

BIODIVERSITY, CONNECTIVITY, AND IMPACTS OF ANTHROPOGENIC BARRIERS
ON VERTEBRATE COMMUNITIES IN THE MEXICO-USA BORDERLANDS

by

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General summary

The Sky Islands region between Mexico and the United States has been recognized as a biodiversity hotspot due to the convergence of Neartic and Neotropical species (Coronel-Arellano et al., 2018; DeBano et al., 1995; Warshall, 1995). For mammals along the US-Mexico border, the northeastern portion of Sonora and the northwestern portion of Chihuahua are considered to be corridors for jaguars (*Panthera onca*), ocelots (*Leopardus pardalis*), and black bears (*Ursus americanus*), all of which use riparian and montane forests to move among the Sky Islands (Atwood et al., 2011; Grigione et al., 2009; Sierra-Corona et al., 2005). Large-scale developments in the region threaten landscape connectivity and the persistence of native wildlife populations (McCormack et al., 2009; Peters et al., 2018). The US-Mexico border wall bisects the distribution range of 346 species of nonflying terrestrial and freshwater animals, including 120 species of mammals, and will impact the cross-border movement of over 100 species under current climate scenarios (Peters et al., 2018; Titley et al., 2021). In this study, we address the ongoing fragmentation of one of the most diverse ecosystems in North America, focusing on the impacts of human barriers, discussing the possibilities of emerging techniques for monitoring terrestrial mammals faster and cost-effective, and investigating the spatiotemporal patterns of apex predators in the region.

In chapter one, we focused on the international border between Arizona and Mexico, which traverses a vast landscape of extreme biodiversity. We aimed to determine how mammals' diversity and habitat use change across significant landscape features: the Cajon Bonito stream, the border wall, and the most transited highway in the area. We installed 85 camera traps and recorded 31 species of terrestrial mammals from 15 families and identified two different jaguar individuals and other cryptic species: the ocelot, porcupine and beaver. Diversity analyses showed that vegetation type influenced the composition of mammals in combination with the presence of cattle and distance to the road. The presence of cars, distance to the border wall, and effort, also affected the

composition as non-interacting covariates. We found that human influence has a negative effect on the habitat use of mammals. Areas closer to the border are less used by larger mammals. However, mesopredators and small herbivores were more tolerant to disturbance and used sites closer to the border and dirt roads, but they exhibited a negative association with the presence of humans and sites closer to the border wall. Also, the presence of cattle negatively affected the habitat use and detectability of large and small carnivores. Our results highlight the need to keep bi-national connectivity for mammal populations using mountain corridors and prioritize locations that provide water sources to wildlife to mitigate highway and border wall impacts. This chapter is formatted for submission to the *Science of the Total Environment* journal.

Given that traditional monitoring methods, particularly camera trapping, can be expensive, labor-intensive, and susceptible to equipment failure or theft, especially when elusive and low-abundant species of interest are present. In the second chapter, we explored the effectiveness of environmental DNA metabarcoding for monitoring terrestrial mammals as a potentially more cost-effective and faster alternative. We surveyed a 20 km section of the perennial Cajon Bonito stream in Mexico, deployed camera traps, and collected eDNA water samples at ten locations along the stream during wet and dry seasons. The camera traps operated continuously for 31 days before each eDNA sampling event. The results indicated that camera traps detected significantly more species (18 in the wet season, 17 in the dry) than eDNA (5 and 4 species, respectively). While some species detected via eDNA were also detected using camera traps, the beaver (*Castor canadensis*) was exclusively detected with eDNA. We analyzed the relationship between camera trap detections and eDNA detection, considering temporal proximity between detection events and spatial proximity. However, no significant correlation was found, contrasting with findings from more humid environments. The lack of correlation suggests that the factors influencing eDNA detection in arid environments, such as DNA persistence, degradation, and transport, make this technique less reliable than in humid environments. Also, the lower structural complexity of arid vegetation compared

to humid environments might reduce DNA persistence and transport. While eDNA metabarcoding shows promise as a supplementary tool, camera traps remain more effective in assessing overall mammalian diversity in this arid ecosystem.

Finally, in chapter three, we investigated the spatiotemporal ecology of three apex predators, black bears (*Ursus americanus*), pumas (*Puma concolor*), and jaguars (*Panthera onca*) in the US-Mexico borderlands. We used a 22-month camera trapping dataset, employing 85 motion-activated cameras placed along a riparian corridor and in a grid parallel to the international border. We focused on (i) spatial overlap, (ii) seasonal activity patterns, (iii) daily activity patterns, (iv) interspecific activity overlap, and (v) the effect of the presence of predators over two prey species, the white-tailed deer (*Odocoileus virginianus*) and the collared peccary (*Dicotyles tajacu*). We found spatial overlap between the three species of predators in riparian forests, and black bears and pumas in pine-oak forests, but pumas were typically the only apex predator in the scrublands and grasslands. We found distinct seasonal activity patterns among the three predators, with black bears showing peak activity in June, pumas exhibiting consistent activity throughout the year, and jaguars demonstrating peak activity from August to January. Daily activity was predominantly diurnal for bears and did not overlap with the two felids. Puma and jaguar activity overlapped, but puma activity peaked at dusk and jaguars during the night. The habitat use of both prey species responded positively to the presence of black bears but not to the felids. We suggest that given the dominance of black bears over both felids, prey species might be using those sites as a refuge from their other predators, exploiting avoidance of bears by the felids that describe the complexity of spatiotemporal partitioning.

Chapter 1. Complex and species-specific impacts of the border wall, roads, and riparian areas on mammal populations along the US-Mexico border

1.1 Abstract

The international border between Arizona and Mexico traverses a vast landscape of extreme biodiversity. Habitat degradation and loss of functional connectivity are potential consequences of increased border-related disturbances and physical barriers. We aimed to determine how mammals' diversity and habitat use change across significant landscape features: the Cajon Bonito stream, the border wall, and the most transited highway in the area. We installed 85 camera traps and recorded 31 species of terrestrial mammals from 15 families and identified two different jaguar individuals and other cryptic species: the ocelot, porcupine and beaver. Diversity analyses showed that vegetation type influenced the composition of mammals in combination with the presence of cattle and distance to the road. The presence of cars, distance to the border wall, and effort, also affected the composition as non-interacting covariates. We found that human influence has a negative effect on the habitat use of mammals. Areas closer to the border are less used by larger mammals. However, mesopredators and small herbivores were more tolerant to disturbance and used sites closer to the border and dirt roads, but they exhibited a negative association with the presence of humans and sites closer to the border wall. Also, the presence of cattle negatively affected the habitat use and detectability of large and small carnivores. Our results highlight the need to keep bi-national connectivity for mammal populations using mountain corridors and prioritize locations that provide water sources to wildlife to mitigate highway and border wall impacts.

1.2 Introduction

The human footprint has impacted almost every ecosystem and ecological process that occurs in the world, including biodiversity and animal movement (Ellis, 2015, 2013; Ripple et al., 2014; Tucker et al., 2018). For terrestrial mammals, human activities and infrastructure have a negative effect on median and long-distance movements, altering distribution ranges, migration routes, predator-prey interactions, genetic diversity, and disease transmission (Tucker et al., 2018). Complete and semi-permeable barriers to wildlife movement have been constructed in recent decades, interrupting the connectivity of landscapes and wildlife movements (Chen and Koprowski, 2019; Jakes et al., 2018; McInturff et al., 2020). Physical barriers constructed in the modern era include the fences and walls along the borders of China-Mongolia, Malaysia-Thailand, India-Pakistan, Germany-Czech Republic, Slovenia-Croatia, Polonia-Belorussia, Turkey-Syria, Hungary-Romania, Iran-Turkmenistan, Botswana-Zimbabwe and US-Mexico (Dallimer and Strange, 2015; Linnell et al., 2016; Trouwborst et al., 2016).

Fences and walls along political boundaries are explicitly intended to be permanent and impenetrable for humans, but that also results in blocked transit of most medium and large wildlife species as well (Ito et al., 2013; McCallum et al., 2014; Woodroffe et al., 2014). In fact, the distribution ranges of 60% of the world's mammals span multiple countries, but the management and conservation actions are usually less effective where international borders are present (Titley et al., 2021).

In addition to the border infrastructure, the world is crisscrossed by roads and fences, which might be actively functioning as barriers and ecological traps depending on an animal's guild and species-specific interactions with the landscape (Gilhooly et al., 2019; Jakes et al., 2018; McInturff et al., 2020; Noonan et al., 2022; Sutherland et al., 2021). The pervasive effects of roads on wildlife movement are due not just to the physical structure but all the human activities associated with their presence, such as vehicle traffic, pollution, increased light exposure, noise, and other indirect effects, including facilitating access to

hunting in remote locations (Chen and Koprowski, 2015; Colchero et al., 2011; Dickson et al., 2005; Ditmer et al., 2018; Fensome and Mathews, 2016; Medinas et al., 2019; Roever et al., 2010). Roads also impact wildlife movements and mortality due to collisions with motor vehicles and pose a risk for wildlife and drivers. In the United States alone, it is estimated that over 58,000 people are injured annually by wildlife collisions (Conover, 2019). Vehicle collisions are especially detrimental for large species with low reproductive rates, such as carnivores, and can reduce their populations locally (Fahrig and Rytwinski, 2009; Gilhooly et al., 2019).

