# Intraguild competition of ocelot (Leopardus pardalis) by coyote (Canis latrans) in Costa Rica

by

Lily Bright

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Approved by ______________________
[Mike Mooring, Co-mentor]

______________________
[Daniel Rocha, Co-mentor]

______________________
[April Cordero, Committee Member]

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**Abstract**

Coyote populations have been expanding southward through Costa Rica and Panama for many decades, raising the threat of intraguild competition with native felid predators. Ocelots are solitary felids that overlap with coyotes in size and diet and are important mesopredators of tropical forests. I asked whether expanding coyote populations in Costa Rica are competing with ocelots through intraguild competition. I used camera trap records from long term surveys, Generalized Linear Models (GLMs) with covariates, and overlap analysis to examine the impact of coyote populations on ocelots. My results provide evidence of a negative influence of coyote occurrence on the presence of ocelots, indicating potential avoidance of coyotes by ocelots. I did not find evidence of temporal avoidance, suggesting that ocelots avoid coyotes geographically. The data are consistent with the hypothesis that coyotes negatively impact ocelot by means of intraguild competition. If true, expanding populations of coyotes could threaten ocelot population persistence.

**Introduction**

Intraguild competition is a type of interspecific competition among predators that perform a similar function in an ecosystem. This type of competition is between a group of species of similar size that hunt similar prey. This group is called a guild (Botts et al. 2020). Because carnivorous guilds typically share similar habitats and geographic ranges, they will often form hierarchies that force smaller carnivores in the guild into altered niches in the ecosystem (Smith et al. 2018; Prugh et al. 2009). One way predators can put pressure on other carnivores within their guild is through direct predation. Predators of a guild can also suppress other guild members via competitive exclusion by competing for limited resources that can result in a change in behavior (Vanak & Gomper 2009; Foster et al. 2013). The presence of strong dominating species can lead to local extinction of inferior species in the ecosystem (Massara et al. 2016; Smith et al. 2018). These inferior species may engage in avoidance of the dominant species either spatially or temporally to allow for niche partitioning (Smith et al. 2018). An example of predator avoidance can be seen in a study of African cheetahs. The cheetahs adapted to a shared environment with African lions by hunting in different territories despite the presence of lower prey availability (Vanak & Gompper 2009).

Intraguild competition can be damaging to species richness and biodiversity in ecosystems. The loss of one species can result in cascading effects and even the collapse of the entire ecosystem. For example, a loss of an apex predator such as jaguar reduces pressures that control local mesopredator populations. It has been found that the absence of an apex predator may allow opportunistic mesopredators to step in and fill that niche in the ecosystem (Prugh et al. 2009; Roemer et al. 2009). Unfortunately, this is not always what occurs. In some cases, the loss of apex predators that control mesocarnivore populations can lead to spatial overlap of carnivorous competitors that results in overhunting and depletion of prey and resources (Davis et al. 2021). When there is a depletion of resources, the carrying capacity of the ecosystem decreases and this can lead to a trophic cascade. A trophic cascade in this example would be a result of the loss of a top-down effect from an apex predator controlling the lower trophic levels in an ecosystem. This would result in the loss of the ability of ecosystems to support themselves as intended unless another species can fill the empty niche. The purpose of this paper is to determine whether the expanding coyote population has an effect on ocelots in Costa Rica, and to explore possible competition consequences for the ecosystem.

The coyote (*Canis latrans*) is a wild carnivore found in both urban and wild habitats. It is a resilient species that can survive on both a meat and plant diet. Coyotes often hunt in packs, are opportunist hunters, and are highly adaptive. Due to the ability to survive in various landscapes, including areas with anthropogenic stressors, coyote populations have been expanding further south in Central America as far as Panama (Cove et tal. 2012). One concern is that the expansion of this resilient species will result in an increase in competition with local predator species for food resources.

Currently, we do not know what that could mean for local populations in the long term. Will coyotes outcompete other guild members?; and will their increased presence result in local extinction of some species? One study in Southern Illinois suggests that there may be a negative relationship between coyotes and other mesopredators (Morin et al. 2022). In the presence of anthropogenic pressures that had already put a strain on local gray fox populations, increasing coyote populations further exacerbated the decline of the gray fox population in that area (Morin et al. 2022). This suggests that coyote presence can have a negative effect on the presence of other mesopredators in an ecosystem, particularly in areas impacted by human influence.

