

Spatiotemporal Behavior & Interactions of Neotropical Felids

By: Chloe Pepke

Advisor: Dr. John Poulsen

Client: Holger Beck, Santa Lucia Cloud Forest Reserve

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Executive Summary

Carnivores, both large and small, are drivers of ecosystem structure. Through cascading trophic effects, carnivores not only influence prey species populations and in turn vegetation composition, but also populations and behavior of other carnivores. The dynamics of these intraguild interactions are varied and often difficult to discern, not only because these relationships vary by region, but because carnivores are typically solitary and elusive species. Carnivores are also often endemic and endangered due to threats like habitat fragmentation, poaching, and global climate change. Robust monitoring of carnivore populations is vital to their effective conservation. In this study, I explore the effectiveness of camera trapping for monitoring elusive carnivores and detecting intraguild interactions of four neotropical felids in Ecuador.

First, I compiled morphological information about each species across Central and South America and created a regional identification guide. This is an important contribution to conservation in the region because three of the study species belong to the same genus and are very similar in appearance, making them difficult to identify in photos. Using the guide and camera trap data from 2016 and 2022 from the Santa Lucia Cloud Forest Reserve (SL) near Quito, Ecuador, I manually sorted camera photos and corrected misidentifications. I found evidence that all three species are present in SL. However, the two smaller species are so similar, that these identifications should be confirmed genetically for certainty. This guide will assist the reserve staff in the identification process, as well as be a useful tool for the reserve's many local educational programs.

Second, I determined the spatial and temporal activity patterns for each species, as well as interspecies differences in these patterns. I modeled the effect of environmental variables including land use/land cover (LULC), elevation, and the distance to the nearest tourist site, on species occupancy and detection probability. I used the results to predict the detection probability of each species. Some species shared patterns, whereas others manifested distinct activity patterns, providing evidence for temporal and spatial niche partitioning among the felids, likely due to a combination of competitive avoidance and predation avoidance. These results will help inform future monitoring at SL and provide a foundation for understanding how felids in SL interact and the potential impacts of ecotourism in the area.

Abstract

The intraguild dynamics of apex and meso-carnivores contribute to the structure and resiliency of ecosystems, but temperature change and habitat loss threaten carnivores globally. This study explores the spatial and temporal behavior of four felid species (*Puma concolor*, *Leopardus pardalis*, *Leopardus wiedii*, and *Leopardus tigrinus*) in the Santa Lucia Cloud Forest Reserve (SL), near Quito, Ecuador. I used camera trap data from 2016 through 2022 to identify felid species and compare temporal trends in activity, distribution, and occupancy in relation to environmental factors. I then used the species-specific models to predict species occupancy in the unmonitored regions of the reserve. These results inform future monitoring efforts and provide insight into the extent of potential interactions among these four felids.

Resumen

Las dinámicas entre carnívoros grandes y los del tamaño mediano definen la estructura y resistencia de un ecosistema, pero el cambio climático y la destrucción del hábitat amenaza a los carnívoros globalmente. Este estudio explora los comportamientos espaciales y temporales de cuatro especies felinas (*Puma concolor*, *Leopardus pardalis*, *Leopardus wiedii* y *Leopardus tigrinus*) que están en la Reserva del Bosque Nublado de Santa Lucia (SL) cerca de Quito, Ecuador. Usé los datos de cámaras trampas colocadas desde 2016 hasta 2022 para identificar las especies felinas y comparar tendencias temporales de la actividad, la distribución, y la ocupación de las especies en relación con factores ambientales. Usé los modelos específicos de cada especie para predecir la ocupación de las especies en las regiones no supervisadas de la reserva. Los resultados informan proyectos futuros de supervisar estas especies y aporta información sobre las interacciones potenciales entre las cuatro felinas.

Introduction

Species interactions across all trophic levels define ecosystems and are critical to measuring their health and resilience for conservation. Identifying these interactions can be difficult, especially for elusive and solitary species like felids. As carnivores, felids can directly and indirectly shape ecosystem structure through top-down effects on prey populations (Winnie Jr, 2017). Apex carnivores also play a role in determining the behavior and niche occupancy of mesocarnivores (Codron, 2018). The intraguild dynamics of felids shape the structure of an ecosystem as much as predator-prey dynamics.

Interspecific interactions of carnivores can take on various forms from commensalism to competition to predation. The type of interaction is influenced by the extent of niche overlap (spatial, dietary, temporal) between species. Many studies on tropical carnivores have found evidence that morphologically similar species tend to have contrasting temporal and spatial activity patterns (Di Bitetti, 2010). Adjusting temporal activity allows species to coexist within a space while sharing the same necessary resources. It also allows smaller carnivores to avoid predation by the larger, apex predators with whom they share fewer resources. These adjustments may become more distinct with human disturbance, which seems to affect large carnivores less strongly than mesocarnivores based on changing activity patterns to avoid humans. (Rodriguez, 2021).

The goal of this study is to evaluate the behavioral patterns of felids in Ecuadorian cloud forests to investigate how species within the same guild interact with their shared environment and each other. To do so, I use camera trap data on four Neotropical felid species: the Puma, Ocelot, Margay, and Northern Tiger Cat. I first explore methods for accurately distinguishing between Ocelots, Margays, and Northern Tiger Cats, which are morphologically similar. I then assess spatial and/or temporal patterns in felid activity across the study area and assess the possible causes of these patterns. This assessment will be used to predict the preferred habitats of each species within the reserve to help inform future monitoring efforts.

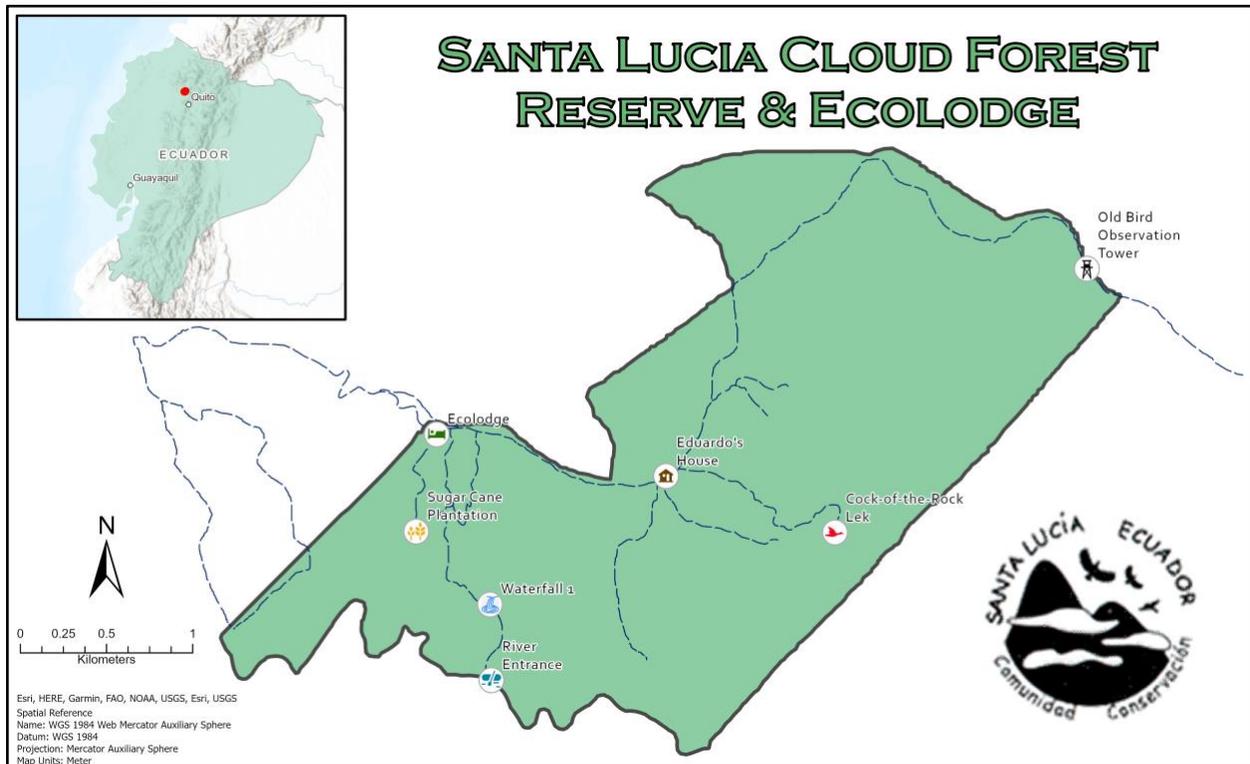
Based on previous studies and observations of the intraguild dynamics of these species, I expect to observe both species-specific and shared activity patterns. Furthermore, I hypothesize that the Ocelot competes with the Puma more than the two smaller species; therefore, the Ocelot behavioral patterns will be spatially and temporally separate from the puma. Likewise, I hypothesize that the two smaller species also compete for resources and will have spatial and temporal differences in activity as well as patterns of avoidance of the two larger carnivores due to predation risk. By identifying the factors that determine felid occupancy, including interactions with other felid species, we can better predict their behavior and habitat preferences to inform conservation efforts.