The Sky Islands region between Mexico and the United States has been recognized as a biodiversity hotspot due to the convergence of Neartic and Neotropical species (Coronel-Arellano et al., 2018; DeBano et al., 1995; Warshall, 1995). For mammals along the US-Mexico border, the northeastern portion of Sonora and the northwestern portion of Chihuahua are considered to be corridors for jaguars (*Panthera onca*), ocelots (*Leopardus pardalis*), and black bears (*Ursus americanus*), all of which use riparian and montane forests to move among the Sky Islands (Atwood et al., 2011; Grigione et al., 2009; Sierra-Corona et al., 2005). Large-scale developments in the region threaten landscape connectivity and the persistence of native wildlife populations (McCormack et al., 2009; Peters et al., 2018). It is estimated that the US-Mexico border wall bisects the distribution range of 346 species of nonflying terrestrial and freshwater animals, including 120 species of mammals, and will impact cross-border movement of over 100 species under current climate scenarios (Peters et al., 2018; Titley et al., 2021). In northern Mexico, the only road that connects the large border cities of Ciudad Juarez and Tijuana is Federal Highway 2, which runs parallel to the international border for 85 km from the eastern slope of the Continental Divide to Agua Prieta, Sonora. Recent black bear mortalities along Mexico's federal Highway 2 in Sonora led to a plea by the state congress to incorporate highway impact mitigation actions (Manteca-Rodríguez et al., 2021; Villarreal et al., 2019). Furthermore, considering current climate change predictions of increased aridity and temperatures, transboundary range movement is critical for the long-term

function and composition of mammal communities along the US-Mexico border (Tittley et al., 2021).

Direct negative impacts of the border wall on the distribution and daily movement have been documented for species such as the Northern pygmy owl (*Glaucidium gnoma*), bighorn sheep (*Ovis canadensis*) (Flesch et al., 2010), puma (*Puma concolor*) and white-nosed coati (*Nasua narica*) (McCallum et al., 2014). The expansion of the border wall along the Arizona-Sonora border in the 2010s bisected several mountainous corridors for mammals, potentially affecting the community of mammals and funneling endangered species through the few remaining corridors (Babb et al., 2022; Grigione et al., 2009; Onorato et al., 2007; Ragan et al., 2022, 2021). Given the importance of this region to sustain broader wildlife populations in both Mexico and the United States, we aimed to assess the effects of the border wall, highways, and natural features in the landscape (e.g. riparian vs upland vegetation) on local mammal communities. We predicted that the presence of humans, vehicles, and cattle would reduce mammalian diversity and use of habitats in proximity. Also, we expected that habitat use and the impacts of human infrastructure would affect species differently depending on their guild and size, e.g., species with larger body size and carnivores would be more impacted by anthropogenic factors than meso-predators and synanthropic species (Chen and Koprowski, 2019), which are more resilient to human influence (Behera et al., 2024).

1.3 Methods

1.3.1 Study site

The study was conducted in northeastern Sonora, Mexico (Figure 1.1). The area is at the western slope of the San Luis mountain range, which is the northern end of the Sierra Madre Occidental in Mexico, and connects with the Madrean archipelago to the north in the United States (González-Elizondo et al., 2012). The camera traps were installed in the properties owned and managed by the non-profit Cuenca de Los Ojos A.C. (hereafter CLO), which is bounded to the

north by the states of Arizona and New Mexico in the United States and on the east by the Janos Biosphere Reserve, Chihuahua, Mexico. CLO lands cover 52,000-ha dedicated to conservation since 1990. Due to the region's outstanding biodiversity and water provision, 25,000 ha were voluntarily dedicated for conservation in 2018 under Mexico's natural protected areas scheme (CONANP 2018). CLO contains nearly 40 km of the international Mexico-USA border. In one section of the border, in the Animas Valley between the states of New Mexico and Sonora, a 1.5 m tall, wildlife-permeable vehicle barrier was installed in 2008 (Figure 1.1). In 2020, construction of a 9.1-meter tall border wall began between Arizona and Sonora along the western portion of CLO, and continued until it was halted in January 2021. This new section of the wall starts at the closest city, Agua Prieta (40 km east), and ends at Guadalupe Canyon, which is close to the border of New Mexico with Arizona and on the CLO (Figure 1.1). The border wall has only 10 cm wide gaps between the bars, with openings at specific washes and river beds to prevent damage during the rainy season, but overall, it appears much less permeable to wildlife than previous vehicle barriers (Figure 1.1). In addition to this border infrastructure, CLO is crossed by two major elements: i) Federal Highway 2, which was recently expanded to four lanes in 2018, and ii) the Cajon Bonito stream, which is the principal water source of the region and one of the best-protected rivers in northwest Mexico. The Cajon Bonito stream is the home of many threatened species, including the Chiricahua leopard frog (*Lithobates chiricahuensis*), Yaqui catfish (*Ictalurus pricei*), roundtail chub (*Gila robusta*) and the Yaqui chub (*Gila purpurea*). Furthermore, four species of mammals listed as endangered in Mexico occur in the Cajon Bonito: beaver (*Castor canadensis*), black bear, ocelot, and jaguar. The jaguar sighting, one of the most northern records in Mexico, occurred 1 km south of the highway and 3 km from the international border with the United States (Ragan et al., 2021).

1.3.2 Camera trap monitoring

We set 100 motion-activated cameras with infrared flash (Bushnell core) to detect medium and large mammal species. Eighty cameras were in a grid arrangement

(20 × 4), parallel to the international border and each camera was separated by 2 km (Figure 1.1). Additionally, we set up 20 camera traps along the Cajon Bonito stream, separated by 2 km following the stream course. We set the cameras at a height of 40 cm above the ground on trees or poles close to trails, dirt roads and where evidence of wildlife movement was evident and we did not use any bait or lure. The cameras were programmed to take 10-second videos when motion and movement were detected with a 5-minute delay between consecutive detections. The time window to consider an independent record for a species at each location was 60 minutes. The trapping took place from October 2020 to August 2022. However, because of theft, flooding, fires, and malfunction, we only used 85 camera traps for further analyses. Two species of cottontails are found in the region, the desert cottontail (*Sylvilagus audubonii*) and the eastern cottontail (*S. floridanus*), which overlap in their distribution in scrublands and oak forests (Hoffmeister, 1986). Morphologically, the dorsal portion of the tail of *S. audubonii* has a broader white rim and the base of the hairs of the *S. floridanus* are red or orangish (Hoffmeister, 1986), but considering the difficulty of distinguishing these characteristics under the variable light conditions of the camera traps and that night videos are in black and white, we merged the records of these two species at the genus level.

1.3.3 Diversity analysis

For the diversity analyses, we only considered native mammal species with a body mass over 1 kg, given the reliable detection range of our motion-activated cameras. We compared the community of mammals using a permutational multivariate analysis of variance using distance matrices, PERMANOVA (Mcardle and Anderson, 2001) with 10,000 iterations and used a non-metric multidimensional scaling (NMDS) using ellipses with multivariate normal distribution with the centroid at the mean of NMDS1 and NMDS2 axes for each vegetation type for graphical representation. To explain the differences in community composition, we incorporated environmental and human influence covariates. The only categorical covariate that we included was the type of

vegetation where the camera was set according to the Mexican national land use and vegetation survey. The types of vegetation found in the area were grassland, scrubland, oak forest, pine-oak forest, and riparian vegetation (INEGI, 2021). The human influence covariates that we included were the number of independent records of cars, the number of independent records of cattle, the linear distance to the closest section of the border wall, the linear distance to the closest section of Highway 2, and the number of independent records of humans on foot or horse-riding. We standardized all the covariates and only included those covariates that were not correlated with each other ($\rho < 0.6$) in the same model. Because the distance to the international border was highly correlated with the distance to the highway ($\rho = 0.88$, P -value < 0.0001), but we wanted to test the effects of both, we incorporated each covariate in two different models and kept the model with the lowest residual value. To identify which species drive the community composition in each vegetation type, we performed the indicator species analysis with the function *multipatt* of the Vegan package. All analyses were performed in R version 4.3.1 (R Core team, 2023).

1.3.4 Species-specific responses

We divided the mammals with enough data ($n > 50$ independent records) to be modeled into five categories based on their ecosystem role. The species in each category were the following: 1) large carnivores: black bear, jaguar and puma; 2) large herbivores: white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*) and collared peccary (*Dicotyles tajacu*); 3) mesopredators: coyote (*Canis latrans*) and bobcat (*Lynx rufus*); 4) small carnivores: striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), hooded skunk (*Mephitis macroura*), hog-nosed skunk (*Conepatus leuconotus*), gray fox (*Urocyon cinereoargenteus*), and white-nosed coati, and 5) small herbivores: cottontail (*Sylvilagus* spp.) and black-tailed jackrabbit (*Lepus californicus*). To test the influence of vegetation types and human influence covariates over the abundance of carnivores, we used the site-specific abundance (N) of each species. The temporal repetition consisted of 1-w during which we counted the number of 60-minute independent

detections. To ensure the population closure assumption, we only modeled the data from the last 40 w of the study (November 1, 2021, to August 1, 2022), when most cameras were active.

We used the latent abundance mixture model proposed by Royle & Nichols (Royle and Nichols, 2003). In this model, the latent abundance N of site i is modeled as Poisson: $N_i \sim \text{Poisson}(\lambda_i)$, where λ_i is the abundance rate at site i and the covariates of λ_i are modeled with the log link: $\log(\lambda) = \mathbf{x}_i\beta$, where \mathbf{x}_i is the vector of site-level covariates and β their corresponding effect parameters. The detection of a single individual w in site i during sample j is modeled as Bernoulli: $w_{ij} \sim \text{Bernoulli}(r_{ij})$ and linked to the detection probability for a single site p_{ij} by: $p_{ij} = 1 - (1 - r_{ij})^{N_i}$, where the covariates of the detection probability for an individual r_{ij} are modeled with the logit link: $\text{logit}(p_{ij}) = \mathbf{v}_{ij}\alpha$ and where \mathbf{v}_{ij} is a vector of observation-level covariates and α is a vector of their effect parameters.