Ocelots (*Leopardus pardalis*) are medium-sized mesopredators often found at elevations below 1200m that prefer thick vegetation habitats (Lopez et al. 2003). Their diet consists mainly of small mammals such as rodents but can include other prey from reptiles to crustaceans and fish. Ocelots are elusive and typically solitary; they prefer to hunt on the ground but can also hunt in trees.

Ocelots can have negative effects on the presence of small felids and other small carnivores in an ecosystem as well (Oliveira et al. 2010). This can result in spatial avoidance, predation, and temporal segregation between ocelot and other predators, sometimes called the "pardalis effect" (Smith et al. 2018; Lombardi et al. 2020). Thus, both coyote and ocelot can participate in intraguild competition resulting in decreased presence of other species. However, Lombardi et al. (2020) found that the presence of coyotes had a positive effect on the occurrence of bobcats and ocelots in Texas. The increased likelihood of bobcat and ocelot presence with the presence of coyotes was likely in part due to the abundance of resources, cover, and olfactory cues in the area (Lombardi et al. 2020).

Coyotes have been present in Central America since the Pleistocene, but recently they have begun to move further south into southern Costa Rica and Panama (Cove et al. 2016; Hildalgo-Mihart 2004). As the coyote population expands within Costa Rica, there is concern for intraguild competition with local species such as the ocelot. As a resilient species, the coyote is highly adaptive and can hunt according to the most abundant species in an area (Eppert 2019; Cove et al. 2016). Eppert's study determined that there was no correlation between habitat preferences between coyotes and ocelots; rather, their presence depended on prey availability. This supports the principle of competitive exclusion and the likelihood of competition for resources. A resilient species like the coyote may be more likely to have a negative effect on species richness and biodiversity in this ecosystem (Di Bitetti et al. 2010; Silveira 2009).

Here I studied the interactions between coyotes and ocelots in Costa Rica. I sought to answer whether there was evidence of temporal or spatial avoidance between the two species. As coyote populations expand and increase, will the coyotes have a negative relationship on the presence of native ocelots in Costa Rica?

I hypothesized that expanding coyote populations will compete with other species within their guild through direct and indirect competition. If true, I predicted that areas supporting high detection of coyotes would have lower relative detection of ocelot, whereas areas with low detection of coyotes should not see a change in detection of ocelots.

Camera trapping has become a popular method to study and observe elusive wildlife because it is cost-efficient and non-invasive (Rovero et al. 2013; Rovero & Zimmerman 2016). In Costa Rica there have been many studies conducted using camera traps over the years (Montalvo et al. 2022; Ahumada et al. 2013; Mooring et al. 2020). In this study, detections of both the coyote and ocelot populations in different regions of Costa Rica were examined using camera traps. I analyzed the relationships between the two species to determine avoidance or competition. This analysis was based on detection of species. It used single species and regional covariates for occupancy and effort calculated from days camera trap units were active as a detection covariate. Measuring abundance of a species can give insight on trends and the carrying capacity of an ecosystem which can be helpful for conservation efforts (Dillon & Marcella 2007). This could help support policy changes and community choices in favor of conservation of ecological communities and species.

## Methods

*Areas Studied*

Data for this study were collected from the Talamanca Cordillera Mountain range in Costa Rica and from sites on the Pacific lowlands (Table 1). Camera trap surveys were monitored by local community members and national parks officials at each site.

Table 1 - Camera trap study sites with location and average elevation.

| Study Site | Latitude | Longitude | Elevation (Region) |
|---|---|---|---|
| Alexander Skutch Biological Corridor | 9.5633 | -83.7839 | Lowland (Central) |
| Bosque de Agua Biological Corridor | 9.265 | -83.421 | Low/Mid/Highland (South) |
| Cabo Blanco National Park | 9.582 | -85.101 | Lowland (Low) |
| Carara National Park | 9.7984 | -84.5979 | Lowland (Low) |
| Proyecto Campanario Biological Station | 8.6397 | -83.7226 | Lowland (Low) |
| Chirripó National Park | 9.4599 | -83.5619 | Highland (Central) |
| El Copal Private Reserve | 9.7804 | -83.7546 | Midland (North) |

| | | | |
|---|---|---|---|
| La Amistad International Park | 9.0539 | -82.9876 | Highland(South) |
| La Cangreja National Park | 9.7001 | -84.3921 | Lowland (Low) |
| La Marta National Wildlife Refuge | 9.7685 | -83.6823 | Lowland (North) |
| Tapantí Macizo de la Muerte National Park | 9.7068 | -83.7793 | Highland (North) |
| Savegre Valley/Los Quetzales National Park | 9.5502 | -83.7911 | Highland (North) |

