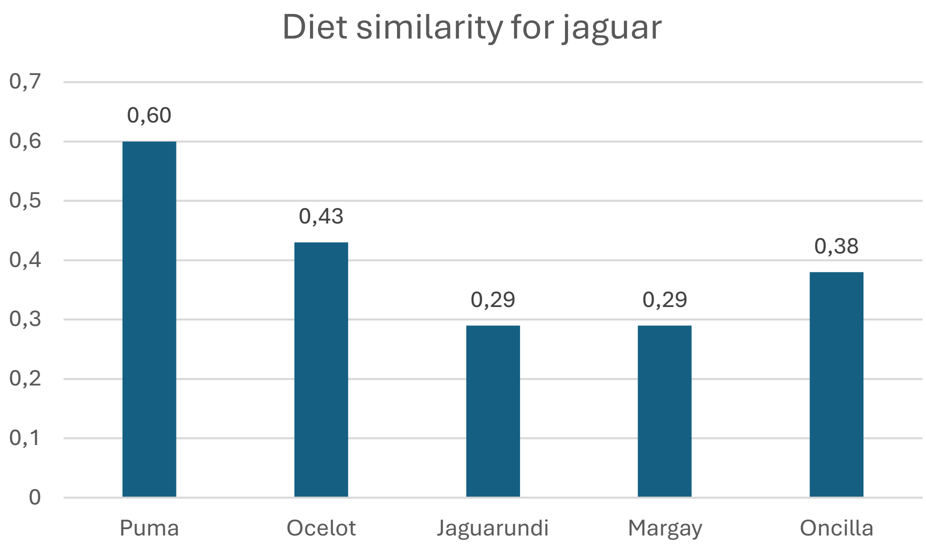
Table 13 Prey species of the Jaguar

Species-I	N1	Species-2	N2	Overall RAI	Overlap Estimate (Δ)	95% Lower	95% Upper
Jaguar	14	Central American Agouti	17	3,70	0.4769	0,2513	0,6955
Jaguar	14	Collared Peccary	1887	205,62	0.5419	0,3525	0,7249
Jaguar	14	Common Opossum	389	55,11	0.7031	0,5191	0,8714
Jaguar	14	Dice's Cottontail	688	84,00	0.6862	0,5105	0,8304

Jaguar	14	Gray Four-eyed Opossum	135	29,30	0.6573	0,4672	0,8377
Jaguar	14	Nine-banded Armadillo	21	4,75	0.6227	0,4032	0,8287
Jaguar	14	Northern Tamandua	24	7,56	0.6176	0,4012	0,8192
Jaguar	14	Paca	320	42,65	0.5773	0,3972	0,7561
Jaguar	14	White-nosed Coati	906	100,40	0.3908	0,2091	0,5868

Looking at the diet similarity for jaguar (Figure 11), the jaguar has the highest overlap with the puma (DS = 0,60), followed by the ocelot (DS = 0,43). These scores correspond with the activity overlap of these three felids.

Figure 11 Diet similarity with other cats for the Jaguar



Diet puma

The main prey for the puma is collared peccary (Δ = 0,54; Overall = RAI 205,62), gray four-eyed opossum (Δ = 0,79; Overall RAI = 29,30), common opossum (Δ = 0,84; Overall RAI = 55,11), and the gray four-eyed opossum (Δ = 0,79; Overall RAI = 29,30) (Table 14). The Overlap Estimate for the northern raccoon could not be calculated since the sample was too small.

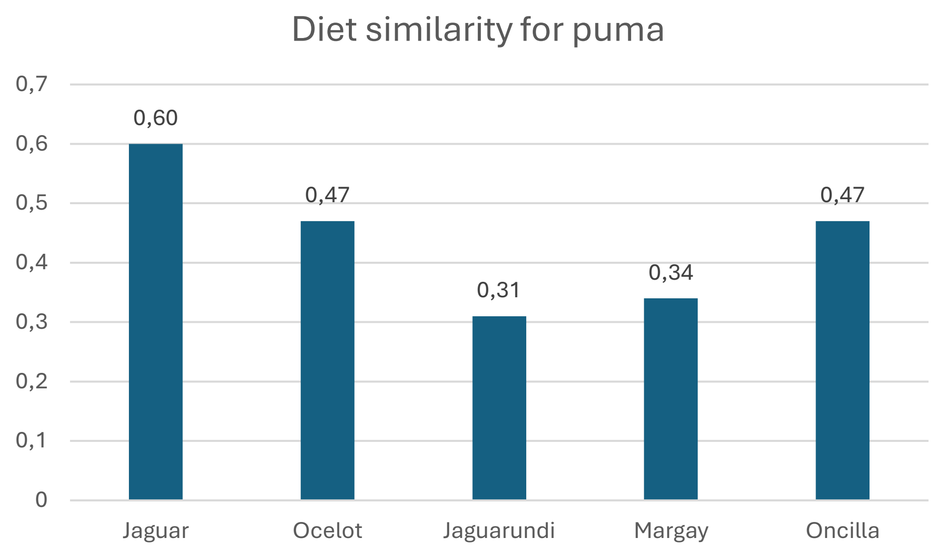
Table 14 Prey species of the Puma

Species-I	N_1	Species-2	N_2	Overall RAI	Overlap Estimate (Δ)	95% Lower	95% Upper
Puma	147	Collared Peccary	1887	205,62	0.5380	0,4726	0,6054
Puma	147	White-nosed Coati	906	100,40	0.3769	0,3095	0,4448
Puma	147	Dice's Cottontail	688	84,00	0.7174	0,6532	0,7756
Puma	147	Common Opossum	389	55,11	0.8437	0,7757	0,9052
Puma	147	Other (small) Rodents*	309	45,02	0.7409	0,6728	0,8046
Puma	147	Paca	320	42,65	0.6952	0,6138	0,7740
Puma	147	Gray Four-eyed Opossum	135	29,30	0.7871	0,7036	0,8644
Puma	147	Tayra	110	15,96	0.3441	0,2602	0,4312

Puma	147	Northern Tamandua	24	7,56	0.7255	0,5774	0,8644
Puma	147	Central American Agouti	17	3,70	0.4697	0,3124	0,6308
Puma	147	Nine-banded Armadillo	21	4,75	0.6026	0,4269	0,7714
Puma	147	Red-tailed Squirrel	1427	154,19	0.2932	0,2299	0,3591
Puma	147	Mouse Opossums*	72	19,05	0.6654	0,5663	0,7550
Puma	147	Mexican hairy dwarf porcupine	10	8,78	0.6590	0,4351	0,8571
Puma	147	Striped Hog-Nosed Skunk	15	4,21	0.6379	0,4498	0,8111
Puma	147	Northern raccoon	3	2,30	NA	NA	NA

According to the diet similarity scores for puma (Figure 12), the jaguar (DS = 0,61) has the most similar diet followed by ocelot (DS = 0,47) and oncilla (DS = 0,47).

Figure 12 Diet similarity with other cats for the Puma



Diet ocelot

The primary prey base for the ocelot consists of dice's cottontail (Δ = 0,72; Overall RAI = 84,00), common opossum (Δ = 0,78; Overall RAI = 55,11), paca (Δ = 0,79; Overall RAI = 42,65), gray four-eyed opossum (Δ = 0,81; Overall RAI = 29,30), and small rodents (Δ = 0,83; Overall RAI = 45,02) (Table 15).

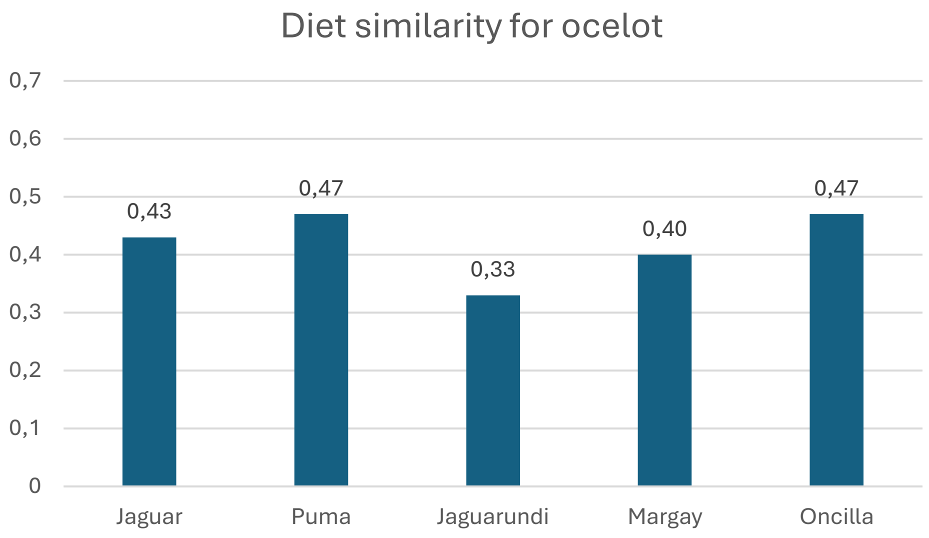
Table 15 Prey species of the Ocelot

Species-I	N1	Species-2	N2	Overall RAI	Overlap Estimate (Δ)	95% Lower	95% Upper
Ocelot	97	Dice's Cottontail	688	84,00	0.7205	0,6537	0,7818
Ocelot	97	Common Opossum	389	55,11	0.7798	0,6855	0,8647
Ocelot	97	Other (small) Rodents*	309	45,02	0.8257	0,7451	0,8952
Ocelot	97	Paca	320	42,65	0.7947	0,7030	0,8789
Ocelot	97	Gray Four-eyed Opossum	135	29,30	0.8079	0,7050	0,9018
Ocelot	97	Central American Agouti	17	3,70	0.2864	0,1326	0,4537
Ocelot	97	Red-tailed Squirrel	1427	154,19	0.1905	0,1314	0,2519
Ocelot	97	Mouse Opossums*	72	19,05	0.7694	0,6588	0,8613

Ocelot	97	Northern Tamandua	24	7,56	0.8339	0,6899	0,9400
Ocelot	97	Nine-banded Armadillo	21	4,75	0.6157	0,4367	0,7836
Ocelot	97	White-nosed Coati	906	100,40	0.2426	0,1838	0,3041
Ocelot	97	Collared Peccary	1887	205,62	0.3790	0,3203	0,4407
Ocelot	97	Tayra	110	15,96	0.1951	0,1189	0,2752

The diet similarity scores for ocelot overlap the most with puma (DS = 0,47) and oncilla (DS = 0,47) (Figure 13).