Methods

Study Area

The study was conducted in the Santa Lucia Cloud Forest Reserve (SL) in Nanegal, Ecuador, located about 80 km northwest of Quito, in the province of Pichincha (*Figure 1*). The reserve lies within the Choco-Andino Biosphere Reserve and a designated ecological corridor for the endangered Andean Bear (*Tremarctos ornatus*). SL has an area of approximately 730 ha and

an elevational range of ~1300 to ~2500 meters above sea level (Santa Lucia Ecolodge, 2020). SL was originally an agricultural collective until the late 1980s when the surrounding region was declared protected forest. The community made the decision to shift from agriculture to community-based conservation and ecotourism. The original families of the collective continue to manage SL including the Ecolodge they built in 1999 and lead various educational programs and research contributing to their mission to sustainably conserve the cloud forest and its natural resources in support of the SL community (Santa Lucia Ecolodge, 2020). Although there are still pastures and plantations within its borders, about 80% of the reserve is primary cloud forest and home to many endemic and endangered species such as the Andean Bear, 300+ orchid species, 400+ bird species, and five felid species (Santa Lucia Ecolodge, 2020); *Puma concolor* (Puma), *Puma yagouaroundi* (Jaguarundi), *Leopardus pardalis* (Ocelot), *Leopardus wiedii* (Margay), and *Leopardus tigrinus* (Northern Tiger Cat / Tigrina / Oncilla), all listed as near threatened or vulnerable in Ecuador (Tirira, 2017). This study focuses on the felid species of SL, excluding the Jaguarundi due to too few observations.



(Figure 1)

Map of the Santa Lucia Cloud Forest Reserve. The red dot in the map of Ecuador indicates the location of SL. Dashed lines indicate hiking trails into and throughout the reserve. Icons represent popular tourist sites with more human activity.

The Puma is a large, tawny-red colored felid that is very distinct from the other species in this study (Figure 2). Pumas are cathemeral, meaning they adjust their temporal activity based on prey availability or the presence of other competitive species (Botts et al., 2020). Their habitat is extensive and ranges from North through South America at all elevations. While the Puma is the apex carnivore in North America, the Jaguar (*Panthera onca*) often outcompetes it in Central and South America. In South America, competition with the Jaguar may have altered the South

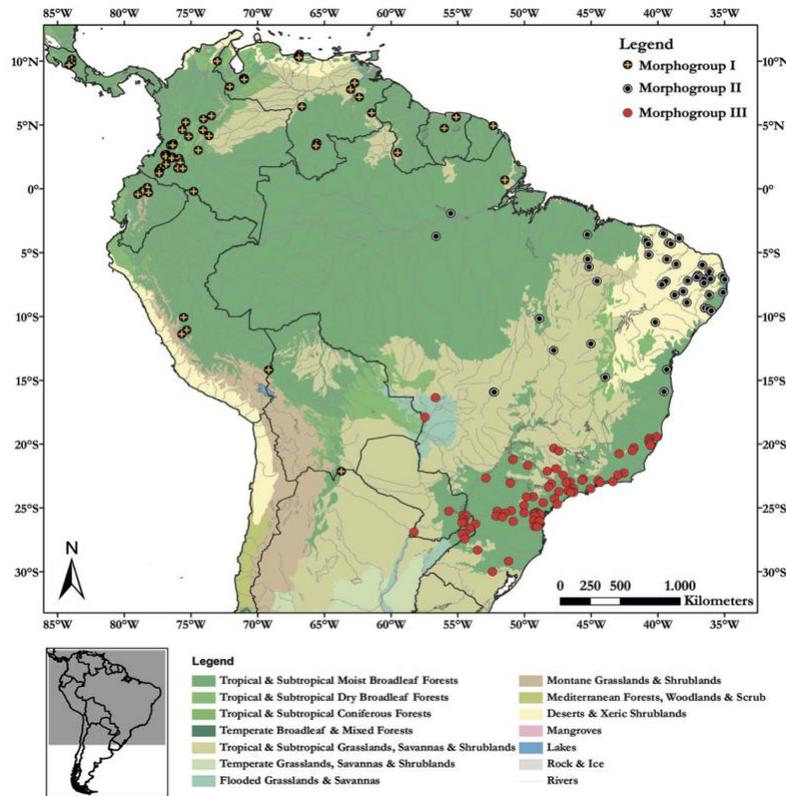
American Puma's diet, leading to its slightly smaller build compared to North American Pumas (Iriarte 1990).



(Figure 2)

Camera trap photo of a Puma in the Santa Lucia Cloud Forest Reserve.

The *Leopardus* genus consists of at least eight species of small- to medium-sized spotted cats that range from southern Texas throughout South America. This genus is generally understudied, especially in montane, tropical forests of the Northern Andes (da Cunha, 2017). In fact, *Leopardus tigrinus* is one of the least understood felids in the Neotropics because of taxonomic uncertainty due to the plesiomorphic morphology of this genus (Gonzalez-Maya, 2022). The physical similarities within this genus make species identification difficult and have led to a trend of combining multiple genetically distinct species into one taxonomic species. In fact, genetic studies have identified seven different haplogroups suggesting as many as six different species or subspecies within the *Leopardus tigrinus* taxonomic group (Ruiz-Garcia, 2017). Today, four subspecies of *Leopardus tigrinus* are recognized despite geomorphological classifications that suggest they are three distinct species (Figure 3) (Nascimento, 2017). Additionally, these species share many behavioral similarities, including dietary overlap of up to 84% in some areas (Silva-Pereira, 2011). They are also generally cathemeral, like the Puma, except for the Margay and Ocelot which are primarily nocturnal (Vanderhoff, 2011) (Nagy-Reis, 2019). As mesocarnivores in varied habitat, this group, particularly the Ocelot, which is the third largest felid in South America, could occupy higher trophic levels (Easter, 2020). The Ocelot may compete with both the smaller *Leopardus* species (often referred to as the “Ocelot effect”) (de Oliveira, 2010) and the Puma depending on prey availability.



(Figure 3)

Distribution of three morphologies of *L. tigrinus* in Central & South America (Nascimento 2017).

Camera Trapping

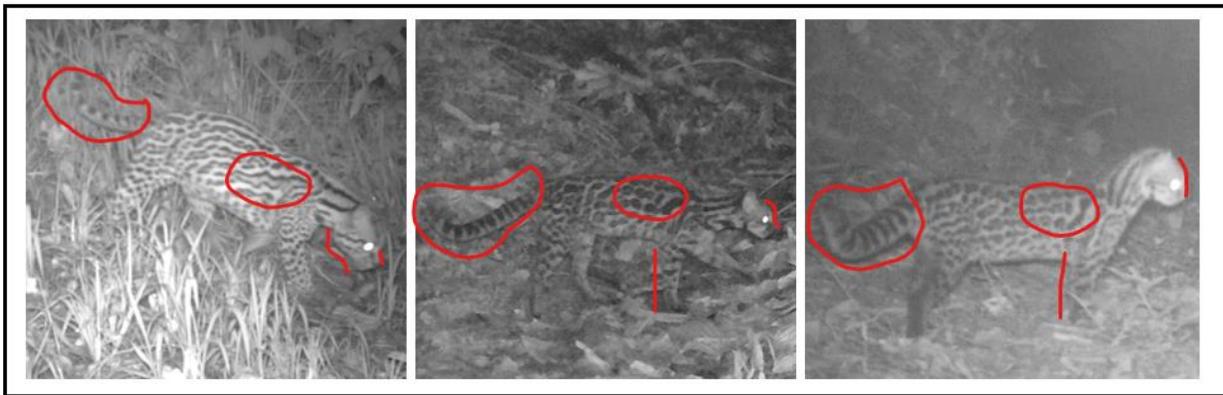
Although radio telemetry and tracking continue to increase in popularity for studies on elusive species with large home-ranges, such as the Puma, this method increases risk to both the animal and researchers and is expensive (Trolliet, 2014). Camera trapping is a more accessible method for observing wildlife and allows for calculations of population parameters in unmarked populations such as population density (Palencia, 2021). Cameras set up in a grid allow for large areas to be monitored and have been found to yield the same results and spatial distributions as GPS collars while also being able to provide insight into interspecific interactions (Triguero-Ocaña, 2020).