*Site Setup*

Camera trapping is used commonly to conduct surveys to inventory biodiversity, establish species' distributions, record activity patterns, and estimate population relative abundance (Frey et al. 2017; Ullrich 2021). This practice allows for the remote recording of elusive species without direct interaction. We used camera traps in up to 12 survey sites from June 2010 to July 2022 for a total of 355,755 photo records that includes 3033 total records of coyote and 592 total records of ocelot. The camera units were Bushnell Trophy Cam (Bushnell Corporation, Lenexa, KS). The cameras were triggered to take a photo using a passive infrared sensor that responded to changes in the temperature and movement of a passing mammal (Welbourne et al. 2016). A total of 193 cameras were included to detect potential avoidance behavior.

Each camera trap site included a scent station constructed with a PVC pipe and a sponge armed with a scent attractant (Calvin Klein's Obsession for Men; Calvin Klein Inc., New York, NY). The purpose of the scent station was to intrigue individuals passing by the camera station, encouraging them to slow down and investigate the scent in front of the camera. This practice ensures a better quality of photo for species identification (Viscarra et al. 2011). Scent attractants are a common practice to increase photographic quality for species studies without affecting temporal activity (Braczkowski 2016). Scent station methodology is further discussed by Mooring et al. (2020).

*Data Analysis*

Data processing began with camera images loaded into the Wild.ID data management application, where photos were identified to species and sorted before being uploaded into a .CSV spreadsheet and subsequent integration into the R-programming language environment (WildID 2021; Ullrich 2021). R is a free software for statistical computing and graphics (R Core Team 2018). This software was used to calculate detections of each species and examine the effects of coyotes on ocelots using Generalized Linear Models (GLMs) and overlap analyses. For exploratory analysis of the data, a figure was generated using Geographic Information Systems displaying all cameras, their location, and whether the presence of coyote or ocelot was detected on the cameras (Figure 1).

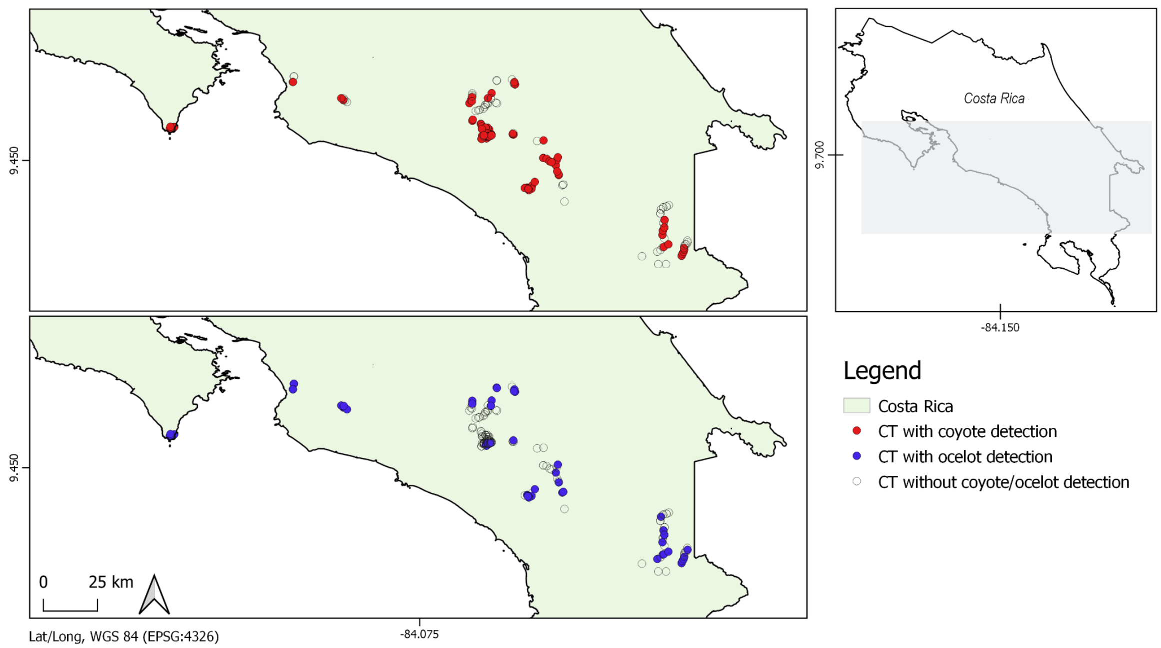


Figure 1 - Camera trap detection of ocelots (blue) and coyotes (red) at posted camera trap locations in the Talamanca region of Costa Rica. The clear dots represent no detection of either species at the site.