Figure 13 Diet similarity with other cats for the Ocelot



Diet jaguarundi

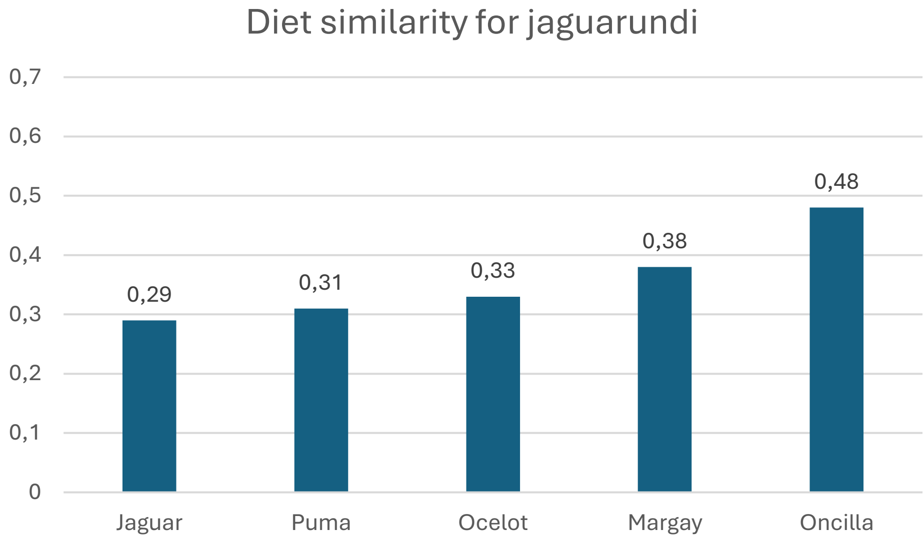
The main prey for the jaguarundi is red-tailed squirrel (Δ = 0,62; Overall RAI = 154,19) and central American agouti (Δ = 0,62; Overall RAI = 3,70) (Table 16). Both prey species are mostly active during the day (94% day; 6% night for red-tailed squirrel and 88% day; 12% night for central American agouti.

Table 16 Prey species of the Jaguarundi

Species-I	N1	Species-2	N2	Overall RAI	Overlap Estimate (Δ)	95% Lower	95% Upper
Jaguarundi	6	Dice's Cottontail	688	84,00	0.2563	0,0669	0,4348
Jaguarundi	6	Common Opossum	389	55,11	0.1938	0,0560	0,3497
Jaguarundi	6	Other (small) Rodents*	309	45,02	0.0990	-0,0167	0,2561
Jaguarundi	6	Paca	320	42,65	0.1041	0,0052	0,2394
Jaguarundi	6	Gray Four-eyed Opossum	135	29,30	0.1381	0,0136	0,2882
Jaguarundi	6	Central American Agouti	17	3,70	0.6196	0,3335	0,8808
Jaguarundi	6	Red-tailed Squirrel	1427	154,19	0.6177	0,2990	0,8658
Jaguarundi	6	Mouse Opossums*	72	19,05	0.1021	-0,0338	0,2780

The diet similarity scores for jaguarundi have a relatively low overlap with the other felids. The most similar diet can be attributed to the oncilla (DS = 48) (Figure 14).

Figure 14 Diet similarity with other cats for the Jaguarundi



Diet margay

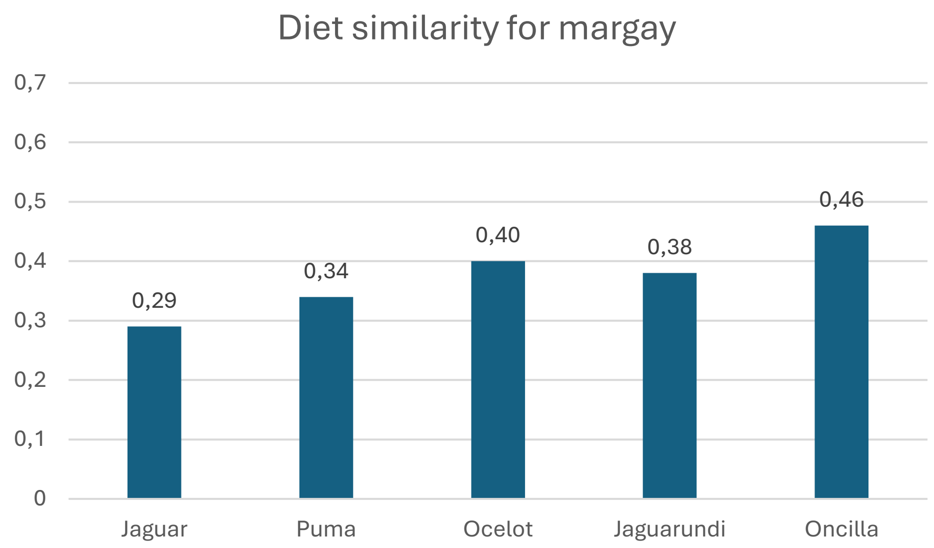
The margay's primary preys consist of dice's cottontail (Δ = 0,69; Overall RAI = 84,00), common opossum (Δ = 0,65; Overall RAI = 55,11), gray four-eyed opossum (Δ = 0,65; Overall RAI = 29,30), mouse opossums (Δ = 0,80; Overall RAI = 19,05), and other small rodents (Δ = 0,67; Overall RAI = 15,00) (Table 17).

Table 17 Prey species of the Margay

Species-I	N_1	Species-2	N_2	Overall RAI	Overlap Estimate (Δ)	95% Lower	95% Upper
Margay	29	Dice's Cottontail	688	84,00	0.6933	0,5552	0,8064
Margay	29	Common Opossum	389	55,11	0.6544	0,4977	0,8041
Margay	29	Other (small) Rodents*	Prey	15	0.6747	0,5250	0,8093
Margay	29	Gray Four-eyed Opossum	135	29,30	0.6515	0,4953	0,8002
Margay	29	Central American Agouti	17	3,70	0.3146	0,1378	0,5032
Margay	29	Red-tailed Squirrel	1427	154,19	0.2112	0,1151	0,3105
Margay	29	Mouse Opossums*	72	19,05	0.8015	0,6717	0,9086

The diet similarity for the margay is attributed to the oncilla (DS = 0,46) (Figure 15). This is also a relatively low score within this felid guild.

Figure 15 Diet similarity with other cats for the Margay



Diet oncilla

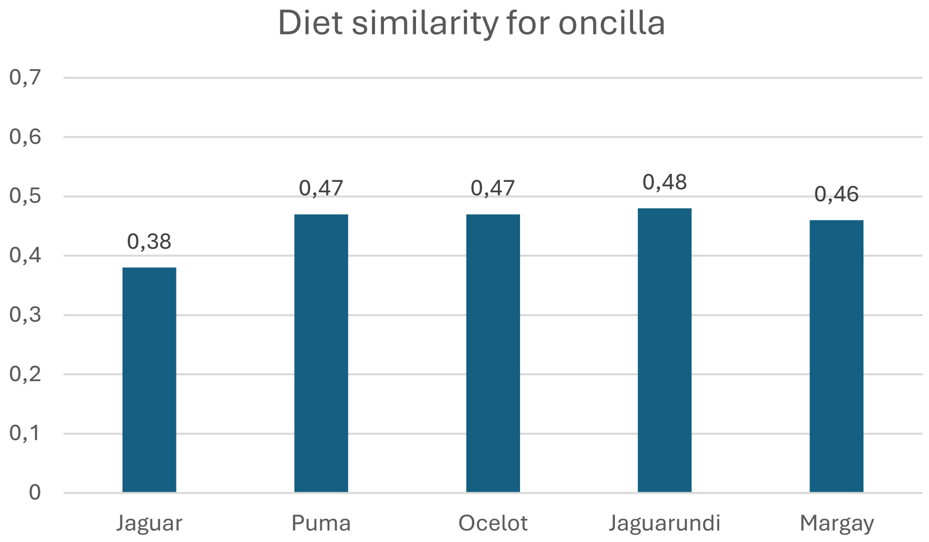
The oncilla has a relatively large prey base consisting of dice's cottontail (Δ = 0,75; Overall RAI = 84,00), common opossum (Δ = 0,88; Overall RAI = 55,11), paca (Δ = 0,74; Overall RAI = 42,65), gray four-eyed opossum (Δ = 0,85; Overall RAI = 29,30), mouse opossums (Δ = 0,74; Overall RAI = 19,05), and other small rodents (Δ = 0,84 Overall RAI = 45,02) (Table 18).

Table 18 Prey species of the Oncilla

Species-I	N1	Species-2	N2	Overall RAI	Overlap Estimate (Δ)	95% Lower	95% Upper
Oncilla	38	White-nosed Coati	901	100,40	0.2870	0,1911	0,3911
Oncilla	38	Dice's Cottontail	688	84,00	0.7458	0,6516	0,8234
Oncilla	38	Common Opossum	389	55,11	0.8834	0,7756	0,9685
Oncilla	38	Other (small) Rodents*	309	45,02	0.8358	0,7333	0,9175
Oncilla	38	Paca	320	42,65	0.7439	0,6137	0,8617
Oncilla	38	Gray Four-eyed Opossum	135	29,30	0.8469	0,7263	0,9481
Oncilla	38	Central American Agouti	17	3,70	0.3582	0,1840	0,5465
Oncilla	38	Red-tailed Squirrel	1427	154,19	0.2113	0,1184	0,3166
Oncilla	38	Mouse Opossums*	72	19,05	0.7369	0,6166	0,8431

The diet similarity for the oncilla is also relatively low (DS = <0,5). The felid with the most overlap in diet is the jaguarundi (DS = 0,48) closely followed by puma (DS = 0,47), ocelot (DS = 0,47) and margay (DS = 0,46) (Figure 16).

Figure 16 Diet similarity with other cats for the Oncilla



3.3 Spatial overlap

The spatial distribution of felid activity in the reserve shows varying patterns across species (Table 19 and Table 20).

The jaguar (Overall RAI = 5.58) exhibited relatively low activity compared to other felid species. The jaguar was recorded on 6 of the 10 trails across 9 camera sites. The jaguar showed a strong preference for the Skutch trail (N = 6), where it was most active in the higher elevation areas. Additional records were made on the Don Victor trail (N = 1), Gavilan trail (N = 2), Los Quetzales trail (N = 3), Montaña trail (N = 1), and Rio trail (N = 1). These observations suggest that while the jaguar is relatively rare in the reserve, it may have specific areas that it favours for its activity.