One of our aims was to investigate the effects of the international border, the border wall and the highway. However, the border and the highway were highly correlated ($\rho > 0.6$), so we initially compared and selected the models with the lowest Akaike Information Criteria (AIC). We used a three-step approach, and first, we compared two full-parametrized models with the distance to the border or the highway and selected the covariate with the lowest AIC for the next step. We considered that the only covariate that might affect detection was the presence of cattle, so for the second step, we compared the performance of one model that included the number of independent cattle detections per week as a covariate of detection versus the null model for detection and selected the model with the lowest AIC. Once we determined if the models would include distance to the highway or distance to the border wall, and the presence of cattle as a covariate for detection, we proceeded to construct 24 models using the R package unmarked version 1.3.2 (Kellner et al. 2023), for the abundance that contained a maximum of 3 additive covariates (Mazzamuto et al., 2019). We report the model-averaged beta estimates considering the models that added had an accumulated AIC weight ≥ 0.90 (Lukacs et al., 2010), and considered as

relevant those covariates whose confidence interval did not include zero (Bauder et al., 2018).

1.4 Results

We set 85 camera traps on the Mexico-US border in northeast Sonora and recorded at least 31 species of terrestrial mammals from 15 families (Table 1.1). Families comprised Canidae, Cervidae, Cricetidae, Didelphidae, Erethizontidae, Felidae, Geomyidae, Heteromyidae, Mephitidae, Mustelidae, Procyonidae, Sciuridae, Tayassuidae and Ursidae. The total effort was 43,482 sampling trap days (median = 541 trap days per site, range = 107–670 days), during which we recorded 21,486 independent videos of mammals. The most abundant species were cottontail, white-tailed deer, and gray fox. In contrast, we detected ocelot twice and American porcupine (*Erethizon dorsalis*) only once (Table 1.1). Excluding the researchers, who went to check the camera traps, humans were detected in 40 locations and cattle were detected in 61 of the 85 locations. Additionally, we recorded domestic horses, dogs, donkeys, pigs, and sheep and documented 46 species of birds. The vegetation type with the most species was the scrubland (24 species), and the vegetation type with the fewest species was the pine-oak forest (20 species). Cottontail was the dominant species in the oak forest and the scrubland, and codominant with the black-tailed jackrabbit in the grasslands. In contrast, the pine-oak and the riparian forest showed more equitable abundances among species (Figure 1.2).

We found strong evidence that vegetation type influenced the composition of mammals in combination with the presence of cattle and distance to the road (Table 1.2). Also, the presence of cars, distance to the border wall, and effort, as non-interacting covariates, affected composition (Table 1.2). Overall, the model explained 56% of the variation in composition, in which the type of vegetation was the covariate that accounted for the highest amount of variation (16%), followed by the interaction of the type of vegetation and the distance to the road

(7%); each of the remaining covariates explained 5% or less of the variation (Table 1.2; Figure 1.3).

The oak, oak-pine, and riparian forests were associated with 12 indicator species and the grasslands with one species (Supplementary Table 1). The oak forest's indicator species were the hooded skunk and the cottontail. The Virginia opossum (*Didelphis virginiana*) was the only indicator species of the pine-oak forest, and the jaguar, the hog-nosed skunk and the white-nosed coati were indicators of the riparian forest (Figure 1.2). The gray fox was an indicator species of the oak and pine-oak forests. The black bear, the Mexican fox squirrel (*Sciurus nayaritensis*) and the puma were indicator species in the pine-oak and riparian forest (Figure 1.2). The white-tailed deer was an indicator species for oak, pine-oak, and riparian forests. Finally, the black-tailed jackrabbit was moderately associated with the grasslands, and no indicator species were associated with the scrubland (Figure 1.2).

The habitat use models for species showed mixed responses for human influence covariates and vegetation types depending on the guild and the species (Supplementary Table 2). For example, the habitat use of the most conspicuous large carnivore and herbivore, the black bear and the white-tailed deer, respectively, were higher at sites far from the international border (Figure 1.4). In contrast, the black-tailed jackrabbit, a small herbivore, had higher abundances at sites closer to the border (Figure 1.4). The white-nosed coati was the only species with higher use far from the highway. The puma and the white-nosed coati used areas closer to the border wall, but the small herbivores used less of these areas. The presence of cars negatively affected the habitat use of pumas and white-nosed coatis, contrasting with the positive influence over the meso-predators and the jackrabbit. Cattle presence negatively impacted carnivores such as pumas, hog-nosed skunk, and white-nosed coati but enhanced coyote's habitat use. The use was higher in sites close to humans for pumas, striped skunks, and white-nosed coatis, but lower for jackrabbits. Most species, except cottontails, had a higher use of riparian forest for vegetation type. Large carnivores were the only guild that exhibited a consistent pattern where habitat

use was higher in forested areas (oak, pine-oak, and riparian forest) and lower in the grasslands. The rest of the species showed species-specific affinities (Figure 1.4). Finally, the presence of cattle had a negative effect on the detection of puma, white-tailed deer, and gray foxes but a positive effect on the detection of black bears (Table 1.3).

1.5 Discussion

The wildlife diversity we found across our study area highlights the region's biodiversity and relevance for conserving mammals amidst the physical and human-activity barriers in the US-Mexico borderlands. The fact that we detected rare species like jaguar, ocelot, and porcupine indicates that long-term and large-scale monitoring efforts in the region will detect species considered absent in the area and track the recolonization of species eradicated during the last century. The species richness was similar across the vegetation types. However, a more detailed look into the habitat use of several species showed a positive association with riparian ecosystems, stressing that the role of water sources in arid landscapes goes further than access to water and includes shelter, food sources, and corridors for multiple species (Hagen and Sabo, 2014; Ragan et al., 2022; Sánchez-Montoya et al., 2017). The indicator species analysis also reflected the strong species-specific habitat associations, where we identified variations in each community's dominant species and habitat affinities. For example, using the individual rosettes pattern of jaguars, we identified two male jaguars that were continuously detected during the surveys and used all the vegetation types, but habitat use and indicator species analyses suggest jaguar affinity for riparian and mountainous habitats. We suspect that without preserving these high-quality habitats, which include the permanent presence of surface water, jaguars would not be using the other ecosystems and would not be residents in the region. In a broader scope, the habitat use patterns we found for large carnivores suggest that the Cajon Bonito stream, in synergy with the mountainous corridor and habitats found at the San Luis and Peloncillo mountain ranges, might be

providing an invaluable refuge for species that depend on extensive areas to survive (Estes et al., 2011; Laliberte and Ripple, 2004; Wolf and Ripple, 2017). Considering the drought the American southwest has been experiencing during the last two decades and the forecasted climatic trends (Cook et al., 2015), mountains will be crucial in buffering the effects of climate change across the elevational gradient (Elsen et al., 2018; Li et al., 2003; Titley et al., 2021).

Overall, we found that human influence has a negative effect on the habitat use of mammals. Still, no covariate that affected more than one species did it in the same direction. Instead, we observed patterns associated with the size or guild of the species. For example, the areas closer to the border are less used by larger mammals, such as the black bear and the deer, supporting our prediction that larger and conspicuous mammals will be more affected by humans. In contrast, the black-tailed jackrabbits, a species more tolerant to disturbance (Markovchick-Nicholls et al., 2008), used sites closer to the border and dirt roads where cars were detected more frequently but exhibited a negative association with the presence of humans and sites closer to the border wall.

Interestingly and worrying, the cottontails, the species most detected overall and a dominant species in all ecosystems except the riparian, also showed a negative association with the border wall. The escape strategies of these two leporid species differ, as the jackrabbit depends on open spaces to outrun the predators, and the cottontail runs and hides in nearby vegetation (Brown and Krausman, 2003; Harrison, 2019). For prey, reduced escaping routes and limited visibility strongly determine habitat preferences (Dorresteijn et al., 2015; Gaynor et al., 2019). These trends urge us to understand better the mechanisms of how the border wall is changing the surrounding ecosystems, considering the ongoing changes in habitat quantity, quality and fragmentation, as well as the induced changes from a behavioral perspective. Because our survey started as the border wall section was in construction, we must consider the temporal mismatch between disturbance and the measurable changes in wildlife populations (Salvatori et al., 2023; Sayre and Knight, 2010; Smith et al., 2021), and expect that most of the effects on the community in the borderlands will be

more evident and widespread in the future as the species react to the changes in the environment.

We only found evidence of the negative impact of the highway over the habitat use of white-nosed coatis, a species that was also negatively impacted by the presence of cars and cattle, but with a positive response to humans. Alterations to the normal movement patterns close to linear features are more complex than crossing or not crossing them (Xu et al., 2021). A study that monitored the use of culverts and underpasses by terrestrial mammals found that 18 species use them frequently (Manteca-Rodríguez et al., 2021), and we detected all species that they reported. It is essential to recognize that in our study site, the highway runs parallel to the international border, making it difficult to discern the effect of each structure; in addition, both sides of the highway are fenced with 4 or 5 lines of barbed wire. All these restrictions on wildlife movement might explain the absence of certain species, such as the pronghorn (*Antilocapra americana*), a species seen on the US side but not detected in our study site. Fence construction across the American West has been shaping and constraining the geographic distribution of pronghorn (Xu et al., 2021), suggesting that a broad spectrum of changes in wildlife communities are imperceptible to camera trap surveys. Future studies dedicated to monitoring the specific response of wildlife to the different border structures and highways will help to illuminate the particular corridors and sites that mammals are avoiding and suggest potential corrective actions and ways to restore and maintain connectivity.