A QuasiPoisson Regression model was determined to be the best GLM for representing count data and accounting for the variation in the days cameras were active. Using this GLM model on the dataset gave the slopes and p-values for each model. Additionally, analysis was performed to explore potential relationships between apex predators jaguar and puma on coyote and ocelot presence using the QuasiPoisson model. I also used the QuasiPoisson model to analyze each overall region of camera stations to determine if one region might be driving the relationship between coyotes and ocelots. Using the package “Overlap” in the R programming language, the temporal overlap between the two target species was investigated. This function assumes that both species are equally likely to be detected throughout any period of their activity (Botts et al. 2020; Wang et al. 2019).

To explore the relationship between ocelot and coyote, single species covariates of coyote against ocelot were used. Additionally, this was also done for the apex predators with ocelot and coyote independently. Since it is possible a species is present but undetected we used a detection covariate based on the days cameras were active. This detection covariate made it more likely that the species was detected over a set period, 7 days.

**Results**

The QuasiPoisson model was run on the coyote and ocelot dataset with covariates, as well as on the apex predators jaguar and puma (Table 2). The results revealed a statistically significant negative relationship between coyotes and ocelot. No significant relationship was found between ocelot and jaguar, or between ocelot and puma, nor did the presence of jaguar have a significant influence on coyote presence (Table 2). The regional analysis indicated no significant difference in relationships among regions (Table 3). In terms of circadian activity patterns, there was an almost complete temporal overlap between coyotes and ocelots (overlap index = 88%), with both species being mostly nocturnal (Figure 2; Botts et al. 2020).

Table 2 - Summary of species models with significance value, standard error, and confidence intervals. For example, "Ocelot ~ Coyote" models the influence of coyote presence on ocelot presence. The asterisk indicates significance of the slope to the model at $p < 0.05$; the models in red were of interest but not significant.

| Species Model | Slope | P-value | Std. Error | Confidence Interval |
|---|---|---|---|---|
| Ocelot ~ Coyote | -0.019 | <0.01** | 0.004 | -0.029,-0.012 |
| Coyote ~ Jaguar | -0.194 | 0.112 | 0.123 | -0.0511, -0.041 |
| Coyote ~ Puma | -0.008 | 0.18 | 0.006 | -0.02,0.003 |
| Ocelot ~ Jaguar | 0.003 | 0.94 | 0.035 | -0.095, 0.056 |
| Ocelot ~ Puma | -0.004 | 0.74 | 0.011 | -0.027,0.017 |

Table 3 - Summary of regional models for the influence of coyotes on ocelot in each study region. The significance at $p < 0.05$ as well as the standard error is included. The asterisk indicates the significance of the slope.

| Ocelot ~ Coyote + Region | Slope | P-value | Std. Error |
|---|---|---|---|
| Northern Region | -0.414 | 0.463 | 0.036 |
| Southern Region | -0.058 | 0.0315* | 0.025 |
| Lowland Region | -0.068 | 0.008* | 0.024 |
| Central Region | -0.187 | 0.005* | 0.059 |