The puma exhibited the highest overall activity across the reserve (Overall RAI = 17.22) and was recorded on 9 of the 10 trails across 27 camera sites. The highest number of observations occurred on the Gavilan trail (N = 54). The puma shows high abundance on most trails compared to other felid species, and it was the most frequently observed cat on Gavilan trail (N = 54), Los Quetzales (N = 15), and Montaña (N = 24). The puma often shares territory with other felids, particularly the ocelot. On several trails, the puma and ocelot have similar numbers of observations, showing that these two species share territory. Notably, both species show similar numbers on the El Jilguero trail (puma N = 29, ocelot N = 40), Rio trail (puma N = 12, ocelot N = 13), and Sentinel trail (puma N = 6, ocelot N = 9). The puma was also observed on the Don Victor trail (N = 7), Jilguero Loop (N = 1), and Skutch trail (N = 5).

The ocelot (Overall RAI = 11.93) was recorded on 9 of the 10 trails across 24 camera sites, nearly matching the puma's distribution. The highest abundance of ocelot observations occurred on the El Jilguero trail (N = 40), which is also a key area for the puma. Other important trails for the ocelot include Jilguero Loop (N = 2), Rio trail (N = 13), and Sentinel trail (N = 9). The ocelot was also observed on the Don Victor trail (N = 7), Gavilan trail (N = 19), Los Quetzales trail (N = 2), Montaña trail (N = 9), and Skutch trail (N = 2).

The jaguarundi (Overall RAI = 2.58) had the lowest overall abundance, making it the least observed felid in the reserve. It was recorded on 4 of the 10 trails and was the only felid species observed on the Heliconia trail. The Don Victor trail (N = 3) had the highest number of jaguarundi observations, while additional records were made on the Gavilan trail (N = 1), Heliconia trail (N = 1), and Jilguero Loop (N = 1).

The margay (Overall RAI = 6.55) was recorded on 5 of the 10 trails across 10 camera sites, indicating moderate abundance. The highest number of margay observations occurred on the El Jilguero trail (N = 10). Other trails where the margay was observed include the Don Victor trail (N = 9), Gavilan trail (N = 4), and Montaña trail (N = 2).

The oncilla (Overall RAI = 13.38) had relatively high abundance, second to the puma. Despite this, it was recorded on only 5 of the 10 trails across 9 camera sites. The highest number of oncilla observations was on the Don Victor trail (N = 22), making it the most observed felid on that trail. Additional records were made on the Gavilan trail (N = 1), Jilguero Loop (N = 1), Los Quetzales (N = 8), and Montaña trail (N = 6).

Table 19 Distribution of cat species on the different trails of Cloudbridge reserve

Trail	**Jaguar**		**Puma**		**Ocelot**		**Jaguarundi**		**Margay**		**Oncilla**	
	N	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**
Don Victor	1	7%	7	5%	5	5%	3	50%	9	30%	22	58%
El Jilguero	0	0%	29	19%	40	40%	0	0%	10	33%	0	0%
Gavilan	2	14%	55	36%	19	19%	1	17%	4	13%	1	3%
Heliconia	0	0%	0	0%	0	0%	1	17%	0	0%	0	0%
Jilguero Loop	0	0%	1	1%	2	2%	1	17%	0	0%	1	3%
Los Quetzales	3	21%	15	10%	2	2%	0	0%	0	0%	8	21%
Montaña	1	7%	24	16%	9	9%	0	0%	5	17%	6	16%
Rio	1	7%	12	8%	13	13%	0	0%	2	7%	0	0%
Sentinel	0	0%	6	4%	9	9%	0	0%	0	0%	0	0%
Skutch	6	43%	5	3%	2	2%	0	0%	0	0%	0	0%
Total	**14**	**100%**	**154**	**100%**	**101**	**100%**	**6**	**100%**	**30**	**100%**	**38**	**100%**

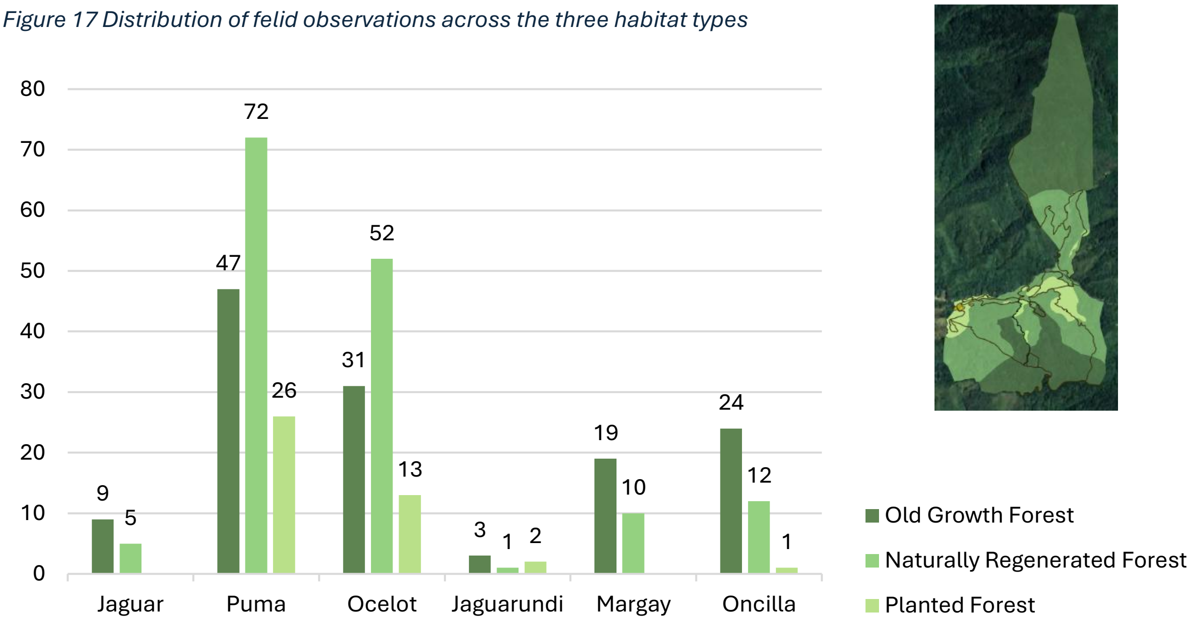
In Table 20 the occurrence of felids at the different trails is shown. Don Victor is more used by the oncilla (47%) than by other cats, El Jilguero is mainly used by the ocelot (51%) and Gavilan (67%), Los Quetzales (54%) and Montaña (53%) are mainly used by the puma. Rio is often used by the puma (43%) and ocelot (46%). Also, Sentinel seemed to be shared between these two species (puma: 40%; ocelot: 60%). Skutch is mainly used by the jaguar (46%) and puma (38%). Heliconia is only used by the jaguarundi, but this is based on one observation. Jilguero Loop has observations of the puma, ocelot, jaguarundi and oncilla, but only a few (N=5).

Table 20 Distribution of cat species on the trails in Cloudbridge reserve

Trail	**Jaguar**	**Puma**	**Ocelot**	**Jaguarundi**	**Margay**	**Oncilla**	**Totaal**	
	%	**%**	**%**	**%**	**%**	**%**	**N**	**%**
Don Victor	2%	15%	11%	6%	19%	47%	47	100%
El Jilguero	0%	37%	51%	0%	13%	0%	79	100%
Gavilan	2%	67%	23%	1%	5%	1%	82	100%
Heliconia	0%	0%	0%	100%	0%	0%	1	100%
Jilguero Loop	0%	20%	40%	20%	0%	20%	5	100%
Los Quetzales	11%	54%	7%	0%	0%	29%	28	100%
Montaña	2%	53%	20%	0%	11%	13%	45	100%
Rio	4%	43%	46%	0%	7%	0%	28	100%
Sentinel	0%	40%	60%	0%	0%	0%	15	100%
Skutch	46%	38%	15%	0%	0%	0%	13	100%

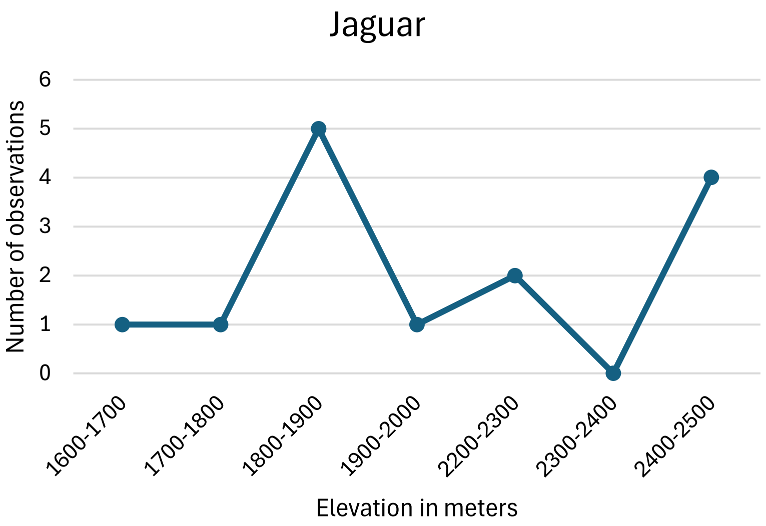
Activity patterns were also analysed based on the habitat types and elevation. Figure 17 presents the distribution of felid observations across three habitat types: Old Growth Forest, Naturally Regenerated Forest, and Planted Forest. The data indicates that Naturally Regenerated Forest has the highest number of detections, followed by Old Growth Forest, while Planted Forest has the lowest overall observations. Jaguars and Margays are more frequently recorded in Old Growth Forest, whereas Ocelots and Pumas appear to utilise Naturally Regenerated Forest to a greater extent. Jaguarundis and Oncillas are observed in all habitat types, albeit in lower numbers.

