Single-Season Occupancy Analysis to Investigate Spatial Segregation of Jaguar and Puma in Costa Rica

by

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ABSTRACT

Jaguar (*Panthera onca*) and puma *(Puma concolor*) are the largest predators in Costa Rica and often share the same habitat and many of the same prey species. Competitive exclusion theory predicts that two species can coexist only if they use different resources, which can be accomplished by partitioning their hunting effort in time and space. Previous studies have implicated both spatial and temporal segregation, with puma often avoiding the dominant jaguar. To investigate whether jaguar and puma avoid each other via spatial versus temporal segregation, I performed an occupancy analysis using single-species, single-season occupancy models with covariates using camera trap records collected from 15 survey locations in Costa Rica over 12 years. I predicted that jaguar presence would influence puma habitat use and avoidance behavior. The occupancy analysis revealed that the habitat use of both jaguar and puma was most influenced by the presence of the other species. Jaguar presence was the covariate with the strongest influence on habitat use of puma (ΔAIC = 0.0), while the presence of puma was the most important covariate influencing the habitat use of jaguar (ΔAIC = 0.0). Environmental covariates that influenced habitat use included forest cover, elevation, and patch size measures. These results provide evidence that spatial segregation is a key factor regulating interspecific competition between these top predators. Previous research has also revealed the importance of temporal segregation in enabling the coexistence of jaguar and puma, with Costa Rican jaguar being more active during daylight hours than puma, which are more nocturnal. I conclude that jaguar and puma can coexist within overlapping habitats through a combination of spatial and temporal segregation.

INTRODUCTION

The jaguar (*Panthera onca*) and puma (*Puma concolor*) are top predators widely present in Mesoamerica and inhabiting a variety of landscapes (Sanderson et al. 2002, LaBarge et al. 2021). As predators, they play a crucial ecological role by regulating and limiting mesopredator and prey species (Labarge et al. 2021). Jaguar and puma have a significant top-down influence on the structure and functionality of ecosystems by controlling herbivore levels which in turn reduces the pressure they put on plants (Foster et al. 2013), thus enabling the world to be green, as proposed by the 'green world hypothesis' (Hairston et al. 1960). Jaguar and puma are sympatric throughout their range, utilizing similar areas and niches (Scognamillo et al. 2003). Niche partitioning has been described as a process whereby natural selection drives competing species into different patterns of resource use or different ecological niches. This suggests that species that exhibit overlapping ecological roles will be pushed to separate niches. This reduces competition and promotes coexistence among species (MacArthur 1958). Species that inhabit the same areas may experience competitive exclusion, in which two species cannot inhabit the same niche because one will consistently outcompete the other (Urban 2009). MacArthur and Levins (1967) predicted that, to overcome the challenges that sympatric species face, species must divide their resources to avoid extinction by competition (limiting similarity theory). As apex predators with similar ecological roles inhabiting many of the same areas, jaguar and puma must exhibit some level of coexistence with each other for them both to continue living in these areas. Coexistence may be possible through several different means related to selection for one or more variables (Scognamillo et al. 2003). Competing predators may coexist by selecting different prey species or different prey sizes (Gittleman 1985; Karanth & Sunquist 1995, 2000; Taber et al. 1997). They may additionally exhibit different activity patterns (Romero-Munoz et al. 2010), choose different habitats (Palomares et al. 1996; Fedriani et al. 1999), or exhibit differential use of space (Creel & Creel 1996; Durant 1998; Palomares et al. 1996; Sollmann et al. 2012).

Panthera onca

The jaguar belongs to the family Felidae and genus Panthera and is the largest felid species in the Americas. As the third largest cat species in the world, following the tiger (*Panthera tigris*) and lion (*P. leo*), the jaguar measures between 1.54 to 2.41 m in length and weighs from 31 to 158 kg (Emmons 1997). The mean body weight of the jaguar varies depending on location, and females weigh less than males (Sunquist & Sunquist 2002). The jaguar's dominant coat is characterized by a tan coloration and covered in rosettes (black interrupted outer rings that surround solid black dots). Jaguars also exhibit a melanistic variation, which is exhibited by black background coloration, although the rosettes are still present and may be seen in the right light (Sunquist & Sunquist 2002). Jaguars typically live in habitats with dense forest cover, which is evidenced by their tropical distribution from northern Mexico through Argentina. Their habitats primarily incorporate primary and secondary forest with bodies of water and a sufficient selection of prey (Swank and Teer 1989, Sanderson et al. 2002). Depending on sex, season, and resources, their home range varies between 20 km^2 to over 100 km^2 (Quigley et al. 2018). Jaguars are known to be solitary hunters and opportunistic predators, which means they select their prey based on availability in their habitat (Sunquist & Sunquist 2002, Weckel et al. 2005). The jaguar's diet consists of mammals, reptiles, and birds, either wild or domestic animals. Some frequent species within their diet include armadillo and ungulates. According to Oliveira & Medellin (2002), jaguar tend to consume larger prey species than puma, although both eat varying sizes. Studies also suggest that larger predator species are constrained by the size of available prey (Sunquist & Sunquist 1989). The jaguar is currently listed as Near

Threatened on the International Union for Conservation of Nature (IUCN) Red List (Quigley et al. 2018).