The presence of cattle negatively affected the habitat use and detectability of large and small carnivores. These patterns suggest that although some habitat preferences might have a role, at least for small carnivores, cattle might act as a risk cue and influence their landscape use (Gaynor et al., 2020; Smith et al., 2021). Cattle predation is minimal in the area and might be due to abundant wild prey. A study conducted in the central Sonoran mountain range found that when natural prey populations are diminished by overhunting, jaguars and pumas exhibit a higher consumption of calves (Cassaigne et al., 2021).

The lack of response of most species to humans might be due to the low numbers of persons on foot or horse-riding moving throughout the landscape. However, puma, white-nosed coati, and ringtails increased habitat use on sites where humans were detected more frequently. The ringtail, a nocturnal and arboreal species, does not overlap with human activities in this area, which are limited to ranching operations mostly during daylight and have been wildlife-friendly for the last two decades. White-nosed coatis are another synanthropic species, and their proximity to humans is well known across their distribution range (Mehrkens et al., 2013; Puebla-Rodríguez et al., 2023). Pumas more frequently use sites far from settlements and highways and where human activity is high (Gray et al., 2016), but they often use moderately-disturbed areas and mid-size habitat patches (Gray et al., 2016), and even use areas where human activity is high (Nickel et al., 2020). Humans on ranches use trails and dirt roads to move across the landscape, and similar to the conclusions in California (Nickel et al., 2020), the effectiveness of using the same trails as humans likely compensates for the costs of closer interactions, especially considering the ruggedness and low frequency of humans' presence that could facilitate temporal avoidance. The low levels of human presence must be regarded with caution since the responses to it could have dramatic changes depending on the species, sometimes with pervasive effects (Behera et al., 2024; Crooks, 2002; Expósito-Granados et al., 2019; Treves et al., 2006). For example, a female black bear that was sighted frequently looking for food in a truck stop area close to the highway was killed in a crash a few months later (J.M. Pérez *pers. comm.*).

Meso-predators showed higher tolerance to human impacts. In fact, coyotes were the only species with a positive response to cattle, as reported elsewhere, usually resulting in human-wildlife conflicts (Chamberlain and Leopold, 2005; Lombardi et al., 2017). Coyotes and bobcats showed higher use in the presence of cars, suggesting the use of dirt roads for travel. This advantage has been exploited for dispersal and colonization in human-dominated landscapes and to traverse between otherwise inhospitable locations (Monroy-Vilchis et al., 2020; Wang et al., 2015). Both species used the flat lands; however,

as reported in other studies where both species are present, the bobcats use grasslands and coyotes require more cover, such as scrubland and oak forest (Jones et al., 2016; Lonsinger et al., 2017). Similarly, habitat use of large herbivores varied by vegetation type. As reported previously in southeastern Arizona, the white-tailed deer was associated with more vegetation types, such as the grasslands, the oak forest, and the riparian forests, compared with the mule deer, which used less open grassland areas (Anthony and Smith, 1977). Finally, as described in other studies in the region, the collared peccary was the only large herbivore that used the scrubland more, in contrast with the white-tailed deer (Coronel-Arellano et al., 2018; Ragan et al., 2022; Villarreal et al., 2019).

Habitat conservation through the establishment of protected areas has been the cornerstone instrument for biological conservation (Figueroa & Sánchez-Cordero, 2008; Butchart et al., 2012; Crooks et al., 2011; Pimm et al., 2014). In this sense, establishing peace parks or transboundary protected areas offers a viable opportunity to maintain structural and functional connectivity (Gray et al., 2016; McInturff et al., 2020). Most of the lands where our study was conducted are private lands federally protected in Mexico; the neighboring area in the San Luis Mountain range is a biosphere reserve, and in the United States easements and forest land have some level of protection for conservation. Hence, a unique opportunity to establish a transboundary park is possible and might boost collaboration in maintaining populations of endangered species and controlling access. International collaboration between Mexico and the United States for wildlife conservation has been effective. For example, black bears, once eradicated in the Big Bend region in Texas, naturally recolonized the US areas after a successful conservation program in Mexico led by private landowners and cattle ranchers (Hellgren et al., 2005; Onorato and Hellgren, 2001). Finally, some of the mitigation measures that must be considered to keep corridors open are to avoid the use of razor coils, barbwire or electric fences that can entangle or electrocute animals in adjacent ranches and border infrastructures; the construction of artificial water sources and wildlife crossing structures; minimize

the human presence across the border with roads, lights, and patrols; and boost local populations of endangered species to maintain genetic diversity and long-term population viability (Linnell et al., 2016; Woodroffe et al., 2014). Such collaborative efforts demonstrate the most promise to affect biodiversity management and each nation's multiple additional objectives.

1.6 Tables

Table 1.1 Mammals recorded with camera traps in US-Mexico borderlands in Sonora, Mexico. Asterisks indicate those species with a body mass < 1 kg that were recorded with the camera traps but removed from the diversity analysis. The code refers to the first two letters of the generic and specific scientific name used in Figure 1.2.

Code	Species	Common name	Naïve occupancy (Total = 85)	Number of Independent videos (n = 21,486)	Relative abundance
SYSP	<i>Sylvilagus</i> spp.	Cottontail	77	3606	0.1678
ODVI	<i>Odocoileus virginianus</i>	White-tailed deer	71	2084	0.0970
URCI	<i>Urocyon cinereoargenteus</i>	Gray fox	71	1802	0.0839
MEMA	<i>Mephitis macroura</i>	Hooded skunk	74	1558	0.0725
LECA	<i>Lepus californicus</i>	Black-tailed jackrabbit	27	1531	0.0713
CALA	<i>Canis latrans</i>	Coyote	54	1240	0.0577
LYRU	<i>Lynx rufus</i>	Bobcat	76	1123	0.0523
OTVA	<i>Otospermophilus variegatus</i>	Rock squirrel	46	1083	0.0504
COLE	<i>Conepatus leuconotus</i>	Hog-nosed skunk	62	801	0.0373
URAM	<i>Ursus americanus</i>	Black bear	46	784	0.0365
PUCO	<i>Puma concolor</i>	Puma	56	654	0.0304
DITA	<i>Dicotyles tajacu</i>	Collared peccary	59	634	0.0295
SCNA	<i>Sciurus nayaritensis</i>	Mexican fox squirrel	23	591	0.0275
PESP	<i>Peromyscus</i> spp.*	Deer mouse	36	573	0.0267
NANA	<i>Nasua narica</i>	White-nosed coati	45	505	0.0235
NESP	<i>Neotoma</i> spp.*	Pack rat	45	505	0.0235
PRLO	<i>Procyon lotor</i>	Raccoon	41	458	0.0213
NEDO	<i>Neotamias dorsalis</i> *	Cliff chipmunk	19	399	0.0186
BAAS	<i>Bassariscus astutus</i>	Ringtail	37	379	0.0176
MEME	<i>Mephitis mephitis</i>	Striped skunk	51	367	0.0171
DIVI	<i>Didelphis virginiana</i>	Virginia opossum	34	289	0.0135
DISP	<i>Dipodomys</i> spp.*	Kangaroo rat	9	179	0.0083
SPGR	<i>Spilogale gracilis</i>	Spotted skunk	28	107	0.0050
AMHA	<i>Ammospermophilus harrisi</i> *	Harris's antelope squirrel	7	81	0.0038
ODHE	<i>Odocoileus hemionus</i>	Mule deer	23	63	0.0029
PAON	<i>Panthera onca</i>	Jaguar	18	59	0.0027

TATA	<i>Taxidea taxus</i>	Badger	10	16	0.0007
THBO	<i>Thomomys bottae</i> *	Botta's pocket gopher	4	7	0.0003
XESP	<i>Xerospermophilus spilosoma</i> *	Spotted ground squirrel	2	5	0.0002
LEPA	<i>Leopardus pardalis</i>	Ocelot	2	2	0.0001
ERDO	<i>Erethizon dorsalis</i>	Porcupine	1	1	0.0000

Table 1.2 Effect of landscape and human influence covariates over the community of mammals in the borderlands of northeastern Sonora, Mexico, using a permutational multivariate analysis of variance (PERMANOVA). *P*-values < 0.01 are bolded.

Covariate	<i>d.f.</i>	<i>S.S.</i>	<i>R</i> ²	<i>F</i>	<i>P</i> -value
Vegetation type	4	3.70	0.158	4.46	< 0.0001
Cars	1	0.55	0.023	2.65	0.0048
Cattle	1	0.77	0.032	3.70	0.0006
Humans	1	0.19	0.008	0.89	0.5277
Distance to the border wall	1	0.75	0.032	3.64	0.0004
Distance to the road	1	0.40	0.017	1.91	0.0376
Effort	1	0.69	0.029	3.32	0.0012
Vegetation type × Cars	4	0.40	0.017	0.49	0.9988
Vegetation type × Cattle	4	1.15	0.049	1.39	0.0533
Vegetation type × Humans	4	0.67	0.028	0.80	0.8174
Vegetation type × Distance to the border wall	4	1.37	0.058	1.65	0.0073
Vegetation type × Distance to the road	4	1.71	0.072	2.05	0.0002
Vegetation type × Effort	4	0.73	0.031	0.88	0.6809
Residual	50	10.38	0.442		
Total	84	23.48	1.000		

Table 1.3. Summary of averaged models that explain the habitat use and detectability of the community of mammals in the US-Mexico borderlands in Sonora, Mexico. Covariates were considered relevant when the standard error of the averaged estimates did not cross zero. The presence of cattle was the only covariate considered for detectability and was calculated as the number of independent cattle detections per week.