Figure 17 Distribution of felid observations across the three habitat types



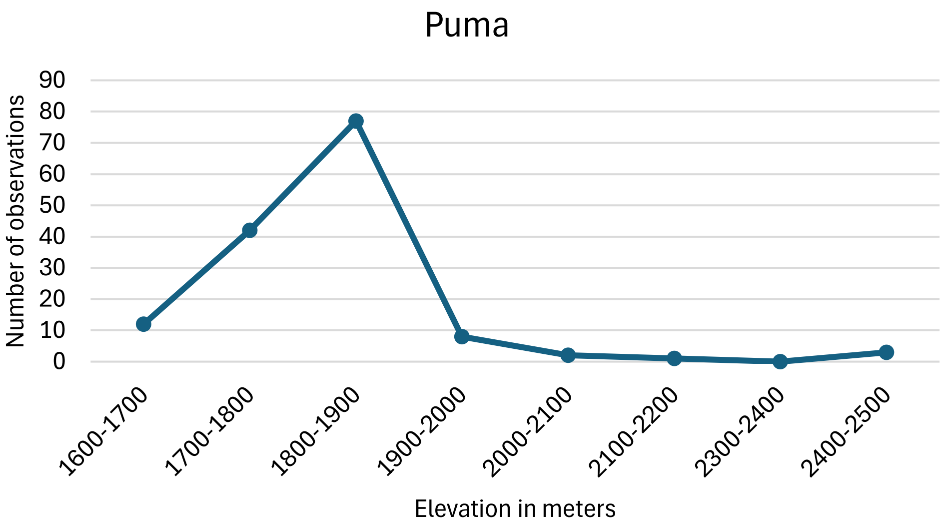
The jaguar was recorded across a broad elevational range, with most detections between 1800 and 1900 metres, but also occurring at both lower (1600–1700 m) and higher elevations (up to 2500 m). The jaguar was among the few species detected above 2400 metres, with four records in this range (Figure 18).

Figure 18 Elevation range of the Jaguar



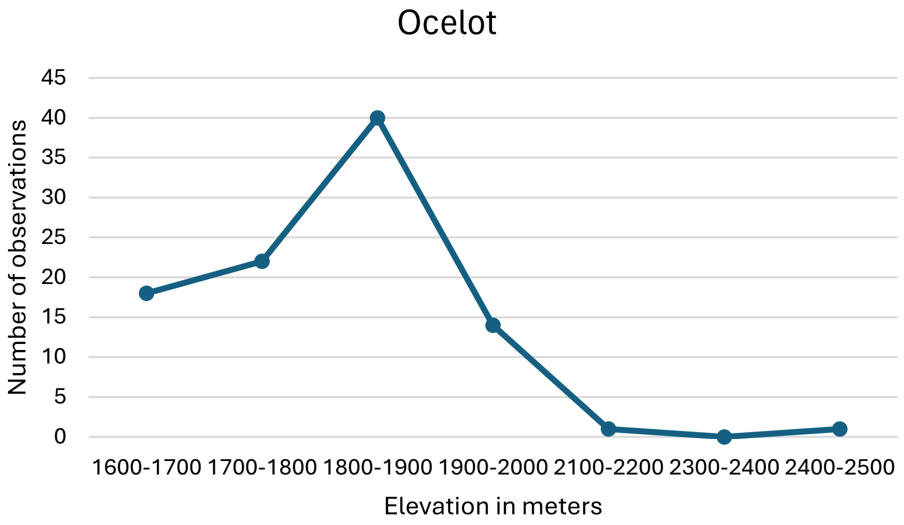
The puma exhibited an average elevational range, with records spanning 1600 to 2500 metres. The highest number of detections occurred at 1800–1900 metres, with additional records at 2400–2500 metres (Figure 19).

Figure 19 Elevation range of the puma



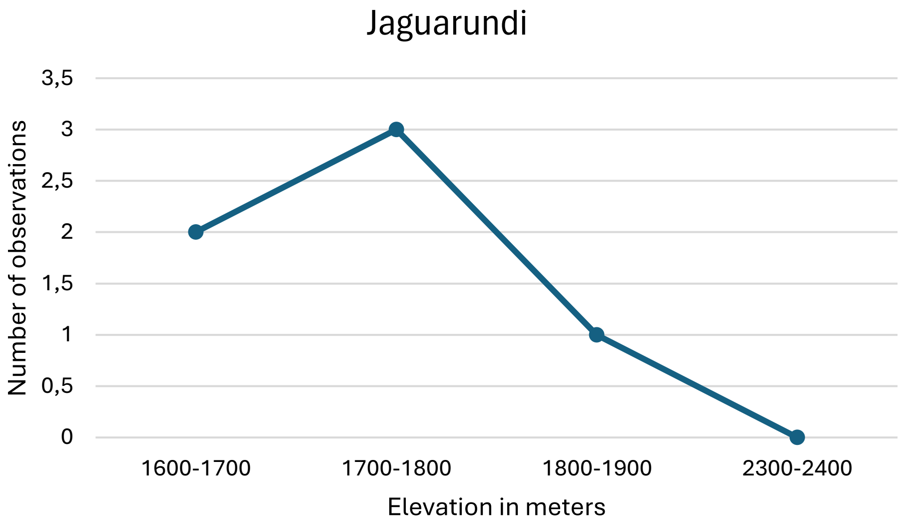
The ocelot was observed across a wide range of elevations, from 1600 to 2500 metres, with the highest number of records between 1800 and 1900 metres. A single detection was recorded at 2400–2500 metres (Figure 20).

Figure 20 Elevation range of the ocelot



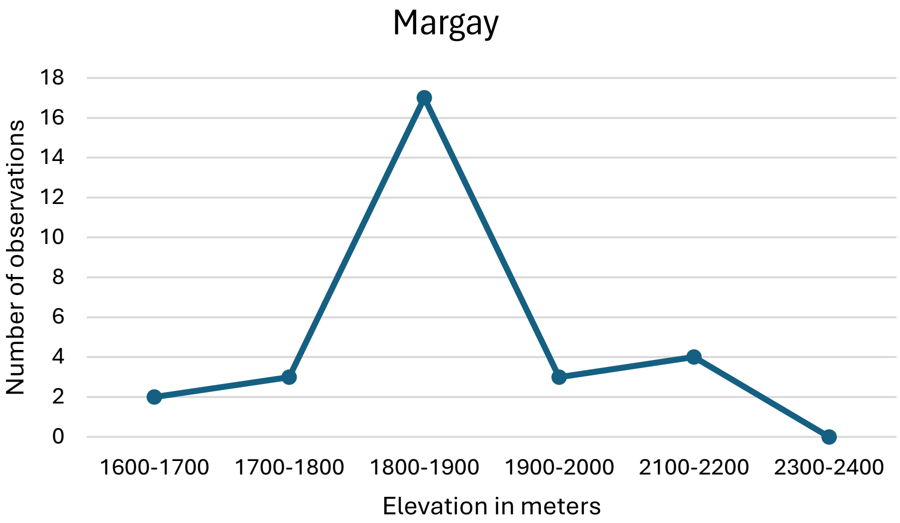
The jaguarundi was detected in small numbers, primarily between 1600 and 1800 metres, with a single record at 1800–1900 metres. No detections were recorded above 1900 metres (Figure 21).

Figure 21 Elevation range of the jaguarundi



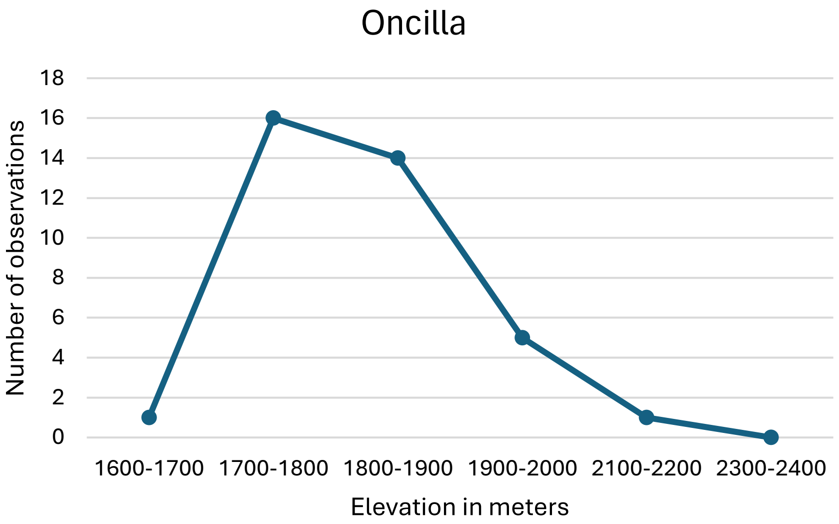
The margay was most frequently recorded at 1800–1900 metres, with additional detections between 1600 and 1800 metres and sporadic occurrences up to 2200 metres. No records were found above this elevation (Figure 22).

Figure 22 Elevation range of the margay



The oncilla showed a broad elevational distribution, with notable observations between 1700 and 1900 metres, but records extending up to 2100 metres. A single detection was recorded at 2400–2500 metres (Figure 23).

Figure 23 Elevation range of the oncilla



3.4 Primary and secondary competitors

The primary and secondary competitors were calculated for each felid species using the variables Body Mass Similarity, Diet Similarity and Competition Overlap (see Table 21 and Appendix II). This only counted if they could also be in the same place at the same time. For the jaguar, the primary competitor was the puma, followed by the ocelot. For the puma, the primary competitor was the jaguar, followed by the ocelot. These three species sit higher on the weight spectrum than the smaller felids and can take on larger prey. The main competitor for the ocelot was the margay, followed by the oncilla, with all three species falling into a similar weight range and being nocturnal. The primary competitor for the jaguarundi was the oncilla, followed by the margay, with the jaguarundi being diurnal and having the most diet overlap with the other small cats. The margay's primary competitor was the ocelot, followed by the oncilla, as all three species share similar body masses and nocturnal activity patterns. Finally, the oncilla’s primary competitor was the margay, followed by the ocelot.

Table 21 Primary and secondary competitors based on final Competition Score (CS)

Species 1	Species 2	Final CS	Primary interactions
Jaguar	Puma	0,618	Primary competitor
Jaguar	Ocelot	0,323	Secondary competitor
Jaguar	Jaguarundi	0,216	
Jaguar	Margay	0,204	
Jaguar	Oncilla	0,291	
Puma	Jaguar	0,618	Primary competitor
Puma	Ocelot	0,435	Secondary competitor
Puma	Jaguarundi	0,314	
Puma	Margay	0,323	
Puma	Oncilla	0,406	
Ocelot	Jaguar	0,323	
Ocelot	Puma	0,435	
Ocelot	Jaguarundi	0,533	
Ocelot	Margay	0,577	Secondary competitor
Ocelot	Oncilla	0,621	Primary competitor
Jaguarundi	Jaguar	0,216	
Jaguarundi	Puma	0,314	
Jaguarundi	Ocelot	0,533	
Jaguarundi	Margay	0,578	Secondary competitor
Jaguarundi	Oncilla	0,642	Primary competitor
Margay	Jaguar	0,204	
Margay	Puma	0,323	
Margay	Ocelot	0,577	Secondary competitor
Margay	Jaguarundi	0,578	
Margay	Oncilla	0,636	Primary competitor
Oncilla	Jaguar	0,291	
Oncilla	Puma	0,406	
Oncilla	Ocelot	0,624	Secondary competitor
Oncilla	Jaguarundi	0,642	
Oncilla	Margay	0,636	Primary competitor

4. Discussion

This study employed camera trapping and overlap statistics to assess the spatial and temporal distribution of six felid species in the Cloudbridge Nature Reserve. While this method provided valuable insights into niche partitioning among felids, it is essential to critically evaluate their strengths and limitations to ensure robust conclusions.