In 2012, the Coordinator of Scientific Research, Holger Beck (HB), started a camera trapping program to determine the species present within SL. In 2016, additional camera traps were distributed across the reserve, and the goal of the program evolved to studies of animal behavior and conservation, particularly as an educational tool for local schools. Since then, a total of 46 cameras across 27 sites along existing trails have been placed in SL (Figure A1, Appendix A). The site, camera name, and start and end date were recorded for each camera trapping session, which varied in length from a single day (due to camera malfunctions or animals knocking them down) to more than a year of continuous monitoring. Several camera makes/models were used including RECONYX, Bushnell, Zecre, and General. All camera models use infrared imaging to capture nighttime activity, which other studies have identified as the most effective method specifically for capturing photos of felids as opposed to flash

photography (Trolliet, 2014). Due to limited resources, accessibility and the risk of poachers/trespassers damaging or stealing equipment, all camera traps were placed on hiking trails. The non-systemic placement of cameras limits our ability to assess the impact of trails on felid detection in this reserve. However, previous research in other regions of Ecuador have found that larger mammals frequently use man-made trails to travel, and large carnivores show negligible avoidance of trails (Blake, 2017). Meanwhile, other studies observed greater avoidance of trails with higher human activity by medium and small-bodied felids (Rodriguez, 2021). For each session, a single camera was placed about knee height (under one meter) facing the trail at a direction that provided the furthest visibility range possible for the camera to detect movement. Camera traps were set to record the date, time, and temperature for each animal observation. Characteristics of each site (geographical location, forest type, elevation, and distance from the ecolodge) were cataloged upon placement.

Species Identification

To identify cat species, HB reviewed all photos and attributed a species name. Due to the physical similarities between the three spotted cat species (*Figure 4*), many of the initial identifications were uncertain or labeled by their common genus. These similarities also prevent use of any species identification software, so all photos were processed manually. To verify the identification of the *Leopardus* species, I first compiled extensive behavioral and morphological information on each species, particularly focused on the morphotypes/subspecies occurring in this region of Ecuador (Tirira, 2017). I then derived an identification taxonomy for this region based on animal size, head profile/face shape, tail size and position, and color/spot pattern (Appendix C) (de Oliveira, 2020). While the consideration of these features may improve species identification methods in Santa Lucia, it should be emphasized that only genetic testing can identify species with absolute certainty, particularly for *L. wiedii* and *L. tigrinus*, as the rate of hybridization is unknown in this study region.



(Figure 4)

L. pardalis, left. *L. wiedii*, center. *L. tigrinus*, right. Red markings indicate clear, distinguishing features. Animal size is not obvious due to the scale of the photos; however, *L. pardalis* has a noticeably thicker, more muscled body and head/neck than the two smaller species.

Occupancy Modelling & Spatial Analysis

Detection and species occupancy probability were assessed based on the presence-absence of each species using tools in the *Unmarked* package (Fisk & Chandler, 2011). To account for differences in the length of trapping effort, i.e., the number of days a camera was operational, observations were condensed into weekly periods (Palmer, 2019). To create the inputs for this model, I first organized the species observations by site and assigned binary values for present/observed (1) and absent/not observed (0). If there was at least one day in a week that a felid was observed, it was marked as present (1). Weeks with no camera present at a given site were marked as “NA”. Next, I created a data frame summarizing the covariates of each site. These covariates included elevation, distance to the nearest tourist site, and land use/land cover (LULC) (i.e., primary forest, secondary forest, varied, pasture/plantation).

First, I ran naïve models for each species that assumed constant detection probability (100% chance of detection) and constant occupancy (100% of sites occupied). The second set of models assumed constant detection probability but investigated the relationship between occupancy and the covariates. The final set of models assumed constant occupancy and assessed the impact of the covariates on detection probability. The covariates can influence both detection and/or occupancy probability, whereas other variables, such as time, would only apply to detection probability (Byrne, 2021). Modeling with two different assumptions was necessary due to the different home-range sizes of each species. The average home ranges of all four species encompass the entire area of SL, meaning observations at any site likely indicate that the species are present throughout the reserve and a model of constant occupancy is a better fit (Kasper, 2016). I determined the best fit models for each species by comparing AIC values (Table B1, Appendix B) which were used to predict the occupancy and detection probability of each covariate (Table B2, Appendix B). All results were visualized spatially which involved three processes: 1. digitizing the reserve features, 2. kernel density estimation (KDE), and 3. spatial predictive modeling.

No geospatial datasets existed for the reserve aside from collections of point coordinates for the camera trap locations and tourist sites. To visualize the results of the camera trap data and occupancy models, I digitized a map of the reserve boundary, LULC, and trails using a photo of a map of the reserve posted at the ecolodge (Figure A2, Appendix A). I used a 2nd order polynomial transformation and 12 control points to accurately align the photo with the true location of the reserve features. I assigned values to each pixel of the georeferenced image according to LULC type. This required three reclassification steps to address the error in the originally assigned pixel values due to image quality and glare/lighting in the photo (Figure A3, Appendix A) The remaining reserve features were created by manually tracing them on the georeferenced image (Figure 1).

To predict and visualize species distributions, I employed KDE, an increasingly common method for distribution and home range estimation across many taxa (Seaman, 1996). This dataset contains many observations at the same geographic locations, so I used the density of observations at each site to identify the trapping locations that had higher proportions of observations for each species. The final product of this step in the analysis was a series of maps showing hotspots of activity for each species (Figure 6).

The goal of the spatial predictive modeling is to predict the preferred habitat for each species by assessing the relationship between occupancy and the covariates (LULC, elevation, and proximity to human activity). I first converted all covariates into raster format. The trails of

SL were included as an additional covariate and assigned predictive value based on literature identifying differences in trail use between large-bodied and medium-bodied felids (Blake, 2017) (Rodriguez, 2021). I assigned initial importance/cost values between 0-100 (100 being most important/preferred/lowest cost) to the different features of each covariate based on the predicted probability of detection/occupancy derived from the models (Table B2, Appendix B). Each variable raster was reclassified to their newly assigned cost values. I then combined the rasters to produce a single image of the reserve area showing the combined importance/cost of all the variables for the species. I repeated this process for each species to assess whether they have different habitat preferences (Figure 7).

Results

Species Identification

In total, 1238 observations of felids were recorded from 2016 – July 2022 in SL. Using the guide (Appendix C) that I developed on morphological identifiers for the *Leopardus* genus, I confirmed the presence of all three species included in this study in SL. After correcting misidentifications and confirming as many *Leopardus* identifications as possible, we confirmed 324 Puma, 131 Ocelot, 41 Margay and 465 Northern Tiger Cat observations. 277 observations were still marked as unidentifiable *Leopardus* species. This was generally due to image quality, despite being able to adjust the exposure and contrast of photos to make the features clearer. It was also because only a small part of the individual was captured by the cameras, such as the very tip of the tail. 244 observations were of melanistic felids (Figure 5), a trait found throughout felid genera and believed to be adaptive (Graipel, 2014). Melanism is generally less common in the Ocelot than the tiger cat and only two studies have claimed to identify melanistic Margays in camera trap photos in Costa Rica and Columbia (González-Maya, 2018). Prior to this discovery in 2018, no record of melanistic margay exists. However, no genetic confirmation took place and identification was solely based on morphological features. Our guide assumes melanistic individuals are Northern Tiger Cat, which was generally supported by the other features of the animal.