Ecosystem role	Species	Number of averaged models	Cumulative AIC weight	Number of relevant covariates for habitat use	Influence of cattle in detectability	Cattle detectability estimate and SE
Large carnivores	Puma	5	0.90	5	Negative	-0.42 ± 0.18
	Jaguar	7	0.92	1	-	-
	Black bear	2	1.00	2	Positive	0.20 ± 0.06
Large herbivores	White-tailed deer	5	0.93	2	Negative	-0.04 ± 0.03
	Mule deer	18	0.904	1	-	-
	Collared peccary	5	0.90	1	-	-
Meso-predators	Coyote	4	0.92	3	-	-
	Bobcat	6	0.91	2	-	-
	Striped skunk	6	0.98	1	-	-
	Ringtail	8	0.90	1	-	-
	Raccoon	6	0.97	1	-	-
	Hooded skunk	5	0.91	1	-	-
	Hog-nosed skunk	4	0.93	2	-	-
	Gray fox	7	0.91	1	Negative	-0.11 ± 0.06
	White-nosed coati	2	0.95	6	-	-
Small herbivores	Black-tailed jackrabbit	1	1.00	5	-	-
	Cottontail	2	0.99	5	-	-

1.7 Figures

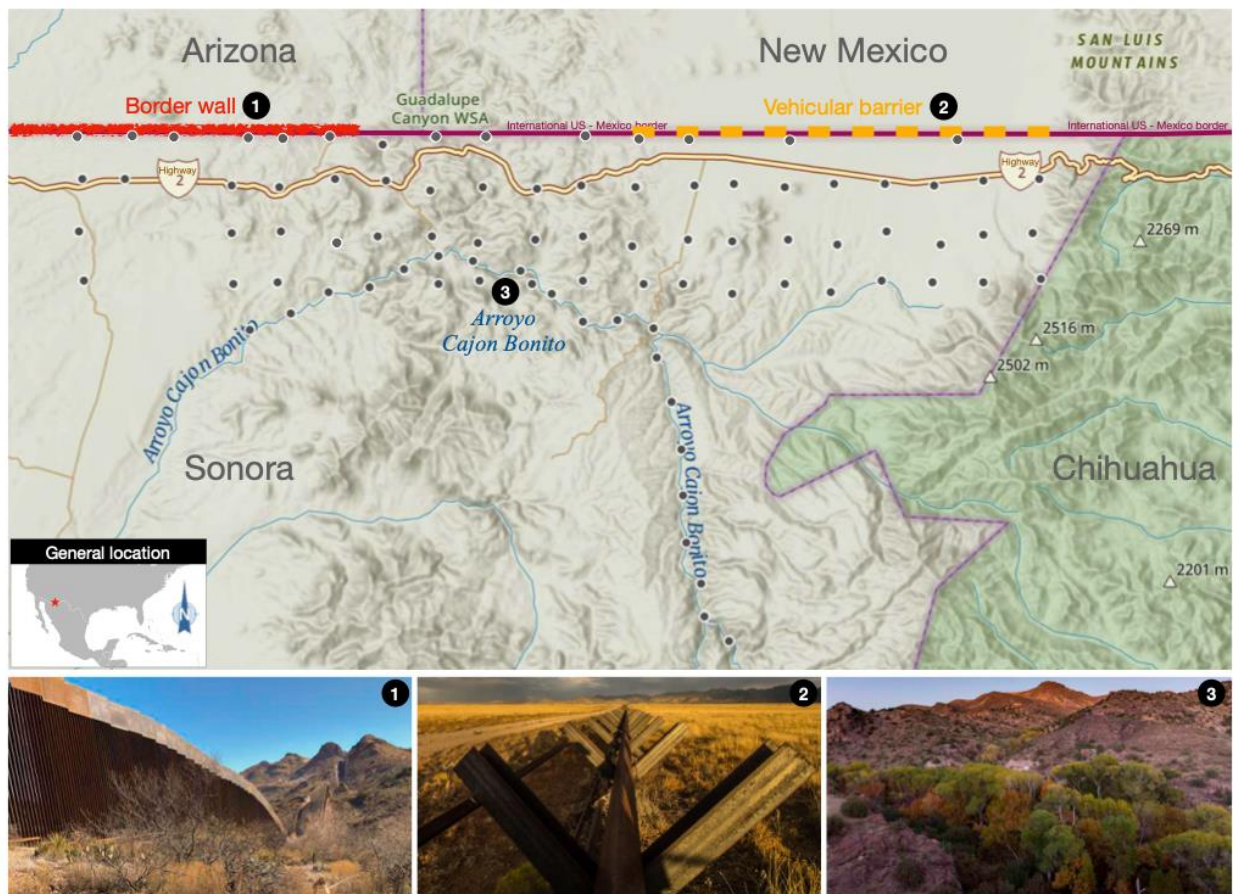


Figure 1.1 Location of the motion-activated cameras with infrared flash aimed to detect medium and large mammal species in northeastern Sonora, Mexico. Eighty cameras were set in a grid arrangement parallel to the international border in front of the different border structures between Arizona and New Mexico and Highway 2 in Mexico. Additionally, 20 cameras are along the Cajon Bonito stream following the stream course.



Figure 1.2 Relative abundance-species rank curves and indicator species for the five ecosystems we surveyed in northeastern Sonora, Mexico borderlands. The code of the species corresponds to Table 1.1 and refers to the four-letter code of the scientific name.

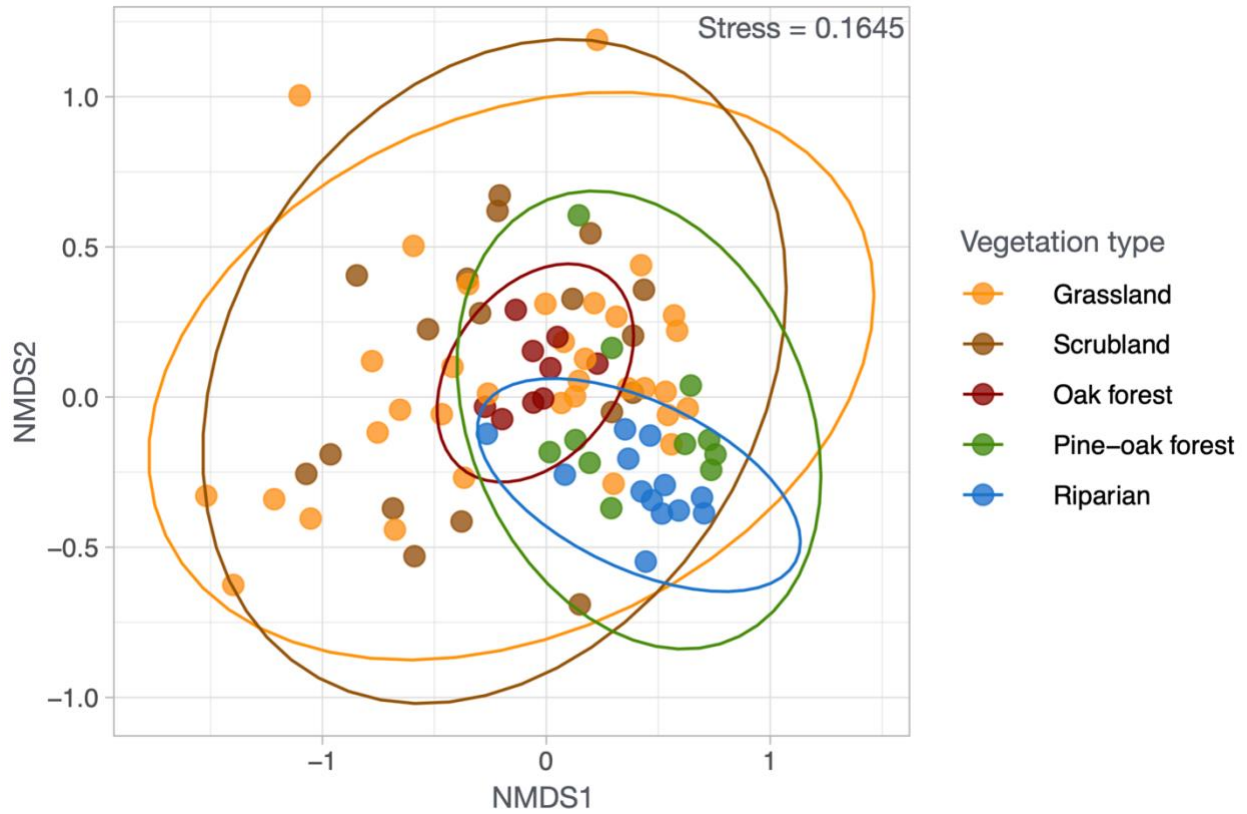


Figure 1.3 Non-metric multidimensional scale analysis of the community of mammals in the borderlands of northeastern Sonora, Mexico. The ellipses represent the grouping for each vegetation type using a multivariate normal distribution. The centroid of each ellipse is the mean of the NMDS1 and NMDS2 axes for each vegetation type.