Puma concolor

The puma also belongs to the family Felidae, but from the Puma lineage and more closely related to jaguarundi (*Herpailurus yagouaroundi*) and cheetah (*Acinonyx jubatus*). Depending on sex, puma have been recorded to measure around 1.09 to 1.23 m and weigh between 28 to 85 kg, but others were recorded as weighing over 100 kg (Torre & Rivero 2017; Sunquist & Sunquist 2002). Puma live in a variety of habitats and have the widest distribution of any native American mammal (Nowak 1999). Their range includes all forest types as well as lowland and montane desert. They typically prefer a habitat with dense vegetation, but can live in open habitats. Their distribution is from Canada and Alaska in the north through southern Argentina and Chile in the south (Nielsen et al. 2015). The puma's home range is mostly dependent on prey density and migration, and varies between 32 km^2 and 1,031 km^2. Their diet typically consists of small to medium sized prey, although they sometimes consume large prey. North American puma have a larger body size and consume larger prey than tropical puma (Iriarte et al. 1990). Species included in their diet are feral pigs, raccoons, armadillos, and particularly in North America, deer. The puma is currently listed as Least Concern on the IUCN Red List (Nielsen et al. 2015).

Harmsen et al. (2009) conducted a camera trap study of interindividual interactions among jaguar and puma. They presented evidence of temporal avoidance between jaguar and puma. While the two species would use the same habitat locations and had the same activity schedules, they avoided coincident times (temporal segregation). One likelihood of this behavior is that the smaller-bodied pumas would avoid jaguars, however the data could not reveal if avoidance was mutual.

A study by Botts et al. (2020) indicated that jaguar and puma had significantly different temporal activity patterns, although they exhibited modest temporal overlap. Both were cathemeral (active both day and night), but jaguar were more diurnal than puma. Jaguar and puma may experience intraguild competition due to competition for the same prey, which implies that they exhibit dietary partitioning.

These prior studies indicate that jaguar and puma may exhibit both temporal segregation and a level of temporal overlap while engaged in dietary competition. I therefore sought to investigate the potential for spatial segregation in jaguar and puma populations in Costa Rica to fill the gap in our understanding of how these top predators interact spatially. Previous studies have indicated that jaguar and puma are generally spatially segregated, often at the microhabitat level (Contreras-Diaz et al. 2021; Foster et al.; Harmsen et al. 2009; Herrera et al. 2018; Palomares et al. 2016; Scognamillo et al. 2003; Sollmann et al. 2012). Several studies have indicated that puma actively avoid jaguar (Harmsen et al. 2009; Romero-Munoz et al. 2010; Sollmann et al. 2012), which makes sense because jaguar are larger and would be the dominant species. To investigate whether jaguar and puma avoid each other via spatial versus temporal segregation, I performed occupancy analysis using single-species, single-season occupancy models with covariates using camera trap records collected from 15 survey locations in Costa Rica over 12 years. I predicted that jaguar presence would influence puma habitat use and avoidance behavior. Understanding the influence of jaguar presence on puma behavior and habitat choice will contribute to the design and implication of conservation policies for these big cats. Overall, understanding these top predators' habitat preferences is important for conservation efforts as it allows us to be aware of where they can be found and which areas need protection.