Camera trapping as a research tool

Camera trapping proved to be an effective non-invasive method for monitoring elusive felids in a cloud forest environment. The dataset spanning multiple years allowed for an in-depth analysis of felid activity, providing a comprehensive overview of how these species coexist. However, camera placement and detection probabilities can introduce biases. As highlighted by Sollmann et al. (2013), detection rates are influenced by factors such as home range size, habitat use, and camera placement along trails versus more secluded areas. In this study, most cameras were positioned along trails, which may have increased detection rates for species that preferentially use trails, such as pumas and ocelots, while underestimating the activity of species that avoid these pathways.

Another significant issue encountered during data collection was the frequent malfunctioning of camera traps. Throughout the study period, multiple camera units broke down and had to be replaced, leading to potential gaps in data collection. These equipment failures may have resulted in missing observations of certain species, affecting the reliability of temporal and spatial activity estimates. Such interruptions in data collection further highlight the importance of redundancy in camera deployment and routine equipment checks to ensure continuous and consistent data gathering.

Additionally, some felid species are particularly elusive and were rarely captured on camera. Smaller cats such as margays and oncillas tend to be more arboreal, reducing their likelihood of being detected by terrestrial camera traps. The same applies to certain prey species that primarily inhabit the canopy. As a result, the study was inherently limited to terrestrial mammals, even though some species within the felid guild and prey base are partially arboreal. This limitation may have led to an underestimation of the dietary range of the felid species, particularly smaller felids that are known to hunt birds and reptiles. Since these prey types are difficult to capture on camera traps, their importance in the felid diet may be underrepresented in this research.

Challenges in data integration

A significant challenge in this research was compiling data from historical databases. Cloudbridge did not have a standardised method for data collection using camera traps, leading to inconsistencies across different datasets. Variations in camera settings, deployment strategies, and data recording formats made it difficult to integrate multiple sources into a single comprehensive database. While this issue was ultimately resolved, some missing data had to be estimated or replaced with average values, reducing the overall reliability of the dataset. These limitations should be considered when interpreting the results and underscore the importance of standardised data collection protocols for future studies.

Data analysis: strengths and limitations

The use of RAI (number of independent captures per unit effort) is widely employed in wildlife research due to its simplicity and applicability across various species. However, as Sollmann et al. (2013) caution, RAI does not account for imperfect detection or variations in species movement patterns. Factors such as species-specific detectability, seasonal variations, and habitat type can bias RAI estimates, making direct comparisons between species or sites potentially misleading. For example, species with larger home ranges, such as jaguars and pumas, may have been detected more frequently simply due to their higher likelihood of encountering camera traps, rather than a true reflection of their relative abundance.

Moreover, seasonality and other temporal factors may have influenced the activity patterns observed in this study. Changes in weather conditions, prey availability, or breeding cycles could impact the frequency and timing of felid activity. Future research should consider analysing activity patterns across different seasons or times of day to capture potential variations that were not fully accounted for in this study.

One way to mitigate these limitations would be to incorporate occupancy modelling or spatially explicit capture-recapture (SECR) techniques, which provide more reliable abundance estimates by accounting for detection probability. While these methods were beyond the scope of this study, future research could benefit from integrating such approaches to validate RAI-based findings.

As expected, the three statistical tests of significance did not always align in their results (see Appendix III). The tests differed in their sensitivity to sample size and distributional variation. Nevertheless, in the majority of cases, all three tests indicated statistically significant overlap. However, in instances where not all three tests agreed, this discrepancy was primarily due to a high overlap estimate combined with differences in sample sizes, where one species typically had a smaller sample size.

Results: Dietary overlap

Dietary partitioning among the felids was present but not absolute. Jaguars and pumas exhibited the highest dietary overlap, both preying on large species such as collared peccary, paca, and opossums. Their diet similarity score (DS = 0.60) and the overlap estimate for collared peccary ($\Delta = 0.54$) suggest that these two apex predators share a significant portion of their prey base. However, pumas had a broader diet that included medium-sized prey such as dice's cottontail (Δ = 0.72) and other rodents (Δ = 0.74), whereas jaguars showed a stronger association with large ungulates. Among the smaller felids (ocelots, margays, and oncillas) exhibited high dietary overlap, feeding primarily on rodents, opossums, and small terrestrial mammals. The highest overlap was observed between ocelots and oncillas (Δ = 0.83), indicating potential competition within this group. The jaguarundi was the most distinct in its dietary habits, primarily preying on diurnal species such as the red-tailed squirrel (Δ = 0.62) and Central American agouti (Δ = 0.62), with little overlap with the other felids. While dietary differentiation helps to reduce competition to some extent, especially for jaguarundi, the high overlap among the other species suggests that additional factors, such as temporal or spatial niche separation, are necessary for coexistence.

Results: Temporal overlap

Temporal niche partitioning among the felid species was not a major factor in reducing competition, as the overlap values suggest a high likelihood of encounters based on species abundance and the extent to which predators and their prey overlap in time and space. Jaguars and pumas were mostly nocturnal, with respectively 71% and 74% of their recorded activity occurring at night, and a high temporal overlap estimate (Δ = 0.75). However, unlike the smaller nocturnal felids, jaguars and pumas exhibited relatively more diurnal activity, with respectively 29% and 26% of their activity occurring during the day. This indicates that while they are primarily nocturnal, they are not as strictly limited to nighttime as the smaller felids. This is just as the literature suggested, allowing for some differentiation in movement and hunting behaviour. The ocelot, margay, and oncilla were all strongly nocturnal, with recorded daytime activity levels of only 9%, 7%, and 11%, respectively. The high overlap between these species, particularly between ocelot and oncilla (Δ = 0.83) and ocelot and margay (Δ = 0.77), suggests that time-based separation is not a primary mechanism of niche differentiation within these groups. The only clear case of temporal partitioning was found in the jaguarundi, which was exclusively diurnal, with 100% of its recorded activity occurring during daylight hours. Its low temporal overlap with all other felids, particularly with ocelot (Δ = 0.18), margay (Δ = 0.21), and oncilla (Δ = 0.23), suggests that it avoids competition primarily by being active when the other species are inactive. However, for the rest of the felid community, the lack of strong temporal separation suggests that they might rely on other forms of niche differentiation.

Results: Spatial overlap

Spatial partitioning was present to some extent, with certain species showing preferences for different areas of the reserve. Jaguars had an overall Relative Abundance Index (RAI) of 5.58 and were primarily detected in higher-elevation areas such as the Skutch trail. Pumas, with the highest overall activity (RAI = 17.22), were recorded on nine out of ten trails, with the highest concentrations on the Gavilan, Montaña, and Los Quetzales trails. The highest number of puma observations occurred on the Gavilan trail (N = 54), suggesting this trail may serve as a key area, possibly indicating a border zone for multiple individuals. Despite these spatial tendencies, the overlap estimate for jaguar and puma (Δ = 0.75) suggests that their coexistence is not solely dependent on spatial separation. Ocelots, with an RAI of 11.93, were widely distributed but were most frequently detected on the Don Victor and Rio trails. Margays and oncillas were recorded less frequently but exhibited overlapping distributions with ocelots, indicating similar habitat use. The jaguarundi was the most spatially distinct species, with an RAI of 2.58, being recorded on only four of the ten trails, including Don Victor (N = 3), Gavilan (N = 1), Heliconia (N = 1), and Jilguero Loop (N = 1). This suggests that jaguarundis avoid areas heavily used by more abundant felids and may favour less frequented trails. However, the low detection rate on Heliconia could also be partially explained by limited camera effort, as this trail had only 390 active camera days over the study period. The limited camera effort suggests that the scarcity of jaguarundi records here does not necessarily indicate a strong habitat preference but could be a reflection of sampling limitations. These findings suggest that while spatial partitioning plays a role, it does not fully segregate species, particularly among jaguar and puma or the smaller nocturnal felids, reinforcing the idea that multiple niche dimensions interact to facilitate coexistence.

For spatial overlap, also ecological factors such as seasonality, migration patterns, and human activity in the reserve likely influenced species distributions in Cloudbridge. While this study primarily examined species occurrences at different trails, further investigation into how these environmental variables shape felid habitat preferences could provide deeper insights into their spatial coexistence strategies.

Results: overlap primary and secondary competitors

The analysis of primary and secondary competitors within the felid guild reveals that potential competition is largely driven by similarities in body mass, diet, and spatiotemporal overlap. As expected based on their size and ecological roles, the jaguar and puma emerged as each other's primary competitors, with the ocelot as a notable secondary competitor for both. These mutual high competition scores suggest substantial overlap in prey base and spatial presence, although variation in habitat use or hunting strategies may reduce direct interactions. Among the smaller felids, the oncilla was identified as the main competitor for the ocelot, margay, and jaguarundi. This is likely due to shared preference for small, nocturnal prey and overlapping activity patterns. Interestingly, the jaguarundi, despite being strictly diurnal, showed high competition scores with more nocturnal species. This indicates that body size and dietary overlap may have weighed more heavily in the competition scores than temporal separation. Overall, these results suggest that while coexistence is facilitated through subtle ecological differentiation, significant potential for competition remains, particularly within similar size classes.

Comparison results with existing studies

The findings of this study align with those of Botts et al. (2020), who examined temporal niche partitioning among predators and prey in Costa Rica. Similar to their results, this study found that smaller *Leopardus* species (ocelot, margay, oncilla) exhibited predominantly nocturnal activity. The only difference is that the larger felids (jaguar, puma) showed more nocturnal than cathemeral behaviour in this research. Factors like relatively high human presence in the Cloudbridge reserve could possibly influence this behaviour. In the Cloudbridge Reserve, human activities predominantly occur during daylight hours. This daytime human presence may lead the large felids to adjust their activity patterns to become more nocturnal, thereby reducing the likelihood of encounters with humans.

Interestingly, Botts et al. (2020) also reported significant temporal overlap among predators, suggesting that prey availability may be a stronger driver of activity patterns than competition alone. This supports the idea that the felid guild in Cloudbridge adapts its activity patterns to maximise hunting efficiency while minimising direct competition.

Moreover, this study confirmed that dietary overlap is an essential component of niche partitioning. Prey selection differed among felid species, with larger species focusing on medium to large prey (e.g., peccaries, coatis), while smaller species relied more on rodents and small mammals. These patterns reinforce previous findings on prey partitioning as a mechanism that facilitates coexistence (Botts et al., 2020).