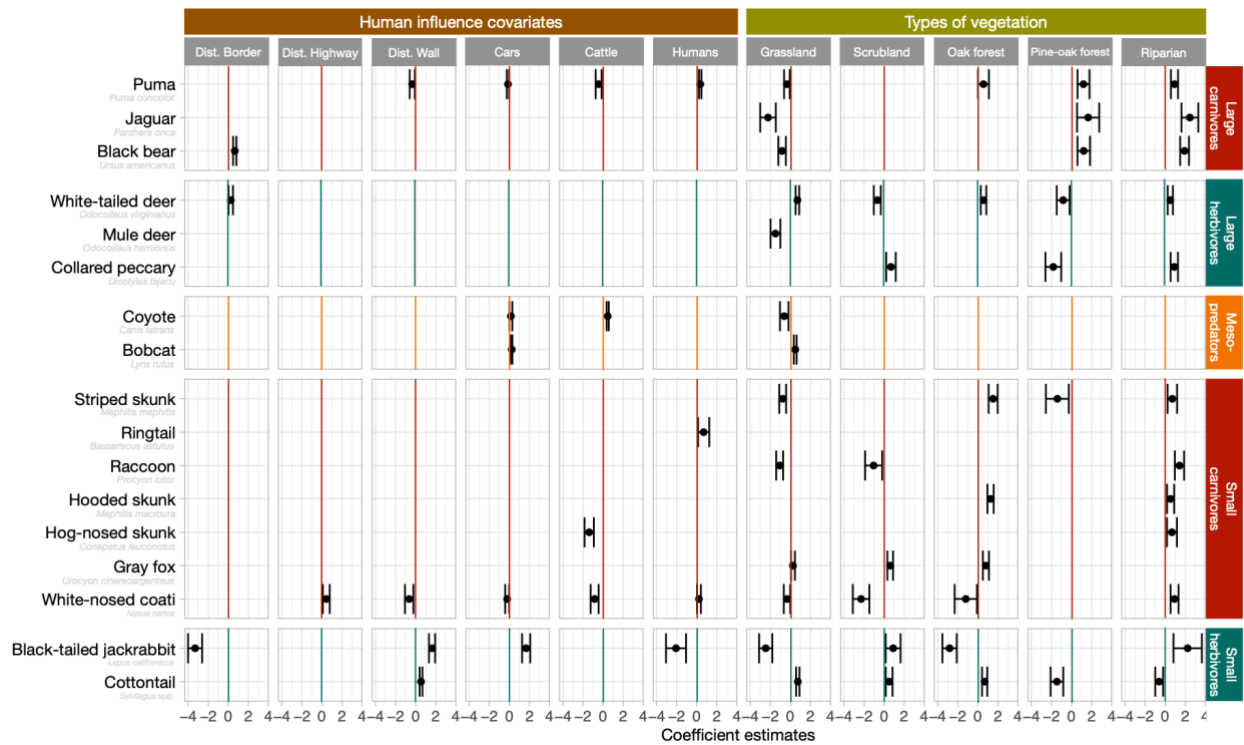


Figure 1.4 Habitat and human influence covariate effects over the abundance of mammals in the Sonoran borderlands, Sonora, Mexico. The detections were obtained using 85 motion-activated cameras with infrared flash aimed to detect medium and large mammal species.

Chapter 2. Mismatched mammal observations using camera traps and environmental DNA in a desert riparian area

2.1 Abstract

Traditional monitoring methods, particularly camera trapping, can be expensive, labor-intensive, and susceptible to equipment failure or theft, especially in challenging environments. Continuously developing environmental DNA (eDNA) metabarcoding techniques offer a potentially more cost-effective and efficient alternative to monitoring wildlife terrestrial species. We compared the effectiveness of camera traps and eDNA for monitoring terrestrial mammal diversity in a desert riparian area along the US-Mexico border. We surveyed a 20 km section of the perennial Cajon Bonito stream, deployed camera traps, and collected eDNA water samples at ten locations along the stream during wet and dry seasons. The camera traps operated continuously for 31 days before each eDNA sampling event. The results indicated that camera traps detected significantly more species (18 in the wet season, 17 in the dry) than eDNA (5 and 4 species, respectively). While some species detected via eDNA were also detected using camera traps, the beaver (*Castor canadensis*) was exclusively detected with eDNA. We analyzed the relationship between camera trap detections and eDNA detection, considering temporal proximity between detection events and spatial proximity. However, no significant correlation was found, contrasting with findings from more humid environments. The lack of correlation suggests that the factors influencing eDNA detection in arid environments, such as DNA persistence, degradation, and transport, make this technique less reliable than in humid environments. Also, the lower structural complexity of arid vegetation compared to humid environments might also reduce DNA persistence and transport. While eDNA shows promise as a supplementary tool, in this arid ecosystem, camera traps remain more effective for assessing overall mammalian diversity.

2.2 Introduction

Reliable assessments of the status of wildlife communities are needed for all conservation efforts and management activities (Swan et al., 2014), especially when wildlife populations are declining at an alarming pace worldwide (Brodie et al., 2021; Ceballos et al., 2017). However, the techniques and effectiveness of monitoring programs vary with the extant number of species and their varying abundances across different ecosystems (Burton et al., 2024). Due to the elusiveness of medium- and large-sized mammals, it has been historically challenging and costly to quantify population and community trends across diverse landscapes (Ceballos and Ehrlich, 2002; Dirzo et al., 2014; Ripple et al., 2014). In recent decades, camera traps have been the quintessential technique for monitoring terrestrial mammals, but they are limited in spatial scale, produce copious amounts of data to be managed, have differences in the detection rates depending on species' body size, and cameras can be damaged in extreme heat and cold, flooding, wildfire, or by vandalism and theft (Hamel et al., 2013; O'Connor et al., 2017). The advent of molecular techniques for detecting species *in situ* promises to overcome some of the challenges of camera traps by increasing detection of elusive species, improving specific identification, and increasing the affordability of monitoring vast areas (Fediajevaite et al., 2021; Takahashi et al., 2023).

For terrestrial mammals, every year, more surveys look for the DNA of mammals in soil, water, and air, where they successfully detect diversity patterns, reveal invasive and cryptic species, and facilitate rapid assessments (Lynggaard et al., 2022; Sales et al., 2020; Ushio et al., 2017; Williams et al., 2018), also known as metabarcoding (Cristescu, 2014). In general, a piece of DNA is used to identify a species based on a standardized section of a highly stable mitochondrial gene established from voucher specimens known as barcodes. Metabarcoding is when high-volume and fast identification of several species is done using degraded samples of DNA material (Cristescu, 2014; Van Der Heyde

et al., 2022). The mechanism of how a mammal is detected using DNA metabarcoding depends on the release of the genetic material of the mammal to the environment by defecation, saliva or mucus in drinking water, swimming or taking dirt baths, shedding, and the continuous release of skin cells or body parts (Ushio et al., 2017; Van Der Heyde et al., 2022). Although technological advances have improved the detection rates of DNA in water and soil samples (Fediajevaite et al., 2021; Takahashi et al., 2023; Van Der Heyde et al., 2022), the successful collection and identification of environmental DNA samples (hereafter eDNA) still poses challenges. Factors that affect eDNA samples include UV degradation of DNA, the transportation of the genetic material away from its source, varying levels of DNA persistence in different substrates, and the amount of DNA that individuals shed in the environment depending on their body size and behavioral habits (Coutant et al., 2021; Harper et al., 2019; Van Der Heyde et al., 2022).

The American Southwest possesses one of North America's most diverse communities of mammals (Coronel-Arellano et al., 2018; Warshall, 1995). The Sonoran and Chihuahuan deserts primarily influence the vast and rugged landscape, but the presence of mountain ranges provides a habitat for montane temperate species along the elevational gradient and perennial water sources (Stromberg et al., 2013). The diversity and abundance of many terrestrial mammals in this arid region is determined in part by the availability of surface water sources and their associated resources of riparian corridors and springs (Herzog and Bateman, 2021; Ragan et al., 2022; Sánchez-Montoya et al., 2022). Because water is a limiting factor in arid lands, water sources and riparian areas are hotspots of diversity in the region and ideal locations for rapid assessments of mammal communities, including endangered, low-abundance, and cryptic species such as jaguar (*Panthera onca*), beaver (*Castor canadensis*), ocelot (*Leopardus pardalis*), and Mexican wolf (*Canis lupus baileyi*) (González-Saucedo et al., 2021; Ragan et al., 2022, 2021).

In the face of warmer and often drier conditions due to climate change (Williams et al., 2022), the distribution of mammals is expected to shift in a mosaic of land use management and varied habitat protection (Peters et al.,

2018; Villarreal et al., 2019). Furthermore, human-made barriers that deter animal movement have been established and expanded in recent years, providing an urgent need for the deployment of rapid and efficient surveys to detect changes in wildlife populations (Chen and Koprowski, 2016; Chen et al., 2011; Koprowski et al., 2005; Tucker et al., 2018). In the American Southwest, these novel anthropogenic barriers include highway construction and expansion and the border wall constructed between the United States and Mexico (Harrity et al., 2024; Peters et al., 2018). However, despite this need for rapid data collection for conservation planning in dynamically changing regions, only a few studies have monitored terrestrial species in arid environments using eDNA surveys (Egeter et al., 2018; Leempoel et al., 2020).