METHODS

Data Collection

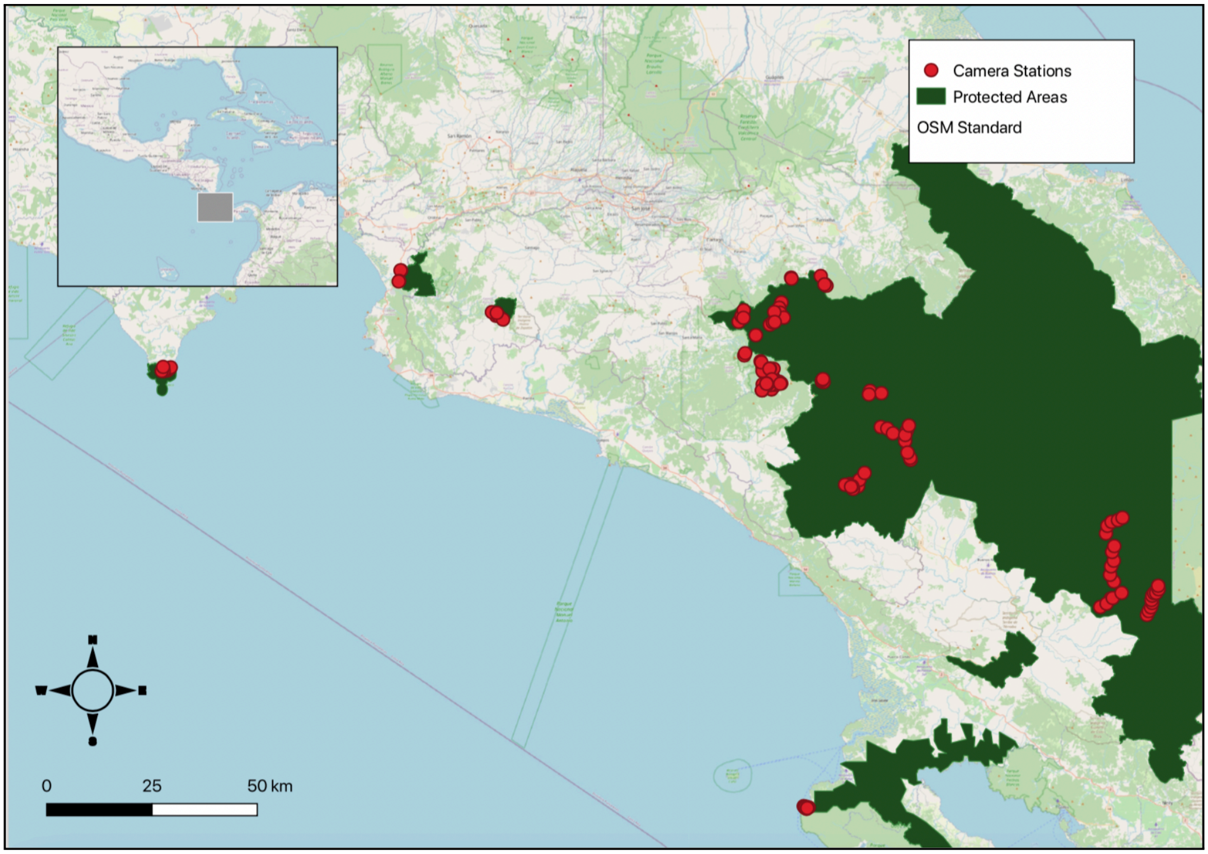

Figure 1. Camera stations used for the study of jaguar and puma within Costa Rica. The gray window gives the larger context of the location of Costa Rica within Mesoamerica. Red dots indicate camera stations and the dark green indicates protected areas. Base map originates from OpenStreetMap and camera station coordinates are projected in WGS 84. Figure courtesy of Emily Bohnet, Sarah Turcic, and Dr. Daniel Gomes Da Rocha.

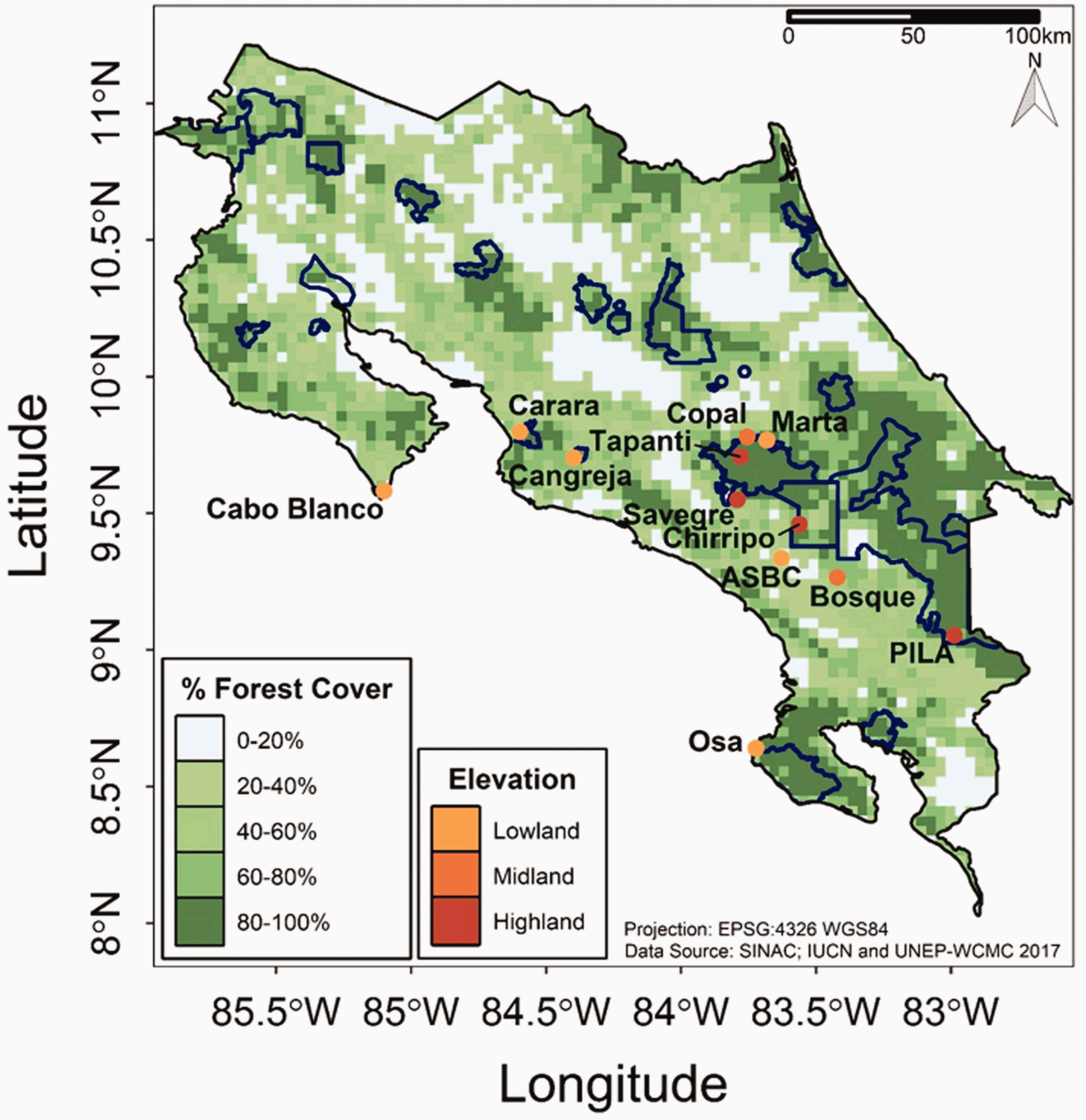

Figure 2. Survey sites used for the study of jaguar and puma in Costa Rica. Camera stations were placed within these sites. Forest cover is shown in green and elevation of sites in orange. Figure courtesy of Ryan Botts, Amy Eppert, and Michael Mooring.