This study exclusively focused on felid species and did not account for other carnivores that may be part of the intraguild competition, such as coyotes (*Canis latrans*), tayras (*Eira barbara*), or mustelids (*Mustelidae*), which could also influence niche partitioning. The presence of these competitors may play a role in shaping the spatial, temporal, and dietary patterns of the felids studied as Botts et al (2020) suggests, adding an additional layer of complexity to their coexistence strategies.

Practical implications of results and scope

The results of this study provide valuable information for conservation efforts in tropical montane forests. Understanding the temporal and spatial behaviour of felids can aid in habitat management strategies, conservation strategies and even reduce human-wildlife conflicts.

For conservationists and wildlife managers, these findings highlight the importance of preserving a variety of habitats to accommodate different felid species. The results also provide a foundation for future studies focusing on more precise monitoring techniques, which could improve the effectiveness of conservation initiatives. Researchers can build on this study by integrating occupancy models and broader prey availability assessments to refine estimates of species interactions and habitat use.

By integrating findings from existing literature and acknowledging methodological constraints, this discussion provides a balanced interpretation of the study results. Future research should build on these insights by incorporating standardised data collection techniques and refining analytical approaches to enhance the accuracy and applicability of findings in wildlife conservation.

5. Conclusion

This study investigated how six felid species—jaguar (*Panthera onca*), puma (*Puma concolor*), ocelot (*Leopardus pardalis*), jaguarundi (*Herpailurus yagouaroundi*), margay (*Leopardus wiedii*), and oncilla (*Leopardus pardinoides*)—coexist in the Cloudbridge Reserve by analysing their dietary, temporal, and spatial partitioning. Understanding these mechanisms provides insight into how these species share resources within the same ecological landscape. The main research question was: *What is the difference in the spatial and temporal distribution, considering the available resources (time, space, and diet), of the six felid species present in the Cloudbridge Nature Reserve?* This was explored through four sub-questions: (1) *"What are the diets of the six felid species and is there any overlap?"* (2) *At which times are the felid species active and is there temporal overlap within this felid guild?* (3) *At which places are the felid species active and is there any spatial overlap within this felid guild?* and (4) *What are the primary and secondary competitors for each felid within the felid guild?*

Dietary overlap

There is evidence of dietary partitioning among felid species, although it is complete. Jaguars and pumas show the greatest similarity in diet, both targeting larger prey species such collared peccary, paca, and opossums. Within the group of smaller cats (ocelots, margays, and oncillas) also a considerable degree of dietary overlap was observed, with diets primarily consisting of rodents, opossums, and small terrestrial mammals. While dietary differentiation helps to reduce interspecific competition, the high overlap among the species indicated that additional factors, such as temporal or spatial niche separation, are necessary for coexistence.

Temporal overlap

Jaguars and pumas are predominantly nocturnal, with 71% and 74%, respectively, of their recorded activity occurring at night. Nonetheless, both species are not strictly limited to nighttime, with respectively 29% and 26% of their activity occurring during the day. The jaguar and puma show a high temporal overlap. In contrast, the ocelot, margay, and oncilla are strongly nocturnal, with daytime activity recorded at just 9%, 7%, and 11%, respectively. The strong temporal overlap within this group, particularly between ocelot and oncilla and ocelot and margay, suggests that time-based activity separation is not the main mechanism of niche differentiation within these groups. The only clear case of temporal partitioning was found in the jaguarundi, that is active exclusively during daylight hours.

Spatial overlap

Jaguar observations (RAI = 5.58) are primarily concentrated in higher-altitude zones, especially along the Skutch trail. Pumas, that show the highest overall activity (RAI =

17.22), were observed on nine out of ten trails, with particularly high concentrations on the Gavilan, Montaña, and Los Quetzales trails. Ocelots (RAI = 11.93) were widely distributed across the reserve, with notable concentrations on the Don Victor and Rio trails. Margays and oncillas were less frequently recorded, but their distribution overlaps considerably with that of the ocelot, indicating similarities in habitat use. The jaguarundi (RAI = 2.58) has the most distinct spatial pattern, being recorded on only four of the ten trails. Altogether, these spatial patterns suggest that while habitat partitioning contributes to reducing competition, it alone is insufficient to explain the coexistence of certain species, particularly among jaguar and puma or the smaller nocturnal felids. This reinforces the idea that multiple niche dimensions interact to facilitate coexistence.

Primary and secondary competitors

Based on body mass similarity, dietary overlap, and spatiotemporal activity patterns, potential competitive relationships were identified within the felid guild. Larger species such as jaguar and puma showed the highest competition scores with one another, likely due to their overlapping prey range and broad spatial presence. The ocelot exhibited strongest overlap with the oncilla and margay, reflecting similarities in body size and nocturnal behaviour. The jaguarundi, while diurnal, had notable dietary overlap with smaller nocturnal species, especially the oncilla. Overall, competition appeared strongest between species of similar size and activity patterns, although temporal partitioning may reduce direct encounters among them.

Overall conclusion

The overall findings of this study provide a nuanced answer to the main research question: *What is the difference in the spatial and temporal distribution, considering the available resources (time, space, and diet), of the six felid species present in the Cloudbridge Nature Reserve.* The hypothesis predicted that the felids would exhibit clear niche partitioning across all three dimensions, thereby reducing direct competition. The results only partially support this hypothesis. While the jaguarundi demonstrates strong niche differentiation through temporal and dietary segregation, the other species exhibit high overlap in at least one or more niche dimensions. Jaguars and pumas show dietary overlap but may reduce competition through prey-switching or microhabitat differentiation. Ocelots, margays, and oncillas are highly similar in both diet and activity patterns, suggesting that fine-scale habitat preferences or prey specialisation may be key to their coexistence.

Recommendations

These findings highlight the complexity of predator coexistence and underscore the importance of habitat heterogeneity in maintaining biodiversity. The Cloudbridge reserve provides a diverse range of habitats that accommodate the ecological requirements of all six felid species, enabling them to share the landscape despite significant niche overlap. Ultimately, this study contributes to a growing body of knowledge on felid ecology in montane cloud forests and reinforces the need for continued conservation efforts to protect these vulnerable and ecologically significant predators.

A recommendation for Cloudbridge reserve for the short term is to cover all trails within the reserve with camera traps, also some places that are off trail and in the canopy. This will help monitoring all cat species, also the smaller cats that are partially arboreal. Installing cameras in hard-to-reach places can be challenging but including smaller felids that are known to hunt birds and reptiles can improve the monitoring of niche partitioning of all cat species. It is important for Cloudbridge to commit themselves to a researcher that is experienced with these methods.

Another recommendation for Cloudbridge for the short term is to conduct research on the influence of human activity on the felids. Compared with the research of Botts et al. (2020), some felids in Cloudbridge tend to be more nocturnal. It would be interesting and important to study if this is influenced by the relatively high presence of humans in the reserve. This would be a good research topic for another researcher or research intern.

A recommendation for Cloudbridge reserve for the longer term is to continue monitoring the six cat species, using a standardised way of data collection. Studying the felids over a long period of time is important to understand their role in the ecosystem and to continue conservation efforts in a way that allows the cat species to thrive.

A recommendation for future research is to study niche partitioning over a long period of time, without the use of historical data. Due to missing data in the historical dataset, some gaps needed to be filled in. By consistently collecting data over a longer period of time, more reliable data on the temporal and spatial distribution of cats and preys could be collected.

Another recommendation for future research is to also include other carnivores that may be part of the intraguild competition, such as coyotes, tayras, or mustelids. These predators could also influence niche partitioning. Furthermore, for spatial overlap factors such as seasonality and migration patterns can influence distributions of species within an area. Further investigation in to how these environmental variables shape felid habitat preferences could provide better insights into their coexistence strategies.

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Appendix I – List of felid preys

Prey base		
Felid	**Prey**	**Sources**
Jaguar (*Panthera onca*)	Collared Peccary (Pecari tajacu), White-tailed Deer (Odocoileus virginianus), Coati (Nasua narica), Armadillo* (Dasypus novemcinctus), Raccoon (Procyon lotor), Central American Red Brocket Deer (Mazama temama), Paca (Cuniculus paca), Tamandua (Tamandua mexicana), Central American Agouti (Dasyprocta punctata), Opossums (Didelphidae), Common Gray four-eyed Opossum (Philander opossum), Dice's Cottontail (Sylvilagus dicei)	Aranda & Sanchez-Cordero (1996); Oliveira (2002); Garla et al. (2001); Medellín et al. (2002); Scognamillo et al. (2003); Novack et al. (2005); Weckel et al. (2006a,b); Foster et al. (2009); Gómez-Ortiz & Monroy-Vilchis (2013); Rueda et al. (2013); Hernández-Saintmartín et al. (2015); Arroyo-Arce et al. (2017); Ávila–Nájera et al. (2018)
Puma (*Puma concolor*)	Rodents (Rodentia), Central American Agouti* (Dasyprocta punctata), Tamandua (Tamandua mexicana), Armadillo* (Dasypus novemcinctus), Raccoon (Procyon lotor), Coati (Nasua narica), Collared Peccary (Pecari tajacu), Opossums (Didelphidae), Tayra (Eira barbara), Common Gray Four-eyed Opossum (Philander opossum), Dice's Cottontail (Sylvilagus dicei), Paca (Cuniculus paca), Central American Red Brocket Deer (Mazama temama)	Aranda & Sanchez-Cordero (1996); Oliveira (2002); Scognamillo et al. (2003); Novack et al. (2005); Moreno et al. (2006); Foster et al. (2010); Monroy-Vilchis et al. (2009); Gómez-Ortiz et al. (2011); Gómez-Ortiz & MonroyVilchis (2013); Rueda et al. (2013); Hernández-Saintmartín et al. (2015); Ávila–Nájera et. al. (2018)
Ocelot (*Leopardus pardalis*)	Rodents* (Rodentia), Opossums (Didelphidae), Four-eyed Opossum (Philander opossum), Paca (Cuniculus paca), Central American Agouti (Dasyprocta punctata), Central American Red Brocket Deer (Mazama temama)	Moreno et al. (2006); Abreu et al. (2008); Bianchi et al. (2010); Silva-Pereira et al. (2011)
Jaguarundi (*Herpailurus yaguarundi*)	Rodents* (Rodentia), Opossums (Didelphidae), Four-eyed Opossum (Philander opossum), Paca (Cuniculus paca), Central American Agouti (Dasyprocta punctata), Central American Red Brocket Deer (Mazama temama)	Bianchi et al. (2011); Silva-Pereira et al. (2011); Giordano (2016); Rinaldi et al. (2015)
Margay (*Leopardus wiedii*)	Rodents* (Rodentia), Opossums (Didelphidae), Four-eyed Opossum (Philander opossum), Central American Agouti (Dasyprocta punctata), Dice's Cottontail (Sylvilagus dicei), White-tailed Deer (Odocoileus virginianus)	Bianchi et al. (2011); Rinaldi et al. (2015); Seibert et al. (2015)
Oncilla (*Leopardus tigrinus oncilla*)	Rodents* (Rodentia), Opossums* (Didelphidae), Four-eyed Opossum (Philander opossum), Paca (Cuniculus paca), Dice's Cottontail (Sylvilagus dicei), Coati (Nasua narica)	Tortato & de Oliveira (2005); Rocha-Mendes et al. (2010); Silva-Pereira et al. (2011); Rinaldi et al. (2015); Seibert et al. (2015);