This study aimed to compare the performance of camera traps versus eDNA for monitoring terrestrial mammals in northern Mexico along the US-Mexico border. We focused the survey on one of the few perennial water sources in the area, the Cajon Bonito stream, due to the previous research in the watershed documenting over 30 species of terrestrial mammals, including endangered species (Pelz-Serrano et al., 2005; Ragan et al., 2022, 2021). We hypothesized that the estimated diversity of terrestrial mammals using camera traps and environmental DNA would be similar, and we expected to find a positive relationship between the number of detections of a species in camera traps and eDNA across our monitoring sites. Secondly, we hypothesized that genetic material would accumulate moving downstream through the watershed (Lyet et al., 2021), so we predicted a higher abundance of species detections in eDNA samples at downstream sites within the watershed. Our third hypothesis was that UV light and heat would disintegrate DNA and reduce detectability (Sales et al., 2020; Van Der Heyde et al., 2022; Wilcox et al., 2021), leading to reduced eDNA detections for a given species as time increased since the species was detected on a nearby camera. Finally, because species that interact frequently with water bodies, e.g. beaver and raccoon (*Procyon lotor*), have more opportunity to shed DNA in water (Coutant et al., 2021; Harper et al., 2019), we expected that aquatic and riparian specialist mammals would be detected most frequently in eDNA

samples. Our overall hope was that our results would inform both the effectiveness and limitations of the using camera trap and eDNA techniques to monitor biodiversity in megadiverse and arid landscapes.

2.3 Methods

2.3.1 Study site

Our study site was located in the northernmost section of the Sierra Madre Occidental, between the Sonoran and the Chihuahuan Desert in northeastern Sonora, Mexico (González-Elizondo et al., 2012). This area between Mexico and the United States of America is in the Sky Islands region and it has been recognized as a biodiversity hotspot due to the convergence of Nearctic and Neotropical species (Warshall, 1995). The landscape is rugged and the elevation defines the vegetation types. Desert grasslands and scrublands are found at lower elevations (<1,400 m asl), and a transition to oak (*Quercus* spp.) and pinyon-juniper (*Pinus discolor-Juniperus arizonica*) forest occurs around 1,600 m asl. Oak and pine forests, mostly *Pinus ponderosa*, are found at higher elevations (1,700-2,300 m asl). The mean annual temperature is 17.2°C, and the mean annual precipitation is 241.1 mm, during the monsoon in July-September (CONAGUA, 2024). In this study, we focused on a section of the Cajon Bonito stream, one of the region's few permanent water sources and one of the most pristine rivers in northern Mexico. The headwaters of Cajon Bonito are at the western slope of the Sierra Madre Occidental mountain range (González-Elizondo et al., 2012). The Cajon Bonito stream is part of the Yaqui river basin (CONAGUA, 2018). The Yaqui drains the western slopes of the Sierra Madre Occidental into the Gulf of California near the city of Obregon and constitutes one of the major river systems of northwestern Mexico (Nicholas & Battisti, 2008). The Cajon Bonito is in the hydrographic sub-basin of the river Batepito-San Bernardino (2,463 km² drainage area), which is a tributary to the Bavispe river (CONABIO, 1998; CONAGUA, 2018). The Cajon Bonito is intermittent in its headwaters, but a perennial section of the stream flows all year from 1,400 to 1,200 m asl over a

30 km stretch. During the dry season (Nov-Jun), baseflow in this perennial stretch is approximately $0.3 \text{ m}^3 \text{ s}^{-1}$; during the wet season (Jul-Oct), monsoon storms can cause floods $>25 \text{ m}^3 \text{ s}^{-1}$ and result in days or weeks of elevated baseflow. This section of the stream has been protected during the last two decades and established as a voluntary area for conservation under the Mexican Natural Protected Areas System (CONANP, 2024). We selected 10 locations along the stream, separated by 2 km each, connected by flowing water during the year to compare the performance of camera traps and eDNA (Figure 2.1).

2.3.2 Camera trap monitoring

We installed a Bushnell core camera trap with infrared flash (Bushnell core DS, Utah, USA), in each of the ten sampling locations at the trail or animal path closest to the stream ($< 30 \text{ m}$ in all locations). The cameras were placed 40 cm above the ground, without bait and aimed to detect medium- and large-sized mammals. The cameras were active 24 h/day and recorded 10-second videos when heat and movement were detected, with a 5-minute delay between detections. These camera trap locations were part of a long-term monitoring effort. When comparing eDNA detections (see below) with camera trap detections at a given site, we considered the camera trap record for the previous 31 days before the eDNA samples were taken. We quantified camera trap detections at a daily scale, meaning we considered an individual species to have been ‘detected’ for that daily period if it appeared in any images during the 24-h period.

2.3.3 Collection of eDNA in the field

We also collected water samples for eDNA at 10 locations across the Cajon Bonito stream in two seasons, sampling water from the stream directly in front of the tree where the associated camera trap was installed on the stream banks. Wet season eDNA water samples were collected on 29 and 30 October 2021, at the end of the monsoon rainy season, and dry season eDNA water samples were collected on 4 and 5 May 2022, during the pre-monsoon dry season. To collect the water samples, we used a self-preserving nitrocellulose filter with a pore size

of 1.2 μm (Smith-Root, Vancouver, WA, USA). We filtered water from the middle point of the stream for 15 minutes using a peristaltic pump (Geotech Geopump peristaltic pump series II, American Falls, ID, USA) at 350 rpm with a liquid delivery rate of 1.67 ml per revolution using a size-15 tube (Table 2.1). The samples were collected in duplicate from downstream to upstream locations, disinfecting the tube with a 5% chlorine solution between each location. The samples were stored in a cabinet in sealed bags at ambient temperature until they were sent to the laboratory for analysis.

2.3.4 DNA extraction and identification of species

The samples were processed by third-party laboratories (Smith-Root, Vancouver, WA, USA, and Jonah Ventures, Boulder, CO, USA) via eDNA metabarcoding. The amplicon sequencing libraries were prepared using the universal MiMammal-U primers as the locus-specific sequences to target a hypervariable region of mammal mitochondria 12S rRNA gene (Ushio et al., 2017). A Fragment Analyzer Automated CE System assessed the library quality and quantity with the dsDNA 935 reagent kit (Agilent Technologies) and Qubit Fluorometer with the Qubit® dsDNA BR Assay kit (Thermo Fisher Scientific). The purified libraries were normalized and combined in an equal molar ratio for sequencing. PhiX (Illumina) was included to serve as an internal control for sequencing, and a control containing 10 different species was included to monitor the entire process. Sequencing was conducted using a MiSeq sequencer with a MiSeq Reagent Kit v2 (Illumina) and 2x250 paired-end cycles. Raw sequence reads were filtered using the MiSeq Sequencer System Software (Illumina) to remove low-quality sequences and trimmed to remove adaptor sequences. The mammal mitochondria 12S rRNA gene sequences were further analyzed using the Geneious software (Biomatters) against sequences in the NCBI RefSeq database.

2.3.5 Comparisons of eDNA versus camera trap performance

We compared the estimated number of species detected in all locations per season and at each location with camera traps-only, eDNA-only, and both

methods. We considered a positive detection event (binary value = 1) with the camera traps when any given species was detected at any given location during a 24-h period. Then, if the same species was detected multiple times during the same day at the exact location, the value was still considered 1. The total number of positive events with camera traps considers all detection events that occurred during the 31 days the cameras were active prior to eDNA water sampling. In the case of eDNA, we considered a positive detection event when a sample detected any given species at any given location. The total number of positive events with eDNA includes all positive detections, considering we took two samples per location.

To examine how detections varied by method and season, we first compared the number of eDNA samples with a detection between seasons within locations. With camera traps, we compared the number of days with a detection during the 31-day wet and dry in wet versus dry seasons. Then, when a species was detected with an eDNA sample, we calculated two metrics. First, we calculated the number of days to the last camera trap detection at that location and then calculated the average of all the locations and all the species as a summary statistic. Second, when we detected a species at a specific location with eDNA samples, we calculated the distance to the closest photographic detection for that species at an adjacent or any camera trap located upstream in the watershed. Then, as a summary statistic, we calculated the average distance between eDNA and adjacent or upstream photo detections using all locations and species.

We tested the relationship between detecting a species with eDNA versus camera traps using a generalized linear model with a binomial link. Given the small number of events per species, we did not include the species identity variable in the model. We considered the detection/non-detection with eDNA as a binary response determined by the number of days that a specific species was detected during the camera trap sampling season at that location, the number of days to the last detection at that location, and the distance to the closest

detection upstream. The analysis was done in R with the glmTMB package, and we considered relevant covariates when P -value < 0.05 .

2.4 Results

We detected at least 20 different species of mammals from 12 families and five orders (Table 2.2). Similar detections were found between the two seasons with camera traps, eDNA, and both methods combined (Table 2.3). Considering both seasons, all the species detected with eDNA were also detected with camera traps except for the beaver, and only seven species were detected with eDNA (Table 2.3).

During the wet season, most of the detection events with eDNA corresponded to beaver, which were detected in all locations and all samples. Other species were detected less frequently with eDNA; deer (*Odocoileus* spp.) were detected in 11 samples at 6 locations, black bear in 3 samples in two locations, and jaguar in one sample. The beaver was the most detected species during the dry season, but only in 6 samples at three different locations. Deer, deer mice (*Peromyscus* spp.), and Mexican fox squirrels (*Sciurus nayaritensis*) were detected in one eDNA sample each. For species detected at a location with eDNA, the average number of days elapsed since the last detection with the camera trap at that exact same sampling location was 10.54 days (SD = 8.44) for the wet season and 11.53 days (SD = 10.07) for the dry season. Additionally, the upstream distance to the next closest detection with a camera was roughly 3 km (Table 2.3). We did not find evidence that the number of days that a species was detected during the camera trap sampling at that location, the number of days to the last detection at that location, or the distance to the closest detection upstream were related to the detection of that species in eDNA samples (Table 2.4; Figure 2.2).