Data for jaguar and puma came from camera trap records collected between 2010–2021. Figure 1 shows the distribution of the camera trap stations throughout Costa Rica. The study areas were primarily located in the high-elevation tropical montane forests of the western Talamanca Cordillera of Costa Rica, with additional survey sites located along the Pacific

Lowlands. Data for this study were collected at the following sites (Figure 2): Alexander Skutch Biological Corridor (ASBC), Corredor Biológico Quetzal Tres Colinas, Chirripó National Park, El Copal Reserve, Cerro Kamuk, La Marta National Wildlife Refuge, Campanario Biological Station, La Amistad International Park, Carara National Park, La Cangreja National Park, Savegre Valley, Tapantí National Park, and Reserva Forestal Río Mach, Sector Villa Mills. These study sites range in elevation from 20 meters to more than 3500 meters above sea level. In Costa Rica, May through November is a distinct wet season while December through April is the dry season. The average annual rainfall at the survey sites was between 3000–8000 mm and the average temperature was between 10–20 °C in the tropical montane forest and 24–32 °C in the Pacific lowlands (Botts et al. 2020). Across these study sites, 141 camera stations (Bushnell Trophy Cam) were deployed along trails. Large mammals such as jaguar and puma typically prefer to travel along trail systems as the most energy efficient means of travel (Harmsen et al. 2010). Cameras were enclosed in a protective case and placed approximately 1 meter above the ground along trails. Each camera was equipped with a scent station consisting of a PVC pipe holding a sponge to which was applied an attractant, Calvin Klein's Obsession for Men (Calvin Klein Inc., New York, NY, USA). The purpose of the attractant was to cause animals to pause within the camera's field of vision to explore the scent, thereby ensuring a clear photo without attracting animals not already on the trail (Braczkowski et al. 2016). The data collected from the camera traps includes species, time of day, and location, among other variables. Cameras were monitored year-round by local collaborators, including national park officials, refuge staff, and community volunteers. For each of these sites, the number of independent jaguar and puma records was determined. Independent records were photos of the same individual or species taken at least 30 min apart from other such records so as to avoid pseudoreplication (Hurlbert 1984).

Covariates

For the occupancy analyses of jaguar and puma, 15 covariates were included: elevation (meters) (GPS), HFI (human footprint index) (Venter et al., 2016), forest cover, NPP (net primary production) (Earth Resources Observation and Science Center 2018), distance to road (meters), distance to river (meters), edge density, patch density, disjunct core (a measure of fragmentation), NDVI (normalized difference vegetation index) (Collection 2 Landsat 8-9 OLI/TIRS), average minimum temperature (°C) (Fick & Hijmans 2017), average maximum temperature (°C) (Fick & Hijmans 2017), average monthly precipitation (mm) (Fick & Hijmans 2017), puma abundance, and jaguar abundance.

To analyze the impact of the two felid species on each other, I created covariates based on the relative abundance index (RAI) of puma and jaguar to estimate the level of competition posed by the other species in a given survey region. For the jaguar occupancy model, I created the puma abundance covariate, and for the puma occupancy model, I created the jaguar abundance covariate. The RAI is calculated as the number of independent detections for each site divided by the total effort for each site (number of days that camera was running) multiplied by 1000 to create a convenient value. Note that the RAI values were grouped by site. This means that the number of records at one site was divided by the combined camera days of all stations within that site. Therefore, 15 unique values were calculated for jaguar abundance and 15 unique values were calculated for puma abundance. For example, for a site with 53 independent puma detections and a total effort of 7039 days, the puma abundance covariate index value for the site is $\frac{53}{7039} \times 1000 = 7.53$.

Table 1. An overview and descriptions of all covariates used in this study.

Covariate	**Description**
Average Maximum Temperature	The average maximum temperature in degrees Celsius
Average Minimum Temperature	The average minimum temperature in degrees Celsius
Disjunct Core	A cell is defined as a core if the cell has no neighbor with a different value than itself. This value counts the disjunct core area, which is a 'patch within the patch' containing only core cells.
Distance to River	The distance (in meters) each camera station is from the nearest river
Distance to Road	The distance (in meters) each camera station is from the nearest road
Edge Density	The edge density equals all edges in the landscape in relation to the landscape area. Landscape edge (m) divided by total landscape area (m^2)
Elevation	The height (in meters) above sea level at each camera station
Forest Cover	The percent coverage of forest, determined by satellite images
HFI	Index for cumulative human presence in the environment, incorporating population density, infrastructure, agriculture, roads, and electric power.
Jaguar	The relative abundance index of jaguar, calculated by dividing jaguar records by camera effort and multiplying by 1,000
NDVI	Normalized difference vegetation index is a comprehensive index that indicates the vegetation levels in a given area via various satellite bands. For this study, bands 4 and 5 were used.
NPP	Net primary production signifies the production of plant biomass
Null	Null model (no covariate)
Patch Density	Number of patches per landscape area (m^2). PD is an 'aggregation metric'. It describes the fragmentation of the landscape.
Precipitation	Average monthly rainfall (mm) calculated from the average of the 12 monthly average rainfall readings at each station
Puma	The relative abundance index of puma, calculated by dividing puma records by camera effort and multiplying by 1,000

Occupancy Modeling

After collecting and processing the camera trap data, an analysis was performed using the R programming language (R Core Team 2021). Single-season single-species occupancy modeling was performed with a time window of four months for each camera station to abide by the closure assumptions. Occupancy models were performed by creating detection tables of site-by-occasion detections, with 0 = non-detection and 1 = detection. To account for imperfect detection in occupancy modeling, the R package "unmarked" was used (Fiske and Chandler 2011). The influence of the covariates on jaguar or puma was compared using the Akaike Information Criterion (AIC). Models with a ΔAIC ≤ 2 were considered to have substantial empirical support (Burnham and Anderson, 2002). Plots were created in the R package "ggplot" (Wickham 2016) to display the relationship between covariates and jaguar and puma occupancy.