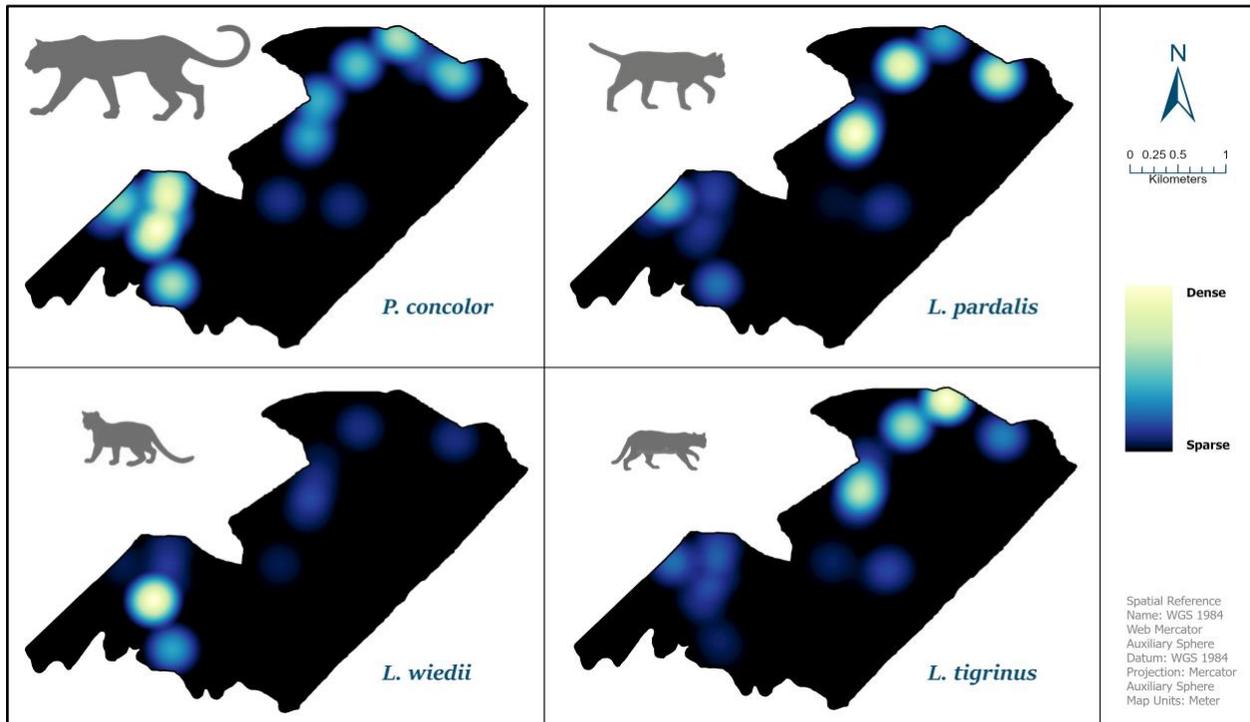
(Figure 5)

Image of melanistic *Leopardus tigrinus* in SL.

Activity & Distribution Patterns

Activity patterns were assessed by hour, month, and temperature. The hourly distribution of felid observations shows primarily nocturnal behavior in all four species, with the Puma having the most daytime activity and a peak in activity earlier in the evening than the other species (Figure A4, Appendix A). This trend is surprising considering both the Puma and Northern Tiger Cat are considered cathemeral but confirms the nocturnal behavior of the Ocelot and Margay. The monthly distribution of observations shows contrasts in annual activity of the species with the Puma and Northern Tiger Cat having a slight peak in activity in the early months of the year (February – April), while the Ocelot and Margay have a distinct peak in observations in the later months (August-October) (Figure A5, Appendix A). This ecosystem has a narrow annual temperature range between about 7-24 degrees Celsius. Despite the small range, the larger bodied felids show a more widespread distribution in activity across the entire temperature range, while the smaller felid species show narrower peaks in activity closer to the average and median temperature (Figure A6, Appendix A).

The KDE maps of the spatial distribution of species observations across camera trapping sites show clear hotspots in felid observations (Figure 6). The Puma shows a higher density of observations in the lower region of the reserve, while the Ocelot has a higher density of observations in the upper part of the reserve. Similarly, the Margay and Northern Tiger Cat show contrasting hotspots of observations with the Margay being seen in the lower region and the Northern Tiger Cat in the upper.

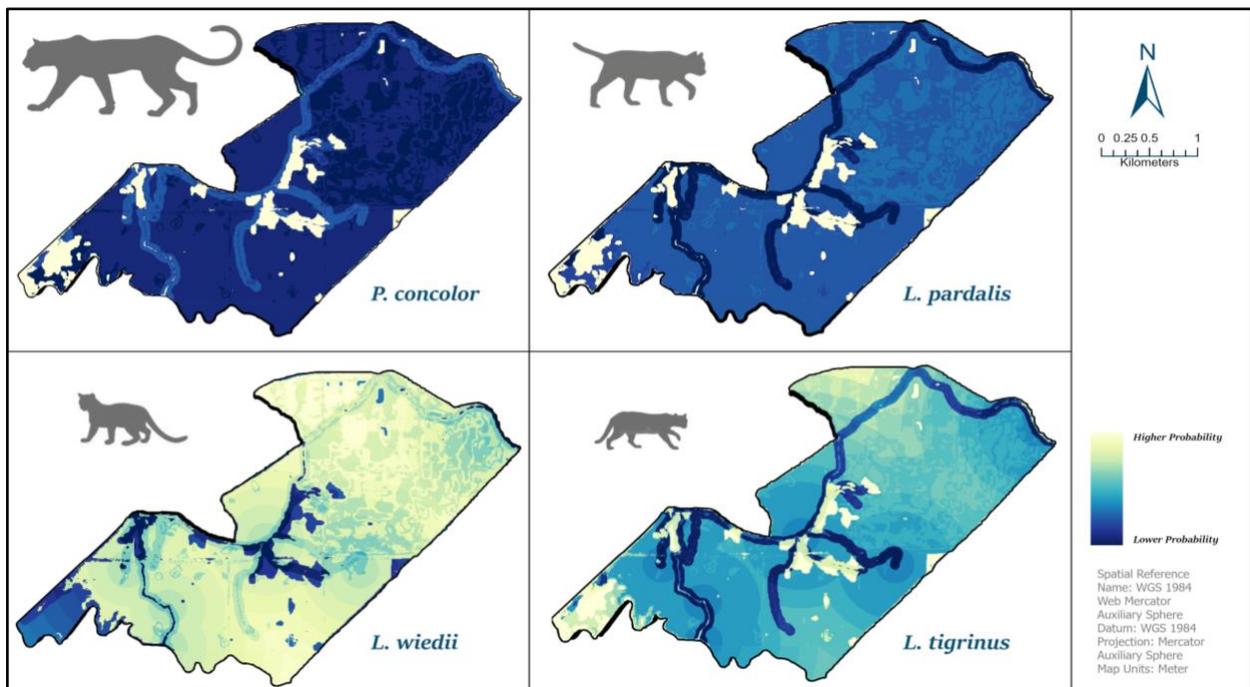


(Figure 6)

KDE maps of felid observations by species. Yellow/light color indicates a greater density of observations, while dark blue/black indicate lower density of observations. Any unmonitored regions automatically display as black - low density (zero observations).

Occupancy & Detection Probability

The model results yielded detection probabilities per week of 10.9% for the puma, 4.44% for the Ocelot, 1.44% for the Margay, and 12.6% for the Northern Tiger Cat. The model indicates that the occupancy and detection probabilities of all four species are strongly related to LULC. Only the Margay and Northern Tiger Cat had significant relationships to the distance from the nearest tourist site (Table B3, Appendix B). Based on the predicted detection probabilities derived from the estimates of the models (Table B2, Appendix B), the Puma, Ocelot, and Northern Tiger Cat all have a higher probability of detection near the pastures and plantations (Figure 7). The Northern Tiger Cat is more likely to be observed in general throughout the reserve. Conversely, the Margay is least likely to be observed near the pastures and plantations with a greater preference for forested areas (Figure 7).



(Figure 7)

Maps of predicted detection probabilities of each species across SL. Yellow/light color indicate a higher probability of detection, while dark blue/black indicates lower probability of detection.

Discussion

Temporal & Spatial Niche Partitioning

The felid species in SL manifested both shared and species-specific spatiotemporal activity patterns. The distinct patterns support the theories of temporal niche partitioning among neotropical felids, specifically between morphologically similar species and mesocarnivores with apex carnivores (Di Bitetti, 2010). The temporal separation of the Ocelot and Puma align with my hypothesis that they compete for resources. In addition to temporal separation, the KDE maps (Figure 6) show contrasting hotspots in species spatial distribution despite the small reserve area, suggesting potential predation avoidance of the puma by the Northern Tiger Cat

which shares a similar temporal distribution with the Puma. This dynamic is also demonstrated with the Ocelot and Margay in SL and could be a result of either competitive avoidance (the “Ocelot effect”) or the Margay avoiding the Ocelot as a predator (de Oliveira, 2010). However, when considering the detection probability predictions across SL (Figure 7), competitive avoidance between the Margay and other species is less likely given the opposite habitat preferences between them. The predicted LULC relationships of the Margay show a preference for forested areas which supports what we know of its arboreal activity and hunting behavior. The higher detection probability of the Puma, Ocelot, and Northern Tiger Cat near plantations is surprising considering a different study found the opposite relationship (Boron, 2020). This other study also included proximity to water and prey abundance, which are main drivers for these species habitat preferences and should be considered in future studies in SL.

The fact that monitoring did not occur throughout SL may have influenced the results because the unmonitored areas are mostly primary forest isolated from human activity from ecotourism. This also limits our ability to assess the impact of human activity on the trails in SL, which was still included in the predicted detection probabilities but based on a study in the Ecuadorian Amazon (Blake, 2017). Furthermore, the LULC data used in the digitization process is from at least 10 years ago and likely needs updating to present more accurate relationships between LULC and felid observation. The results support species preferences for different LULC types, but the models for all species fit best under the assumption of 100% occupancy since the species were observed at most sites.