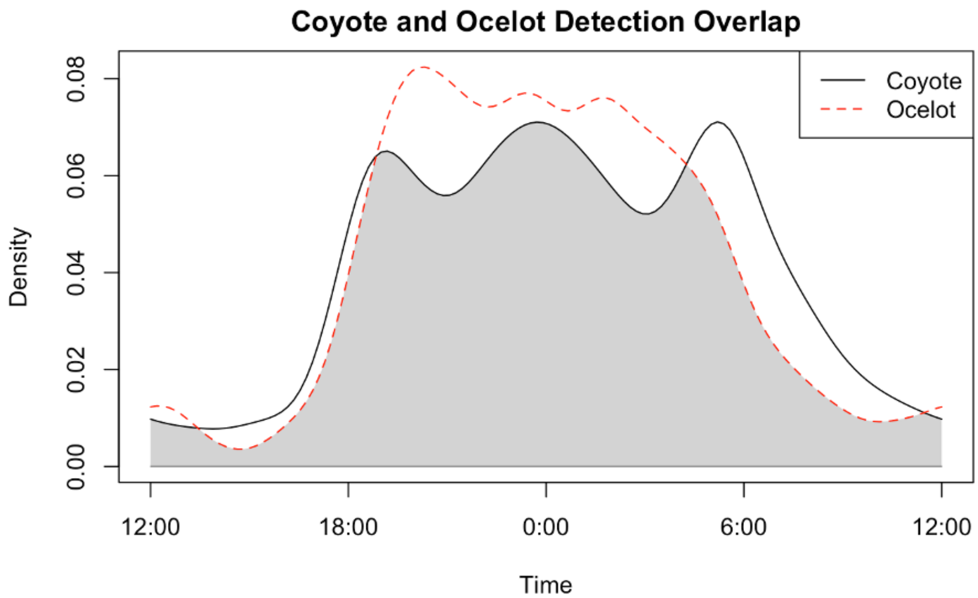


Figure 2 - Temporal overlap showing the activity patterns of coyotes (black solid line) and ocelot (red dotted line) at varying times of the day from all study sites.

**Discussion**

This study attempted to determine whether expanding coyote populations could have a negative effect on the presence of ocelot populations in Costa Rica. The results are consistent with the hypothesis that intraguild competition is driving spatial avoidance of coyotes by ocelot, which could threaten ocelot population persistence. There is thus evidence to reject the null hypothesis that expanding coyote populations will have no effect on ocelot presence and abundance in Costa Rica – it is unlikely that coyotes will not impact ocelots and perhaps other mesocarnivores in the path of their range expansion

The temporal activity comparison did not indicate temporal avoidance as seen by the high degree of overlap between coyote and ocelot activity patterns (88%; Figure 2). This makes sense because both species are mostly nocturnal. Botts et al. (2020) explored the circadian rhythms of mammals in Costa Rica and concluded that similar-sized predators within a guild are likely hunting the same prey at the same time, which would make temporal avoidance unlikely between the coyote and ocelot. As expected, the GLM analysis found significant evidence of a negative relationship between coyote and ocelot (Table 2). This is in line with the prediction of intraguild competition and the competitive exclusion principle shown by many studies among predators (Moreno-Sosa et al. 2022; Linnell & Strand 2008; Caro & Stoner 2003).

Separating the data by region did not indicate that one region is driving the results (Table 3). Additionally, there did not appear to be a significant relationship between these two mesopredators and the two larger predators, the jaguar and puma.

Despite not having statistical significance, there may be a negative correlation between jaguar and coyote and a positive correlation between ocelot and jaguar presence, meaning that when jaguar are present coyote presence is less likely and, conversely, ocelot presence is more likely. Results similar to this have been observed in the study on the co-occurrence of ocelot, bobcats and coyotes in which ocelot activity correlated with jaguar activity, likely because of similar habitat preferences (Lombardi et al. 2020). This is interesting because it suggests that the absence of jaguar in tropical forests may trigger mesopredator release of coyote populations, which in turn may be driving a decline in ocelots due to competitive avoidance (Oliveira et al. 2010).

Some limitations of this study include having more coyote records than ocelot records, and even fewer jaguar records. Another consideration is that the ocelots may have adapted to different ways of hunting to avoid competition with coyotes. The ocelot is an excellent climber, and it is possible that ocelot have adapted to the presence of coyotes by practicing spatial avoidance through arboreal hunting. This concept is supported by a study that found that leopards, another arboreal felid, appeared to hoist prey into trees to avoid other predators such as lions and African wild dogs (Stein et al. 2015). Because camera traps were not placed in the canopy of the trees in this study, ocelot presence would be less likely to be detected, thereby underestimating ocelot presence and abundance.

**Conclusions**

Overall, my analysis suggests that coyote presence has a negative effect on ocelots through intraguild competition. I conclude that the results are consistent with the hypothesis that intraguild competition is driving spatial avoidance of coyote by ocelot, which may threaten ocelot populations. Although the results of this analysis are inconclusive, further investigation can provide more definitive results. In recent years, ecological conservation has begun to focus on ecosystems over individual species (Linnell & Strand 2008). Therefore, the implications of this study are important for conservation efforts overall. If coyote populations are causing a decrease in ocelot populations in Costa Rica there may need to be new policies or practices introduced to preserve the ecosystem. Competitive exclusion within guilds can help explain why some predators may be more susceptible to extinction than others (Creel 2008), thus providing new insights regarding species protection policies and future efforts.

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