RESULTS

Panthera onca

Jaguar were recorded at 9 of the 15 study sites. The puma RAI covariate was the best fit model for jaguar occupancy, with the lowest AIC value of all covariates. Puma RAI showed a negative correlation with jaguar occupancy, with a statistically significant p-value of 0.039. The second top covariate was forest cover, which had a negative correlation and statistically significant p-value equal to 0.032. Table 2 provides a summary of the occupancy model results for jaguar.

Table 2. Occupancy model results for the covariates investigated with jaguar. AIC refers to the Akaike information criterion and p-value gives significance of plot correlations.

JAGUAR OCCUPANCY

Covariate	**AIC**	**ΔAIC**	**p-value**
Puma RAI	277.80	0.00	0.039
Forest Cover	279.50	1.70	0.032
Edge Density	280.04	2.25	0.022
Patch Density	280.57	2.78	0.037
HFI	281.86	4.06	0.051
Disjunct Core	283.29	5.50	0.152
NDVI	283.38	5.59	0.138
Null	283.44	5.65	<0.01
NPP	283.77	5.97	0.248
Distance to River	284.40	6.60	0.359
Distance to Road	285.10	7.31	0.575
Average Maximum Temperature	285.23	7.44	0.647
Precipitation	285.26	7.46	0.583
Average Minimum Temperature	285.42	7.62	0.869
Elevation	285.44	7.64	0.969

The following figures show the trends of these two top covariates and how they are suggested to relate with jaguar occupancy. Figure 3 reveals the correlation between puma relative abundance index and jaguar occupancy probability, denoted as habitat use. As puma abundance increases, the probability of a jaguar inhabiting that area decreases.

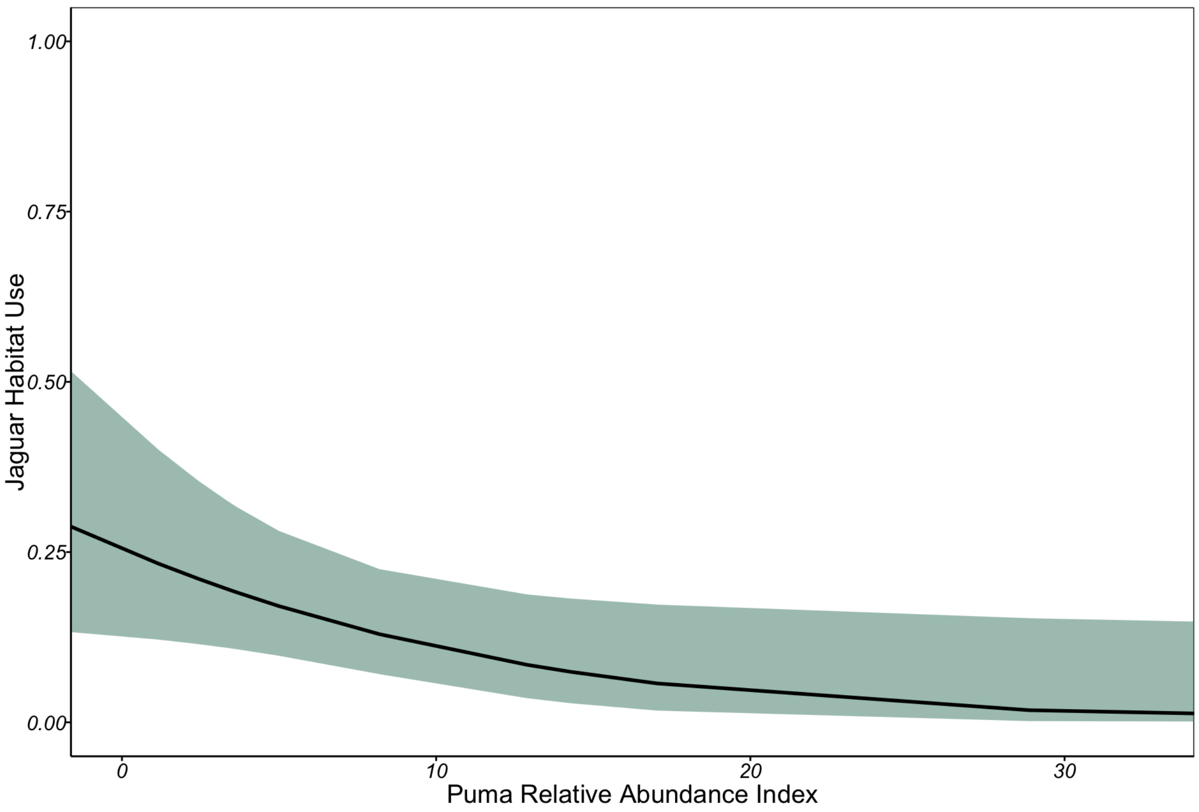

Figure 3. The relationship between puma RAI and the probability of jaguar occupancy, denoted as habitat use.