Hybridization

Given the physical similarities in the three *Leopardus* species, it is impossible to identify the species with absolute certainty. While my *Leopardus* species identification guide (Appendix C) showcases more obvious examples of the traits that distinguish the species, most of the photos were not at a good angle to view every feature or were blurry from the animal’s movement. Additionally, Margay and Northern Tiger Cat are most similar morphologically in the Northwestern Andes compared to other areas where both are prevalent, such as the Amazon or Southern Brazil/Northern Argentina (de Oliveira, 2020). Evidence of a variety of hybridization events between several of the *Leopardus* species has been identified in several regions of South America including the Andean Northern Tiger Cat with Margays and Ocelots, Bolivian tigrina with Geoffrey’s cat (*Leopardus geoffroyi*) (Trigo, 2008), and Brazilian/Uruguayan pampas cat (*Leopardus colocola*) and tigrinas (da Silva Santos 2018). Gaining knowledge of the rate of hybridization between these species in SL through genetic sampling methods will help refine this identification guide as the physical traits are confirmed by genetic species identification. Considering the near threatened and vulnerable status of the Margay and Northern Tiger Cat worldwide (de Oliveira, 2015) (Payan, 2016), we must be able to accurately identify populations of both species to help conserve and protect them.

Implications for Conservation

Apart from the necessity of improving species identification within morphologically similar genera, the two small *Leopardus* species are specialists within this mountainous ecosystem making them especially susceptible to the effects of global climate change (Vale, 2015). In addition to niche shrinkage, many studies of the impacts of climate change on wildlife

hypothesize that as global temperatures rise, species habitat ranges will shift to higher elevations (Chen, 2011). In SL, this presents the risk of Jaguars, which are not currently found at this elevation, moving into the region. This would have potentially detrimental impacts on the Puma as the current apex predator, as well as the prey populations, and the local farmers and their livestock. To prepare for this possibility, SL should continue to monitor these felid species throughout the reserve to further their understanding of the felid's interactions.

Going forward, I would recommend modifying the reserves current camera trap protocol which would improve detection of felids and enable more robust analysis of SL wildlife populations. Setting up camera traps in a grid format with measurements of the angle and distance of detection for the camera will allow SL to calculate population metrics such as abundance and density. Furthermore, setting up an additional camera across from another will capture both flanks of an animal and improve our chances of capturing better quality photos. My hope is that these findings and the species identification guide can be incorporated into the various educational programs at SL and used as a tool to reach their conservation goals.

Acknowledgement

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References

- Blake, J. G., Mosquera, D., Loiselle, B. A., Romo, D., & Swing, K. (2017). Effects of human traffic on use of trails by mammals in lowland forest of eastern Ecuador. *Neotropical Biodiversity*, 3(1), 57-64.
- Boron, V., Xofis, P., Link, A., Payan, E., & Tzanopoulos, J. (2020). Conserving predators across agricultural landscapes in Colombia: Habitat use and space partitioning by jaguars, pumas, ocelots and jaguarundis. *Oryx*, 54(4), 554-563. doi:10.1017/S0030605318000327
- Botts, R. T., Eppert, A. A., Wiegman, T. J., Rodriguez, A., Blankenship, S. R., Asselin, E. M., ... & Mooring, M. S. (2020). Circadian activity patterns of mammalian predators and prey in Costa Rica. *Journal of mammalogy*, 101(5), 1313-1331.
- Byrne, Morgan, and James Golden. "Occupancy Models." *Occupancy Modeling*, 29 Nov. 2021, https://kevintshoemaker.github.io/NRES-746/Occupancy.html#Occupancy_Models.
- Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science*, 333(6045), 1024–1026. <https://doi.org/10.1126/science.1206432>
- Codron, D., Radloff, F. G. T., Codron, J., Kerley, G. I. H., & Tambling, C. J. (2018). Meso-carnivore niche expansion in response to an apex predator's reintroduction; a stable isotope approach. *African Journal of Wildlife Research*, 48(1), 1–16. <https://doi.org/10.3957/056.048.013004>
- da Cunha, C. J., Moreira, D. O., Seibert, J. B., & Gatti, A. Research gaps and trends on the feeding ecology of *Leopardus wiedii* and *Leopardus guttulus*.
- da Silva Santos A, Trigo TC, de Oliveira TG, Silveira L, Eizirik E. Phylogeographic analyses of the pampas cat (*Leopardus colocola*; Carnivora, Felidae) reveal a complex demographic history. *Genet Mol Biol*. 2018;41(1 suppl 1):273-287. doi: 10.1590/1678-4685-GMB-2017-0079. PMID: 29668017; PMCID: PMC5913729.
- de Oliveira, T. G., Tortato, M. A., Silveira, L., Kasper, C. B., Mazim, F. D., Lucherini, M., ... & Sunquist, M. (2010). Ocelot ecology and its effect on the small-felid guild in the lowland neotropics. *Biology and conservation of wild felids*, 559-580.

- de Oliveira, T., Paviolo, A., Schipper, J., Bianchi, R., Payan, E. & Carvajal, S.V. 2015. *Leopardus wiedii*. The IUCN Red List of Threatened Species 2015: e.T11511A50654216. <http://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T11511A50654216.en>
- de Oliveira, T. 2020. Identificación de Felinos por Fototrampeo: una ciencia compleja. Conferencia para la conservación de la Fundación Patino de Santa Cruz. 25/06/2020. Virtual.
- Di Bitetti, M. S., De Angelo, C. D., Di Blanco, Y. E., & Paviolo, A. (2010). Niche partitioning and species coexistence in a Neotropical felid assemblage. *Acta Oecologica*, 36(4), 403-412.
- Easter, T., Bouley, P., & Carter, N. (2020). Intraguild dynamics of understudied carnivores in a human-altered landscape. *Ecology and Evolution*, 10(12), 5476-5488.
- Fiske, Ian, Chandler, Richard (2011). unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. *Journal of Statistical Software*, 43(10), 1-23. URL <https://www.jstatsoft.org/v43/i10/>.
- González-Maya, J. F., Arias-Alzate, A., Granados-Peña, R., Gómez-Hoyos, D. A., Schipper, J., Manjarrés-Morrón, M., & Manjarrés Pinzón, G. (2018). Margays also hide their spots: first records of melanistic *Leopardus wiedii* from Colombia and Costa Rica. *Revista mexicana de biodiversidad*, 89(2), 587-589.
- Graipel, M. E., Oliveira-Santos, L. G. R., Goulart, F. V. B., Tortato, M. A., Miller, P. R. M., & Cáceres, N. C. (2014). The role of melanism in ocellas on the temporal segregation of nocturnal activity. *Brazilian Journal of Biology*, 74, S142-S145.
- Iriarte, J. A., Franklin, W. L., Johnson, W. E., & Redford, K. H. (1990). Biogeographic variation of food habits and body size of the American puma. *Oecologia*, 185-190.
- Kasper, C. B., A. Schneider, and T. G. Oliveira. "Home range and density of three sympatric felids in the Southern Atlantic Forest, Brazil." *Brazilian Journal of Biology* 76 (2016): 228-232.
- Nagy-Reis, M. B., Iwakami, V. H., Estevo, C. A., & Setz, E. Z. (2019). Temporal and dietary segregation in a neotropical small-felid assemblage and its relation to prey activity. *Mammalian Biology*, 95, 1-8.
- NASCIMENTO, F. O., & Feijó, A. (2017). Taxonomic revision of the tigrina *Leopardus tigrinus* (Schreber, 1775) species group (Carnivora, Felidae). *Papéis Avulsos de zoologia*, 57, 231-264.