Appendix II – Body Mass Similarity, Diet Similarity and Competition Overlap

species1	**species2**	**Body Mass Similarity**	**Diet Similarity**	**Competition Overlap**	**Final Competition Score**
Jaguar	Puma	0,745	0,60	0,51	0,618
Jaguar	Ocelot	0,108	0,43	0,43	0,323
Jaguar	Jaguarundi	0,068	0,29	0,29	0,216
Jaguar	Margay	0,033	0,29	0,29	0,204
Jaguar	Oncilla	0,023	0,38	0,47	0,291
Puma	Jaguar	0,745	0,60	0,51	0,618
Puma	Ocelot	0,364	0,47	0,47	0,435
Puma	Jaguarundi	0,323	0,31	0,31	0,314
Puma	Margay	0,289	0,34	0,34	0,323
Puma	Oncilla	0,279	0,47	0,47	0,406
Ocelot	Jaguar	0,108	0,43	0,43	0,323
Ocelot	Puma	0,364	0,47	0,47	0,435
Ocelot	Jaguarundi	0,938	0,33	0,33	0,533
Ocelot	Margay	0,932	0,40	0,4	0,577
Ocelot	Oncilla	0,922	0,47	0,47	0,621
Jaguarundi	Jaguar	0,068	0,29	0,29	0,216
Jaguarundi	Puma	0,323	0,31	0,31	0,314
Jaguarundi	Ocelot	0,938	0,33	0,33	0,533
Jaguarundi	Margay	0,975	0,38	0,38	0,578
Jaguarundi	Oncilla	0,965	0,48	0,48	0,642
Margay	Jaguar	0,033	0,29	0,29	0,204
Margay	Puma	0,289	0,34	0,34	0,323
Margay	Ocelot	0,932	0,40	0,4	0,577
Margay	Jaguarundi	0,975	0,38	0,38	0,578
Margay	Oncilla	0,988	0,46	0,46	0,636
Oncilla	Jaguar	0,023	0,38	0,47	0,291
Oncilla	Puma	0,279	0,47	0,47	0,406
Oncilla	Ocelot	0,922	0,47	0,48	0,624
Oncilla	Jaguarundi	0,965	0,48	0,48	0,642
Oncilla	Margay	0,988	0,46	0,46	0,636

Appendix III – Activity overlap for cat and potential intraguild competitors and prey species for all sites

Species-I	N_1	Species-2	Predator-Prey	N_2	Trails Recorded	Sites Recorded	Overall RAI	Overlap Estimate	95% Lower	95% Upper	Watson U^2	P-U^2	Wr	P-Wr	Fisher's Exact	Primary Interactions
Jaguar	14	Puma	Predator	147	9	27	17,22	0.7523	0,5618	0,9152	0,0571	0,6464	0,7337	0,0000	0,7186	primary compe
Jaguar	14	Ocelot	Predator	97	9	24	11,93	0.7187	0,5243	0,8911	0,1376	0,1286	4,5157	0,0000	0,1584	secondary com
Jaguar	14	Margay	Predator	29	5	10	6,55	0.7043	0,5015	0,8759	0,0646	0,5718	1,0710	0,0000	0,2464	
Jaguar	14	Jaguarundi	Predator	6	4	5	2,58	0.3579	0,1191	0,6082	0,2339	0,0155	8,4457	0,0000	0,1410	
Jaguar	14	Oncilla	Predator	38	5	9	13,38	0.7663	0,5776	0,9261	0,0809	0,4136	1,7833	0,0000	0,6721	
Jaguar	14	Central American Agouti	Prey	17	6	7	3,70	0.4769	0,2513	0,6955	0,2895	0,0033	10,7546	0,0000	0,0944	
Jaguar	14	Collared Peccary	Prey	1887	10	27	205,62	0.5419	0,3525	0,7249	0,2950	0,0048	9,5948	0,0000	0,0010	primary prey
Jaguar	14	Common Opossum	Prey	389	9	15	55,11	0.7031	0,5191	0,8714	0,1672	0,0708	4,2604	0,0000	0,0440	secondary prey
Jaguar	14	Dice's Cottontail	Prey	688	10	20	84,00	0.6862	0,5105	0,8304	0,0847	0,3740	1,2964	0,0000	0,0958	
Jaguar	14	Gray Four-eyed Opossum	Prey	135	6	7	29,30	0.6573	0,4672	0,8377	0,2754	0,0073	8,4431	0,0000	0,0078	
Jaguar	14	Nine-banded Armadillo	Prey	21	8	9	4,75	0.6227	0,4032	0,8287	0,0822	0,4155	1,3445	0,0000	0,8247	
Jaguar	14	Northern Tamandua	Prey	24	5	5	7,56	0.6176	0,4012	0,8192	0,1930	0,0419	6,8459	0,0000	0,4140	
Jaguar	14	Paca	Prey	320	9	17	42,65	0.5773	0,3972	0,7561	0,3874	0,0004	13,1086	0,0000	0,0004	
Jaguar	14	White-nosed Coati	Prey	906	10	26	100,40	0.3908	0,2091	0,5868	0,5593	0,0000	15,1776	0,0000	0,0000	

Species-I	N_1	Species-2	Predator-Prey	N_2	Trails Recorded	Sites Recorded	Overall RAI	Overlap Estimate	95% Lower	95% Upper	Watson U^2	P-U^2	Wr	P-Wr	Fisher's Exact	Primary Interactions
Puma	147	Jaguar	Predator	14	6	9	5,58	0.7523	0,5638	0,9167	0,0571	0,6453	0,7337	0,0000	0,7177	primary compe
Puma	147	Ocelot	Predator	97	9	24	11,93	0.7684	0,6688	0,8582	0,3552	0,0017	10,0214	0,0000	0,0118	secondary com
Puma	147	Margay	Predator	29	5	10	6,55	0.6692	0,5077	0,8162	0,2322	0,0196	4,1932	0,0000	0,0672	
Puma	147	Jaguarundi	Predator	6	4	5	2,58	0.3098	0,1338	0,4947	0,2952	0,0019	9,8061	0,0000	0,0028	
Puma	147	Oncilla	Predator	38	5	9	13,38	0.8521	0,7397	0,9464	0,0689	0,5149	0,4395	0,0001	0,9431	
Puma	147	Collared Peccary	Prey	1887	10	27	205,62	0.538	0,4726	0,6054	3,4867	0,0000	124,8520	0,0000	0,0000	primary prey
Puma	147	White-nosed Coati	Prey	906	10	26	100,40	0.3769	0,3095	0,4448	5,8169	0,0000	190,5496	0,0000	0,0000	secondary prey
Puma	147	Dice's Cottontail	Prey	688	10	20	84,00	0.7174	0,6532	0,7756	0,3234	0,0042	3,5033	0,0000	0,0000	
Puma	147	Common Opossum	Prey	389	9	15	55,11	0.8437	0,7757	0,9052	0,3141	0,0028	8,0191	0,0000	0,0002	
Puma	147	Other (small) Rodents*	Prey	309	9	15	45,02	0.7409	0,6728	0,8046	0,5813	0,0000	9,4713	0,0000	0,0000	
Puma	147	Paca	Prey	320	9	17	42,65	0.6952	0,6138	0,7740	1,1914	0,0000	39,5529	0,0000	0,0000	
Puma	147	Gray Four-eyed Opossum	Prey	135	6	7	29,30	0.7871	0,7036	0,8644	0,4794	0,0001	15,0684	0,0000	0,0005	
Puma	147	Tayra	Prey	110	8	16	15,96	0.3441	0,2602	0,4312	3,1584	0,0000	122,6916	0,0000	0,0000	
Puma	147	Northern Tamandua	Prey	24	5	5	7,56	0.7255	0,5774	0,8644	0,2099	0,0334	7,3254	0,0000	0,3964	
Puma	147	Central American Agouti	Prey	17	6	7	3,70	0.4697	0,3124	0,6308	0,6201	0,0000	22,3865	0,0000	0,0001	
Puma	147	Nine-banded Armadillo	Prey	21	8	9	4,75	0.6026	0,4269	0,7714	0,3375	0,0026	11,5946	0,0000	0,0172	
Puma	147	Red-tailed Squirrel	Prey	1427	10	29	154,19	0.2932	0,2299	0,3591	7,1418	0,0000	222,1806	0,0000	0,0000	
Puma	147	Mouse Opossums*	Prey	72	5	6	19,05	0.6654	0,5663	0,7550	0,3847	0,0013	5,5298	0,0000	0,0000	
Puma	147	Mexican hairy dwarf porcu	Prey	10	4	4	8,781559	0.659	0,4351	0,8571	0,1423	0,1175	4,1669	0,0000	0,6167	
Puma	147	Striped Hog-Nosed Skunk	Prey	15	5	7	4,205214	0.6379	0,4498	0,8111	0,2230	0,0207	7,0553	0,0000	0,0821	
Puma	147	Northern raccoon	Prey	3	2	2	2,298851	Sample toc	Sample toc	Sample toc	Sample toc	Sample toc	3,1127	0,0000	0,4955	