Figure 4 reveals a negative trend in forest cover and jaguar habitat use. As forest cover increases, the probability of jaguar occupancy decreases.

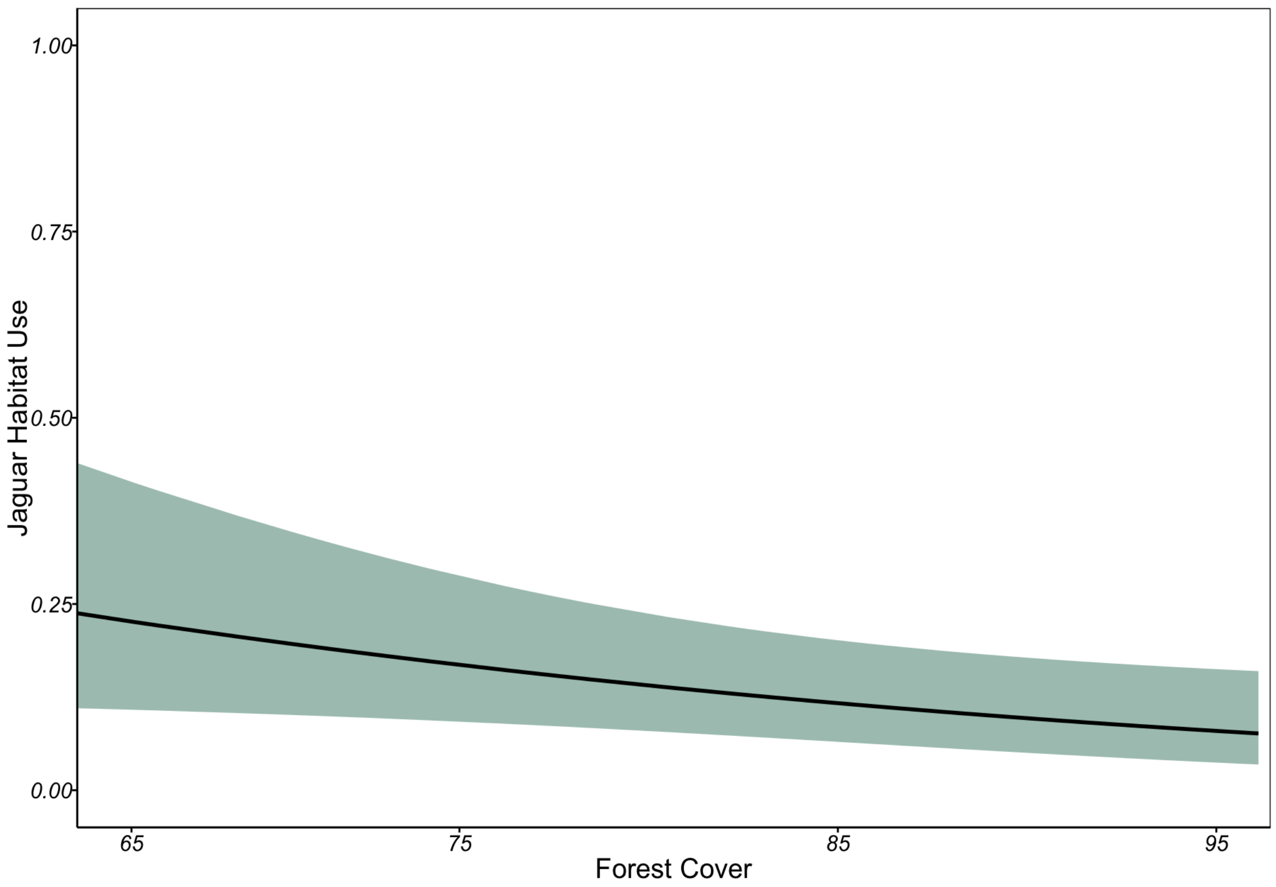

Figure 4. The relationship between forest cover and the probability of jaguar occupancy, denoted as habitat use.

Puma concolor

Puma were recorded at 13 of the 15 study sites. The jaguar RAI model was the top covariate for the puma occupancy model, having the lowest AIC and ΔAIC values. Showing a negative correlation with puma occupancy, jaguar RAI had a p-value of 0.059. The second top covariate for puma occupancy was elevation, which also had a negative correlation and a p-value of 0.126. The p-values for both models were not statistically significant. Table 3 provides a summary of the puma occupancy model results.

Table 3. Occupancy model results for the covariates investigated with puma. AIC refers to the Akaike information criterion and p-value gives significance of plot correlations.

PUMA OCCUPANCY

Covariate	**AIC**	**ΔAIC**	**p-value**
Jaguar RAI	1093.21	0.00	0.059
Elevation	1094.60	1.39	0.126
Null	1095.03	1.82	0.612
Average Minimum Temperature	1095.36	2.15	0.203
Average Maximum Temperature	1095.55	2.34	0.230
Patch Density	1095.88	2.67	0.309
Forest Cover	1096.17	2.96	0.362
Precipitation	1096.32	3.11	0.376
NDVI	1096.32	3.11	0.406
Distance to River	1096.44	3.23	0.437
HFI	1096.81	3.60	0.646
Distance to Road	1096.96	3.75	0.799
NPP	1096.98	3.77	0.823
Edge Density	1096.99	3.78	0.842
Disjunct Core	1097.00	3.79	0.874

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The following figures show the relationship between these top two covariates and the probability of puma occupancy, or their habitat use. Figure 5 reveals a negative trend in jaguar relative abundance and puma probability of occupancy, meaning puma habitat use decreases as jaguar abundance increases.