- Palencia, P., Rowcliffe, J. M., Vicente, J., & Acevedo, P. (2021). Assessing the camera trap methodologies used to estimate density of unmarked populations. *Journal of Applied Ecology*, 58(8), 1583-1592.
- Palmer, Meredith S. "VERY BASIC occupancy analyses with camera trap data". LionStats, 22 Sep. 2019; <https://lionstats.wordpress.com/2019/09/22/very-basic-occupancy-analyses-with-camera-trap-data/#more-139>.
- Payan, E. & de Oliveira, T. 2016. *Leopardus tigrinus*. The IUCN Red List of Threatened Species 2016: e.T54012637A50653881. <http://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T54012637A50653881.en>
- Rodriguez JT, Lesmeister DB, Levi T. Mesocarnivore landscape use along a gradient of urban, rural, and forest cover. *PeerJ*. 2021 Apr 6;9:e11083. doi: 10.7717/peerj.11083. PMID: 33868809; PMCID: PMC8034353.
- Ruiz-García, M., Pinedo-Castro, M., & Shostell, J. M. (2018). Small spotted bodies with multiple specific mitochondrial DNAs: existence of diverse and differentiated tigrina lineages or species (*Leopardus* spp: Felidae, Mammalia) throughout Latin America. *Mitochondrial DNA Part A*, 29(7), 993-1014.
- Seaman, D. E., & Powell, R. A. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, 77(7), 2075-2085.
- Silva-Pereira, J. E., Moro-Rios, R. F., Bilski, D. R., & Passos, F. C. (2011). Diets of three sympatric Neotropical small cats: Food niche overlap and interspecies differences in prey consumption. *Mammalian Biology*, 76(3), 308-312.
- Sustainable tourism: Santa lucía ecolodge: Nanegal. Santa Lucia Ecolodge. (2020). Retrieved August 15, 2022, from <https://www.santaluciaecuador.com/>
- Tirira S, Diego, & Asociación Ecuatoriana de Mastozoología. (2017). A field guide to the mammals of Ecuador: Including the Galapagos Islands and the Ecuadorian Antarctic zone.
- Trigo, T. C., Freitas, T. R. O., Kunzler, G., Cardoso, L., Silva, J. C. R., Johnson, W. E., ... & Eizirik, E. (2008). Inter-species hybridization among Neotropical cats of the genus *Leopardus*, and evidence for an introgressive hybrid zone between *L. geoffroyi* and *L. tigrinus* in southern Brazil. *Molecular ecology*, 17(19), 4317-4333.

- Triguero-Ocaña, Roxana, et al. "Quantifying wildlife-livestock interactions and their spatio-temporal patterns: Is regular grid camera trapping a suitable approach?." *Ecological Indicators* 117 (2020): 106565.
- Trolliet, F., Vermeulen, C., Huynen, M. C., & Hambuckers, A. (2014). Use of camera traps for wildlife studies: a review. *Biotechnologie, Agronomie, Société et Environnement*, 18(3).
- Vale, Mariana & Lorini, Maria Lucia & Cerqueira, Rui. (2015). Neotropical wild cats susceptibility to climate change. *Oecologia Australis*. 19. 63-88. 10.4257/oeco.2015.1901.05.
- Vanderhoff, E. N., Hodge, A. M., Arbogast, B. S., Nilsson, J., & Knowles, T. W. (2011). Abundance and activity patterns of the margay (*Leopardus wiedii*) at a mid-elevation site in the eastern Andes of Ecuador. *Mastozoología neotropical*, 18(2), 271-279.
- Winnie Jr, J., & Creel, S. (2017). The many effects of carnivores on their prey and their implications for trophic cascades, and ecosystem structure and function. *Food Webs*, 12, 88-94.

Appendix A

Figure A1: Map of camera trap placements across SL.

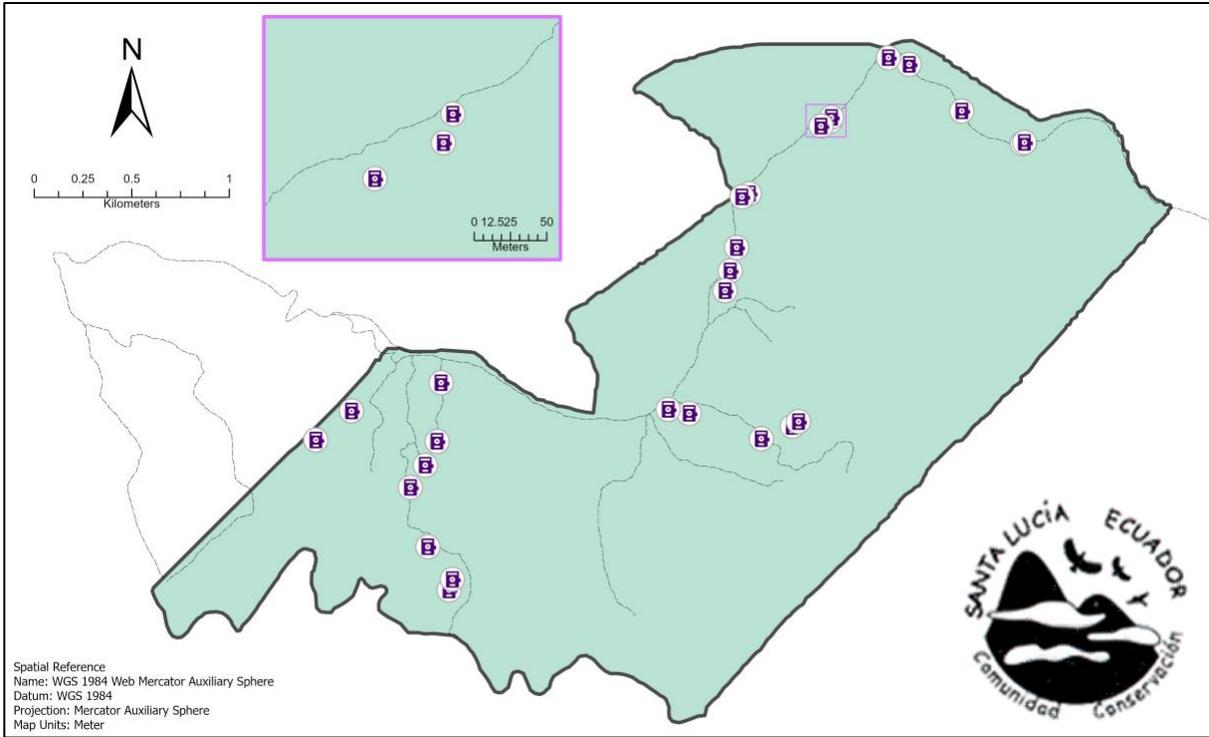


Figure A2: Image of map of SL used for digitization of all reserve features.

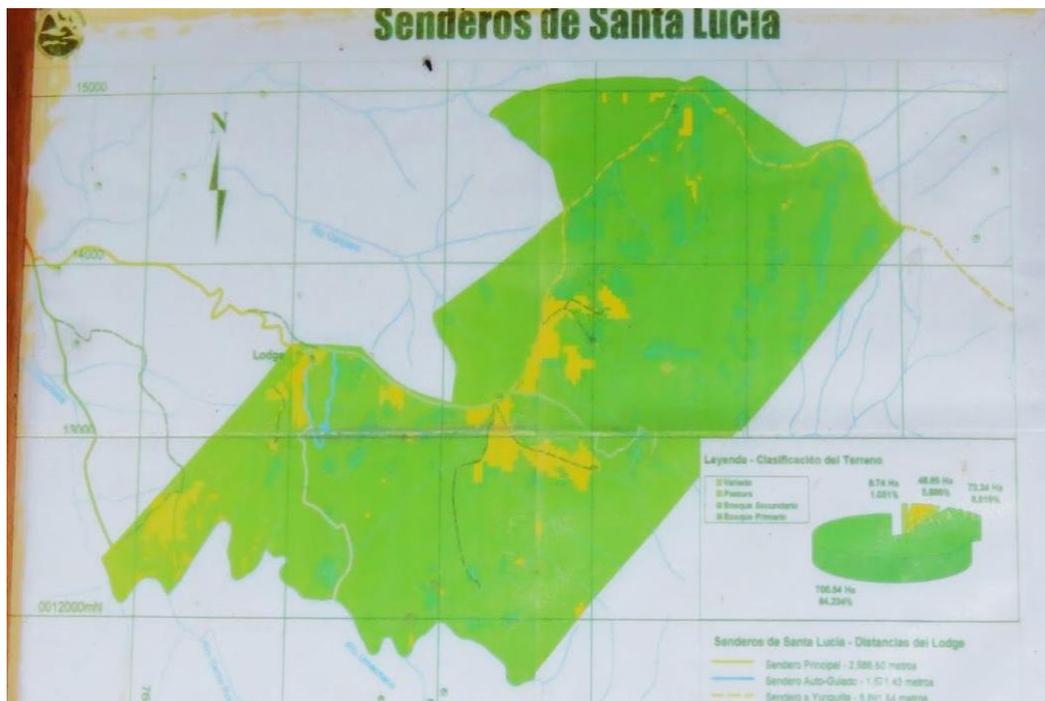


Figure A3: Three-step reclassification process of LULC raster from digitized image.