Species-I	N_1	Species-2	Predator-Prey	N_2	Trails Recorded	Sites Recorded	Overall RAI	Overlap Estimate	95% Lower	95% Upper	Watson U^2	P-U^2	Wr	P-Wr	Fisher's Exact	Primary Interactions
Ocelot	97	Puma	Predator	147	9	27	17,22	0.7684	0,6700	0,8575	0,3552	0,0020	10,0214	0,0000	0,0130	
Ocelot	97	Jaguar	Predator	14	6	9	5,58	0.7187	0,5200	0,8929	0,1376	0,1243	4,5157	0,0000	0,1606	
Ocelot	97	Margay	Predator	29	5	10	6,55	0.7703	0,6249	0,8950	0,1314	0,1533	3,9109	0,0000	0,4657	primary
Ocelot	97	Jaguarundi	Predator	6	4	5	2,58	0.1786	0,0252	0,3586	0,4322	0,0000	12,3154	0,0000	0,0000	
Ocelot	97	Oncilla	Predator	38	5	9	13,38	0.83	0,6989	0,9348	0,0783	0,4192	1,9553	0,0000	0,4081	secondary
Ocelot	97	Dice's Cottontail	Prey	688	10	20	84,00	0.7205	0,6537	0,7818	0,3468	0,0015	7,1363	0,0000	0,0000	secondary
Ocelot	97	Common Opossum	Prey	389	9	15	55,11	0.7798	0,6855	0,8647	0,2826	0,0078	7,9434	0,0000	0,0003	primary
Ocelot	97	Other (small) Rodents*	Prey	309	9	15	45,02	0.8257	0,7451	0,8952	0,1503	0,1076	2,4424	0,0000	0,0002	
Ocelot	97	Paca	Prey	320	9	17	42,65	0.7947	0,7030	0,8789	0,5442	0,0001	17,5016	0,0000	0,0000	
Ocelot	97	Gray Four-eyed Opossum	Prey	135	6	7	29,30	0.8079	0,7050	0,9018	0,2549	0,0134	8,3527	0,0000	0,0040	
Ocelot	97	Central American Agouti	Prey	17	6	7	3,70	0.2864	0,1326	0,4537	0,8774	0,0000	28,6083	0,0000	0,0000	
Ocelot	97	Red-tailed Squirrel	Prey	1427	10	29	154,19	0.1905	0,1314	0,2519	6,3999	0,0000	189,6795	0,0000	0,0000	
Ocelot	97	Mouse Opossums*	Prey	72	5	6	19,05	0.7694	0,6588	0,8613	0,0984	0,2849	0,7874	0,0000	0,0196	
Ocelot	97	Northern Tamandua	Prey	24	5	5	7,56	0.8339	0,6899	0,9400	0,0827	0,3957	1,9353	0,0000	0,7380	
Ocelot	97	Nine-banded Armadillo	Prey	21	8	9	4,75	0.6157	0,4367	0,7836	0,2642	0,0088	6,9641	0,0000	0,0013	
Ocelot	97	White-nosed Coati	Prey	906	10	26	100,40	0.2426	0,1838	0,3041	5,5175	0,0000	179,6136	0,0000	0,0000	
Ocelot	97	Collared Peccary	Prey	1887	10	27	205,62	0.379	0,3203	0,4407	3,8776	0,0000	137,6343	0,0000	0,0000	
Ocelot	97	Tayra	Prey	110	8	16	15,96	0.1951	0,1189	0,2752	3,7618	0,0000	146,5490	0,0000	0,0000	

Species-I	N_1	Species-2	Predator-Prey	N_2	Trails Recorded	Sites Recorded	Overall RAI	Overlap Estimate	95% Lower	95% Upper	Watson U^2	P-U^2	Wr	P-Wr	Fisher's Exact	Primary Interactions
Jaguarundi	6	Puma	Predator	147	9	27	17,22	0.3098	0,1322	0,4982	0,2952	0,0028	9,8061	0,0000	0,0026	
Jaguarundi	6	Ocelot	Predator	97	9	24	11,93	0.1786	0,0259	0,3623	0,4322	0,0000	12,3154	0,0000	0,0000	
Jaguarundi	6	Margay	Predator	29	5	10	6,55	0.2051	0,0168	0,4246	0,3473	0,0006	11,6525	0,0000	0,0006	secondary
Jaguarundi	6	Jaguar	Predator	14	6	9	5,58	0.3579	0,1210	0,6173	0,2339	0,0126	8,4457	0,0000	0,1411	
Jaguarundi	6	Oncilla	Predator	38	5	9	13,38	0.2296	0,0606	0,4284	0,3513	0,0004	11,6573	0,0000	0,0020	primary
Jaguarundi	6	Dice's Cottontail	Prey	688	10	20	84,00	0.2563	0,0669	0,4348	0,3981	0,0001	11,5846	0,0000	0,0001	
Jaguarundi	6	Common Opossum	Prey	389	9	15	55,11	0.1938	0,0560	0,3497	0,4069	0,0000	11,7134	0,0000	0,0000	
Jaguarundi	6	Other (small) Rodents*	Prey	309	9	15	45,02	0.099	-0,0167	0,2561	0,4570	0,0000	12,1075	0,0000	0,0000	
Jaguarundi	6	Paca	Prey	320	9	17	42,65	0.1041	0,0052	0,2394	0,4541	0,0000	12,2275	0,0000	0,0000	
Jaguarundi	6	Gray Four-eyed Opossum	Prey	135	6	7	29,30	0.1381	0,0136	0,2882	0,4790	0,0000	12,4611	0,0000	0,0000	
Jaguarundi	6	Central American Agouti	Prey	17	6	7	3,70	0.6196	0,3335	0,8808	0,0409	0,8795	0,5357	0,0000	0,8247	
Jaguarundi	6	Red-tailed Squirrel	Prey	1427	10	29	154,19	0.6177	0,2990	0,8658	0,0744	0,4699	1,5387	0,0000	0,1907	
Jaguarundi	6	Mouse Opossums*	Prey	72	5	6	19,05	0.1021	-0,0338	0,2780	0,4541	0,0000	12,6742	0,0000	0,0000	

Species-I	N_1	Species-2	Predator-Prey	N_2	Trails Recorded	Sites Recorded	Overall RAI	Overlap Estimate	95% Lower	95% Upper	Watson U^2	P-U^2	Wr	P-Wr	Fisher's Exact	Primary Interactions
Margay	29	Puma	Predator	147	9	27	17,22	0.6692	0,5074	0,8148	0,2322	0,0206	4,1932	0,0000	0,0671	
Margay	29	Ocelot	Predator	97	9	24	11,93	0.7703	0,6245	0,8923	0,1314	0,1468	3,9109	0,0000	0,4633	secondary
Margay	29	Jaguar	Predator	14	6	9	5,58	0.7043	0,4971	0,8783	0,0646	0,5682	1,0710	0,0000	0,2474	
Margay	29	Jaguarundi	Predator	6	4	5	2,58	0.2051	0,0186	0,4224	0,3473	0,0006	11,6525	0,0000	0,0005	
Margay	29	Oncilla	Predator	38	5	9	13,38	0.719	0,5457	0,8650	0,1691	0,0689	5,0060	0,0000	0,3456	primary
Margay	29	Dice's Cottontail	Prey	688	10	20	84,00	0.6933	0,5552	0,8064	0,1556	0,0943	1,5979	0,0000	0,0640	
Margay	29	Common Opossum	Prey	389	9	15	55,11	0.6544	0,4977	0,8041	0,3194	0,0032	9,3159	0,0000	0,0058	
Margay	29	Other (small) Rodents*	Other (sma	Prey	309	9	15	0.6747	0,5250	0,8093	0,3400	0,0020	10,7061	0,0000	0,0019	
Margay	29	Gray Four-eyed Opossum	Prey	135	6	7	29,30	0.6515	0,4953	0,8002	0,4167	0,0003	13,5225	0,0000	0,0022	
Margay	29	Central American Agouti	Prey	17	6	7	3,70	0.3146	0,1378	0,5032	0,5559	0,0000	20,0615	0,0000	0,0000	
Margay	29	Red-tailed Squirrel	Prey	1427	10	29	154,19	0.2112	0,1151	0,3105	2,0541	0,0000	57,3031	0,0000	0,0000	
Margay	29	Mouse Opossums*	Prey	72	5	6	19,05	0.8015	0,6717	0,9086	0,1222	0,1823	3,6085	0,0000	0,3825	

Species-I	N_1	Species-2	Predator-Prey	N_2	Trails Recorded	Sites Recorded	Overall RAI	Overlap Estimate	95% Lower	95% Upper	Watson U^2	P-U^2	Wr	P-Wr	Fisher's Exact	Primary Interactions
Oncilla	38	Puma	Predator	147	9	27	17,22	0.8521	0,7412	0,9473	0,0689	0,5186	0,4395	0,0002	0,9430	
Oncilla	38	Ocelot	Predator	97	9	24	11,93	0.83	0,6992	0,9356	0,0783	0,4295	1,9553	0,0000	0,4059	secondary
Oncilla	38	Margay	Predator	29	5	10	6,55	0.719	0,5476	0,8651	0,1691	0,0686	5,0060	0,0000	0,3480	primary
Oncilla	38	Jaguarundi	Predator	6	4	5	2,58	0.2296	0,0597	0,4272	0,3513	0,0004	11,6573	0,0000	0,0022	
Oncilla	38	Jaguar	Predator	14	6	9	5,58	0.7663	0,5751	0,9230	0,0809	0,4215	1,7833	0,0000	0,6699	
Oncilla	38	White-nosed Coati	Prey	901	10	26	100,40	0.287	0,1911	0,3911	2,1567	0,0000	64,7898	0,0000	0,0000	
Oncilla	38	Dice's Cottontail	Prey	688	10	20	84,00	0.7458	0,6516	0,8234	0,1473	0,1068	2,6544	0,0000	0,1778	
Oncilla	38	Common Opossum	Prey	389	9	15	55,11	0.8834	0,7756	0,9685	0,0705	0,4938	1,5411	0,0000	0,3619	
Oncilla	38	Other (small) Rodents*	Prey	309	9	15	45,02	0.8358	0,7333	0,9175	0,0766	0,4399	1,4486	0,0000	0,0116	
Oncilla	38	Paca	Prey	320	9	17	42,65	0.7439	0,6137	0,8617	0,3266	0,0037	11,1977	0,0000	0,0003	
Oncilla	38	Gray Four-eyed Opossum	Prey	135	6	7	29,30	0.8469	0,7263	0,9481	0,1463	0,1083	4,7059	0,0000	0,0717	
Oncilla	38	Central American Agouti	Prey	17	6	7	3,70	0.3582	0,1840	0,5465	0,6832	0,0000	25,3716	0,0000	0,0001	
Oncilla	38	Red-tailed Squirrel	Prey	1427	10	29	154,19	0.2113	0,1184	0,3166	2,4239	0,0000	66,7334	0,0000	0,0000	
Oncilla	38	Mouse Opossums*	Prey	72	5	6	19,05	0.7369	0,6166	0,8431	0,1367	0,1335	2,8752	0,0000	0,0222	