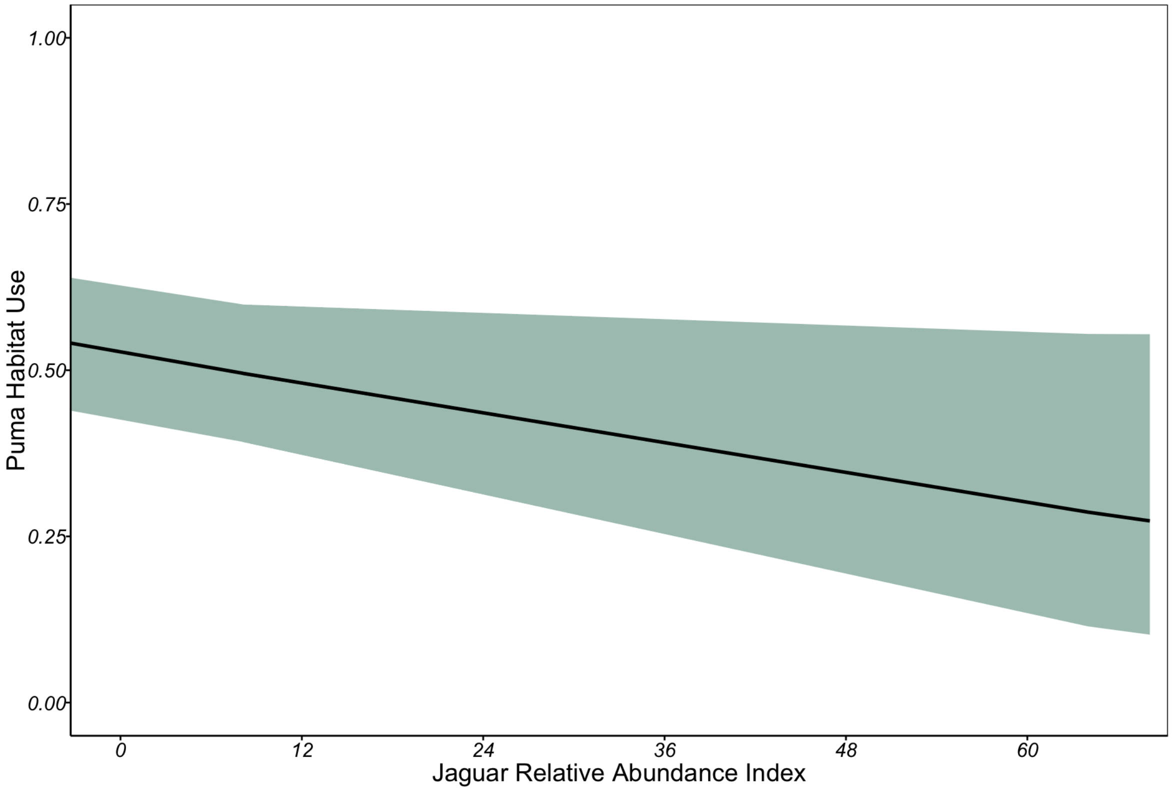

Figure 5. The relationship between jaguar RAI and puma probability of occupancy, denoted as habitat use.

Figure 6 shows a negative relationship between elevation and puma probability of occupancy. Puma tend to inhabit areas of lower elevation.