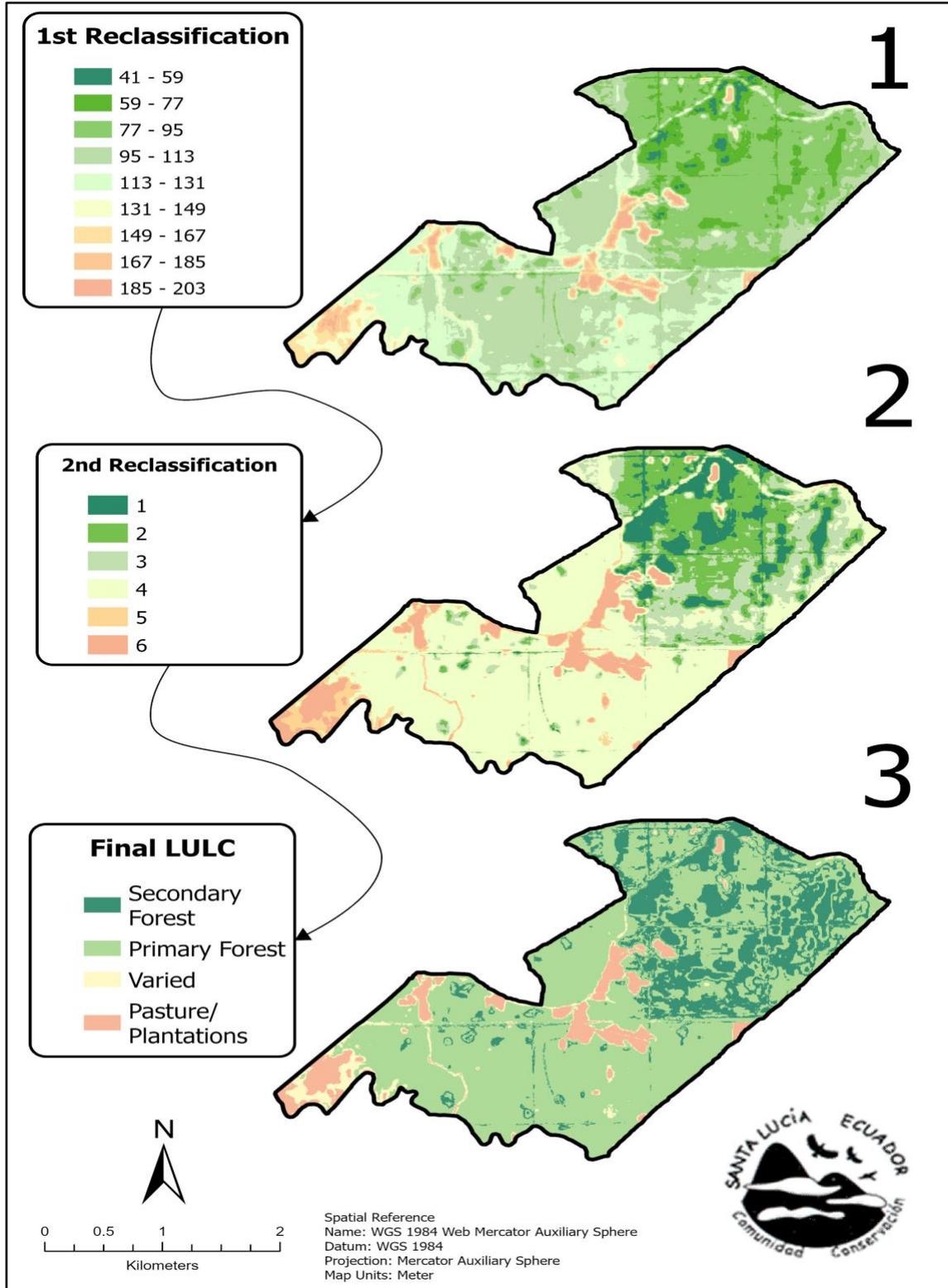


Figure A4: Density plot of observations by hour of day starting at sunrise.

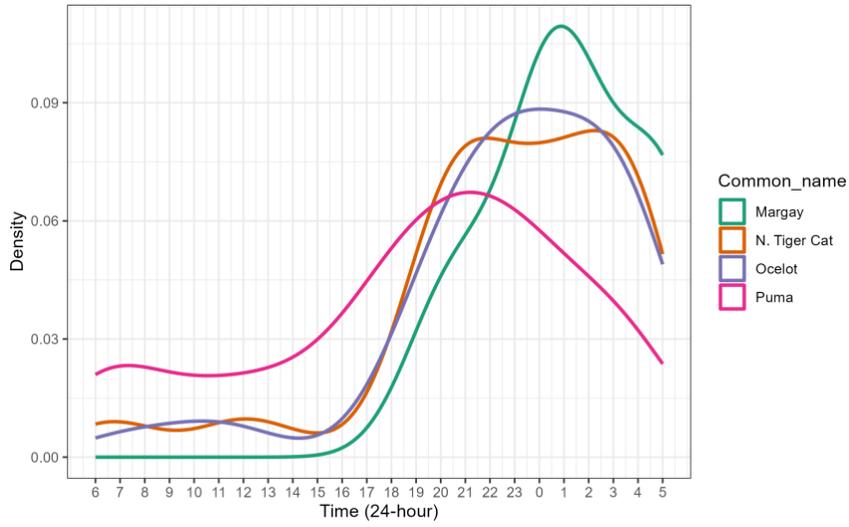


Figure A5: Density plot of observations by month.

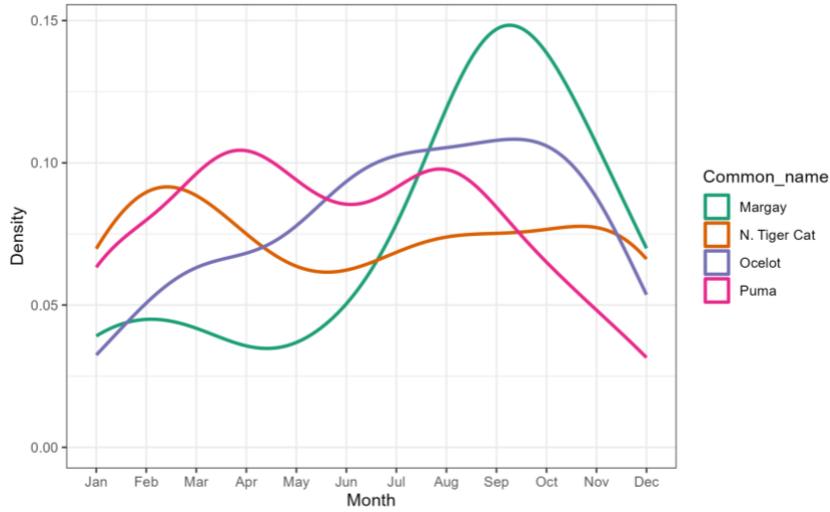
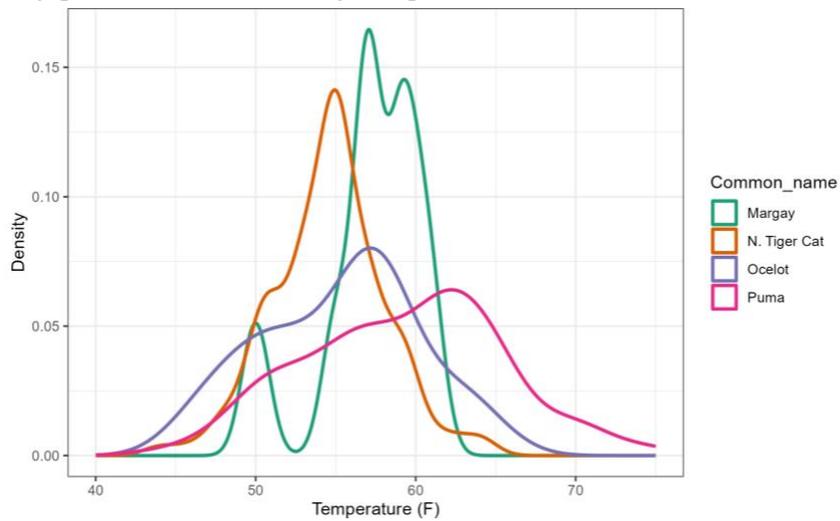


Figure A6: Density plot of observations by temperature at time of observation.



Appendix B

Table B1: Best fit models of site variables and AIC value for each species.

Species	Best Model	AIC
<i>Puma concolor</i>	~ LULC ~ 1	1814.47
<i>Leopardus pardalis</i>	~ LULC ~ 1	917.49
<i>Leopardus wiedii</i>	~ Distance_to_Nearest_Tourist_Site + LULC ~ 1	379.66
<i>Leopardus tigrinus</i>	~ Distance_to_Nearest_Tourist_Site + LULC ~ 1	1910.14

Table B2: Predicted probability of detection based on model variables (0.1120 = 11.2%).

Covariate	Feature	<i>Puma concolor</i>	<i>Leopardus pardalis</i>	<i>Leopardus wiedii</i>	<i>Leopardus tigrinus</i>
LULC	Primary Forest	0.1120	0.0371	0.0209	0.0821
	Secondary Forest	0.0895	0.0611	0.0044	0.1074
	Varied	0.1024	0.0244	0.0000	0.1974
	Pasture/Plantation	0.2558	0.3487	0.0000	0.4724
Distance to Nearest Tourist Site (m)	0	NA	NA	0.0327	0.0822
	200	NA	NA	0.0249	0.0878
	400	NA	NA	0.0189	0.0938
	600	NA	NA	0.0143	0.1001
	800	NA	NA	0.0108	0.1068
	1000	NA	NA	0.0082	0.1139
	1200	NA	NA	0.0062	0.1214
	1400	NA	NA	0.0046	0.1293
	1600	NA	NA	0.0035	0.1377
	1800	NA	NA	0.0026	0.1465
	2000	NA	NA	0.0020	0.1558

Table B3: P-values of covariates from best fit models for each species.

Covariate	<i>Puma concolor</i>	<i>Leopardus pardalis</i>	<i>Leopardus wiedii</i>	<i>Leopardus tigrinus</i>
Distance to Nearest Tourist Site (m)	NA	NA	9.390e-6	0.0053
LULC	Primary Forest	0.0022	2.232e-14	0.8946
	Secondary Forest	0.0051	1.894e-8	0.9150
	Varied	0.0012	1.299e-11	0.9884
	Pasture/Plantation (Intercept)	0.0042	0.0508	0.8454

Appendix C

Guide to identify Ocelot, Margay, and Northern Tiger Cat in Santa Lucia in English and Spanish.

LEOPARDUS SPECIES

SANTA LUCIA *af* LUCIA

OCELOT

Leopardus pardalis



SIZE

Medium-Large
Thicker, muscular body

SPOTS

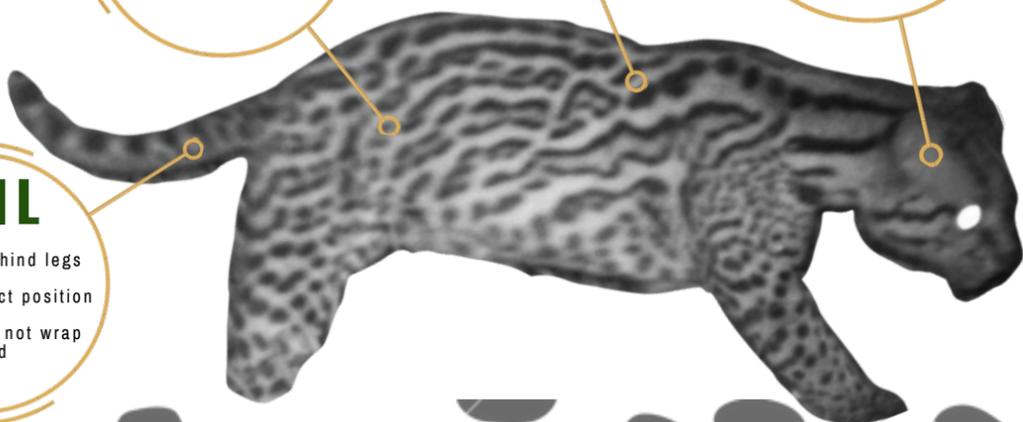
Large & Long Rosettes
Rosettes form a strip pattern along the flank
"Pawprint" Rosettes

HEAD

Large head in proportion to body
Long snout
Long forehead
Wide/thick jaw

TAIL

Shorter than hind legs
Held up in erect position
Tail spots do not wrap around



NORTHERN TIGER CAT

Leopardus tigrinus



COLOR

Melanism:
Black coat color with spots often still visible

SPOTS

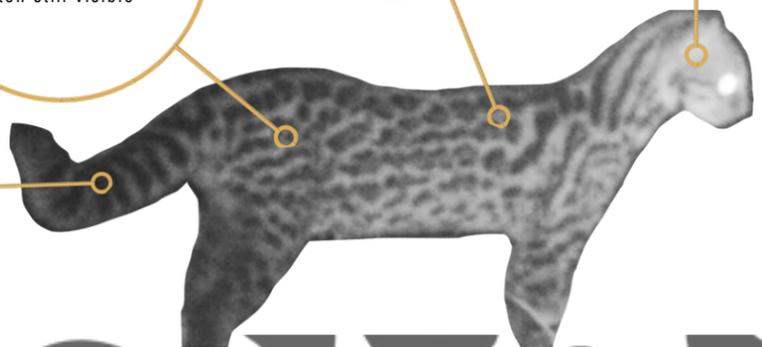
Small Rosettes
Rosettes are close together & blend together
"Donut"/"Cluster" Rosettes

HEAD

Small head
Proportional to body
Straight/Triangular shape from the front
Convex facial profile

TAIL

Longer or equal to length of hind legs
Tail rings
"Fluffy" appearance



MARGAY

Leopardus wiedii



TAIL

Longer than hind legs
Tail rings
Thin

SPOTS

Medium-sized Rosettes
Rosettes are distinct
Slightly more separation between Rosettes
"Donut" Rosettes

HEAD

Slightly large head in proportion to body
Concave facial profile
Round face shape from the front
Large ears & eyes

HEIGHT

Long legs
Thinner, delicate body



LAS ESPECIES LEOPARDUS

de

SANTA LUCIA

OCELOTE

Leopardus pardalis



TAMAÑO

Mediano
Cuerpo grueso y muscular

MANCHAS

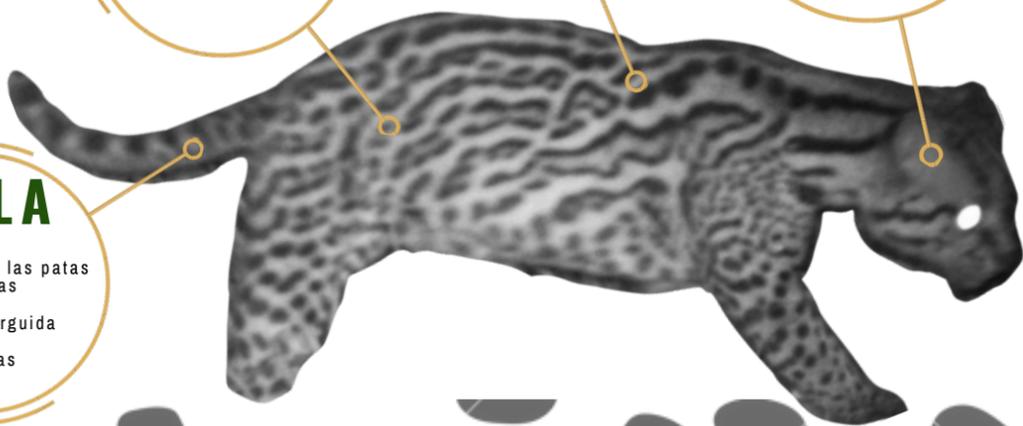
Rosetas grandes y largas
Las rosetas forman un patrón de rayas en la ijada
Estilo de "Huella"

CABEZA

La cabeza es grande en proporción de cuerpo
El morro largo
La frente larga
Mandíbula gruesa

COLA

Más corto que las patas traseras
Posición erguida
Manchas



ONCILLA

Leopardus tigrinus



COLOR

Melanismo:
Pelaje negro pero las manchas siguen siendo visibles

MANCHAS

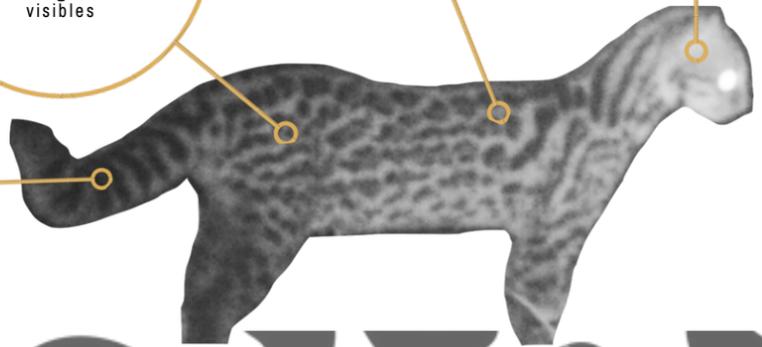
Rosetas pequeñas
Rosetas densas y mezclado
Estilo de "Dónut"/"Cluster"

CABEZA

Cabeza pequeña
Es proporcional al cuerpo
Cara triangular
Perfil facial convexo

COLA

Egual o más largo que las patas traseras
Anillos
Parece "esponjoso"



MARGAY

Leopardus wiedii



COLA

Más largo que las patas traseras
Anillos
Delgada

MANCHAS

Rosetas medianas
Rosetas son distintas
Rosetas son más separadas
Estilo de "Dónut"

CABEZA

La cabeza es un poco grande en proporción al cuerpo
Perfil facial cóncavo
Cara redondo
Orejas y ojos grandes

ESTATURA

Patas largas
Cuerpo delgado y delicado