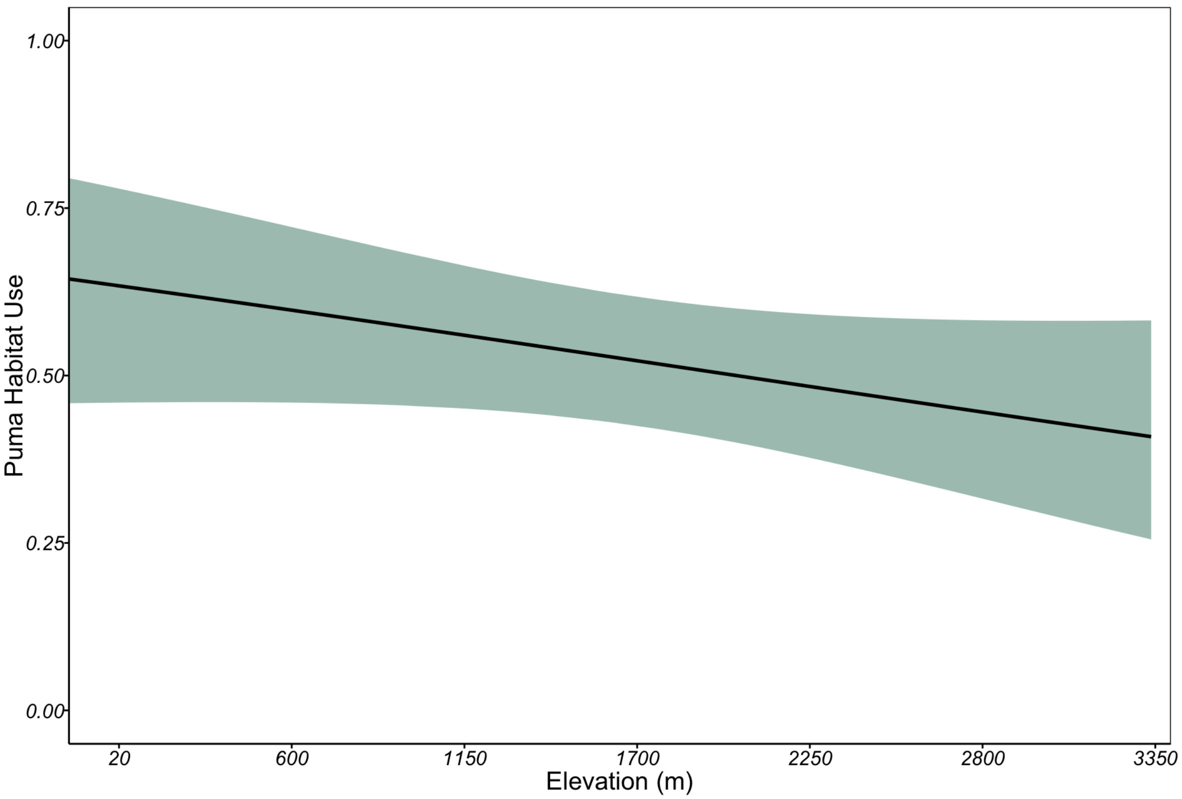

Figure 6. The relationship between elevation and puma probability of occupancy, denoted as habitat use.

DISCUSSION

Jaguar and puma have coexisted together in many different habitats, areas, and timelines (Sanderson et al. 2002, LaBarge et al. 2021). Since they live in a wide area in the Americas and coexist in many of the same locations, it is expected that they will share different resources. To better understand how they can coexist, I sought to explore the relationship between these two big cats specifically within Costa Rica. Previous studies have suggested that species inhabiting the same niche may be able to coexist through one or multiple means. These include exhibiting different temporal activity patterns (Romero-Munoz et al. 2010), selecting different prey species (Gittleman 1985; Karanth & Sunquist 1995, 2000; Taber et al. 1997), selecting different habitats (Palomares et al. 1996; Fedriani et al. 1999), or using different spaces by way of spatial segregation (Creel & Creel 1996; Durant 1998; Palomares et al. 1996; Sollmann et al. 2012). A study by Romero-Munoz et al. (2010) researched the activity patterns of jaguar and puma. They found a statistically significant difference in their activity patterns, which indicates temporal segregation. They did not find any trends of activity following prey species, suggesting that the segregation was influenced by avoidance behavior between the two species. However, another study indicates that patterns of jaguar and puma habitat use were best explained by prey availability, rather than habitat structure or species interactions (Santos et al. 2019). Prey abundance was the most important indicator for the felids' spatial and temporal partitioning. Sollmann et al. (2012) found a difference in space use by jaguars and pumas in Brazil, showing that spatial avoidance and differences in habitat use can both take place between the species. Evidence of interspecific segregation was seen in a study by Harmsen et al. (2009). Jaguar and puma avoided each other more than they avoided conspecifics, indicating a level of interspecific competition. Additionally, they avoided using the same location at the same time. Overall, it is apparent that jaguar and puma throughout the Americas exhibit differences in segregation as a method of coexistence in their overlapping habitats.

In my study, I sought to explore spatial segregation by investigating the effects of the presence of one cat on the detection probability of the other. Additionally, I investigated 13 different habitat covariates to determine how these influence occupancy. The results revealed that the most highly correlated covariate for both species were the jaguar and puma presence covariates based on relative abundance (RAI). This indicates that jaguar and puma exhibit some level of spatial segregation. As the relative abundance of one species increased, the probability of habitat use by the other species decreased.

Another significant covariate for jaguar occupancy was forest cover, which was the only anomalous and unexpected result of this study. As forest cover increased, the probability of a jaguar using that habitat decreased. While all of the camera stations were within forested areas, occupancy probability decreased with greater density of forest cover. This is contrary to a study by Arroyo-Arce et al. (2014), who suggested that jaguar tend to prefer dense forest. One possible reason for this contradiction may be that the jaguar's hunting behavior was more important than the density of forest cover. Some researchers suggest that jaguar may seek prey outside of forested habitat if influenced by habitat loss or illegal hunting (Miller & Everett 1986; Núñez et al. 2002; Hoogestijn & Hoogestijn 2010).

An important environmental covariate for puma was elevation. As elevation increased, the probability of occupancy of the puma decreased. This result is consistent with a study in Panama by Craighead et al. (2022), who found that puma presence was negatively associated with elevations greater than 250 m. Understanding their habitat preferences is important for conservation efforts as it allows us to understand where they can be found and which areas need to be protected.

One limitation encountered in this study was an outlier in the occupancy model of puma relative abundance index versus jaguar probability of occupancy. This may have skewed the result for this relationship and further analyses may need to be done. Additionally, having a wider range of data would give us greater confidence in our results. Further study of forest cover and jaguar habitat use would prove useful to better understand this correlation. However, this study provides valuable insights into the habitat preferences of jaguar and puma and can be applied to future research going forward.

This study suggests that jaguar and puma experience spatial segregation and will avoid areas where the opposite species is detected. I conclude that jaguar and puma can coexist within overlapping habitats through a combination of spatial and temporal segregation.

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