2.5 Discussion

2.5.1 Diversity of mammals detected with eDNA and camera traps

Environmental DNA monitoring of terrestrial species is still an emerging technique but it has proven effective across different types of ecosystems (Lyet et al., 2021; Mena et al., 2021; Sales et al., 2020; Ushio et al., 2017). We surveyed a riparian ecosystem in an arid region and found that the camera traps detected three times more species than eDNA water samples during both dry and wet seasons. These results contrast with the higher eDNA detection levels found in water samples from more humid environments, where surface water also is more abundant on the landscape (Coutant et al., 2021; Lyet et al., 2021; Mena et al., 2021). For example, two vole species (*Arvicola amphibius* and *Microtus agrestis*) and the red deer (*Cervus elaphus*) were more likely to be detected in water samples from a riverine system in the Scottish Highlands than in camera traps or terrestrial sediment samples (Sales et al., 2020). Additionally, in the Amazon rainforest of French Guyana, more species were detected with eDNA compared to line transects that used visual surveys to detect mammals (Coutant et al., 2021). The same pattern of higher detection of species in eDNA was reported in the temperate rainforest of British Columbia using water samples from the lower part of the watershed compared to camera traps (Lyet et al., 2021). Furthermore, in the Peruvian rainforest, more small mammal species were detected with eDNA from water samples than with camera traps; however, more medium and large mammals were detected with camera traps than with eDNA in the same study (Mena et al., 2021). Our results from an arid watershed are most similar to one of the few other eDNA studies in arid ecosystems, where researchers detected only two of nine mammal species known to be present around the focal water holes (Egeter et al., 2018).

The stream we surveyed has water year-round, yet we detected a few terrestrial species using eDNA from water samples. One of the main differences between arid and humid landscapes is vegetation's structural complexity, which might be relevant for the transportation and persistence of DNA in arid

environments. Several authors have suggested that the multiple vegetation layers in humid environments provide more shaded places, in which DNA is less exposed to direct sunlight and experiences fewer temperature shifts, providing ideal places to find higher quantities of conserved DNA material (Fediajevaite et al., 2021; Van Der Heyde et al., 2022; Webb and Leake, 2006). However, recent research suggests that sun exposure and temperatures do not greatly impact DNA degradation compared to the effects of microbial degradation (Guthrie et al., 2024; Mächler et al., 2018). We effectively detected beavers and black bears (*Ursus americanus*) in most samples, even though we know they are not abundant at our study site (Lara-Díaz et al., 2018; Pelz-Serrano et al., 2005). These two species frequently live in or interact with the stream, so we suspect that the interaction of the organisms with surface water might be crucial for the liberation of DNA in the environment. The infrequency of rain and runoff events that *wash* the mammals or carry their DNA in dry environments might be why we failed to detect many resident mammal species in our region that have limited interactions with surface water (Harper et al., 2019; Williams et al., 2018).

Previous work has shown that the size of the catchment correlates with the amount of DNA collected from streams and the number of mammals detected with camera traps (Lyet et al., 2021). In the 20 km section we surveyed in Cajon Bonito, we found no correlation between the camera trap and the eDNA surveys regarding the sampling location upstream or downstream in the catchment, in contrast with other similar studies (Coutant et al., 2021; Leempoel et al., 2020; Lyet et al., 2021). If we were to expand the length of our transect beyond 20 km, it is possible that we would see more substantial differences in mammal detections between headwaters and downstream reaches. However, most streams in the American Southwest do not have a surface flow year-round and are only connected hydrologically during brief and rare flood events (Webb and Leake, 2006). In the Cajon Bonito stream, downstream we would find only isolated pools of water rather than flowing connected reaches, so the accumulation of DNA at downstream locations would only be possible during destructive flood events.

2.5.2 *The specific mismatches between eDNA and camera traps*

The diversity found with the one-month camera trap deployments at each location in this study was similar to the results of a two-year study using the same locations and upland slopes nearby, which found 22 species of mammals (Marín et al. *In prep.*). The species that our shorter-term survey failed to detect were those that are cryptic and have low abundances, including ocelot, or species that are common in nearby ecosystems but rarely encountered in riparian ecosystems, such as the American badger (*Taxidea taxus*), mule deer (*Odocoileus hemionus*), and the black-tailed jackrabbit (*Lepus californicus*). We succeeded in detecting some of the most abundant species that use the riparian forest with the eDNA samples, such as deer, black bear, javelina (*Dicotyles tajacu*), and Mexican fox squirrels. The detection of the jaguar in our study, a low-abundance species in the region, was surprising, and its detection might be due to their high affinity with water. Jaguars have been detected before using eDNA in water (Coutant et al., 2021; Mena et al., 2021; Wilcox et al., 2021); however, felines generally are more challenging to detect due to their general avoidance of water (Lyet et al., 2021). For example, puma (*Puma concolor*) and bobcats (*Lynx rufus*) are common in the riparian area and were detected consistently with the camera traps. However, we did not detect them with eDNA water samples. Previous studies using soil samples reported an overrepresentation of both puma and bobcat in their eDNA soil samples due to their latrine and marking habits, suggesting that species' affinities and behaviors determine their detectability in water, soil, or air (Leempoel et al., 2020; Williams et al., 2018). Combining soil and water eDNA approaches would yield a more comprehensive species list for a location given species-specific differences in behavior (Lyet et al., 2021) and detectability with each approach (Takahashi et al., 2023).

2.5.3 *Future monitoring efforts in arid and biodiverse landscapes*

Our models found no relationship between eDNA survey detection and the distance that a mammal was detected with a camera trap upstream. The

questions of how long the eDNA remains in the aquatic system and how far it is transported before it can be detected are still open and more likely would depend on a variety of local conditions, including antecedent flow conditions and temperature, light, and microbial activity levels (Jo and Yamanaka, 2022; Lynggaard et al., 2022; Sales et al., 2020). In agreement with previous studies that suggested that the downstream transport of eDNA does not exceed a few kilometers (Coutant et al., 2021), we found that the average distance to the closest detection with camera traps upstream once we detected a species with eDNA was around 3 km. However, understanding transport distances and the degradation rates of DNA material in this stream would take significant further study to disentangle.

In conclusion, our study indicates that camera trap surveys are more effective for detecting mammals than water-based eDNA in the riparian system we surveyed. Despite the homogeneous species richness detected across our samples, some precautions might be helpful when focusing only on obtaining an inventory of species. For example, pooling the samples across the stream to mitigate the consequences of reduced DNA yield at downstream locations (Takahashi et al., 2023) and increasing the volume of water filtered (Lyet et al., 2021) might help increase the detection rates. Selecting the appropriate medium to sample (water, soil, air) while considering the focal species' habits is essential to maximizing the detection of focal species in any given region. As previous authors have suggested (Cristescu, 2014; Fediajevaite et al., 2021; Van Der Heyde et al., 2022), further comparisons of DNA metabarcoding surveys against traditional methods will help to refine this still-developing technique. The mismatches we found via eDNA metabarcoding and the camera traps offer insights into the main challenges and considerations for monitoring in arid conditions, suggesting that, for now, traditional surveys using camera traps are still more effective for quantifying mammal diversity in our biodiverse region.

2.6 Tables

Table 2.1 Volume of water filtered per sample used to characterize the community of mammals in the US-Borderlands using environmental DNA from the Cajon Bonito stream in Sonora, Mexico. Each sample (S1 and S2), was obtained by filtering water from the stream for 15 minutes using a peristaltic pump.

Location	Dry season		Wet season	
	S1 water volume (L)	S2 water volume (L)	S1 water volume (L)	S2 water volume (L)
NG19	1.0	1.2	2.0	2.1
NG18	3.3	4.2	2.0	1.3
NG17	2.3	2.2	1.8	1.8
NG16	1.4	1.4	2.4	2.0
NG15	2.2	2.1	4.0	2.4
NG14	2.0	1.5	2.2	2.5
NG13	1.9	1.7	3.5	2.9
NG12	3.9	2.1	2.9	1.1
NG11	2.8	2.9	1.9	2.5
NG10	3.1	4.4	2.8	2.4
Total water volume filtered per season	47.6 L		46.5 L	
Average water volume filtered per location	4.76 L (SD = 1.85)		4.65 L (SD = 1.06)	
Average water volume filtered per sample	2.38 L (SD = 0.98)		2.32 L (SD = 0.68)	

Table 2.2 Species of terrestrial mammals detected with camera traps (CT), and environmental DNA during wet and dry seasons in the Cajon Bonito, Sonora, Mexico.

Family	Species	Common name	Wet season		Dry season	
			CT	eDNA	CT	eDNA
Order Artiodactyla						
Cervidae	<i>Odocoileus</i> spp.	Deer	X	X	X	X
Tayassuidae	<i>Dicotyles tajacu</i>	Collared peccary	X	X	X	
Order Carnivora						
Canidae	<i>Canis latrans</i>	Coyote	X		X	
	<i>Urocyon cinereoargenteus</i>	Gray fox	X		X	
Felidae	<i>Lynx rufus</i>	Bobcat	X		X	
	<i>Panthera onca</i>	Jaguar	X	X		
	<i>Puma concolor</i>	Puma	X		X	
Mephitidae	<i>Conepatus leuconotus</i>	Hog-nosed skunk	X		X	
	<i>Mephitis macroura</i>	Hooded skunk	X		X	
	<i>Mephitis mephitis</i>	Striped skunk	X		X	
Procyonidae	<i>Bassariscus astutus</i>	Northern ringtail	X		X	
	<i>Nasua narica</i>	Coati	X		X	
	<i>Procyon lotor</i>	Raccoon	X		X	
Ursidae	<i>Ursus americanus</i>	Black bear	X	X	X	
Order Didelphimorphia						
Didelphidae	<i>Didelphis virginiana</i>	Opossum				X
Order Lagomorpha						
Leporidae	<i>Sylvilagus</i> spp.	Cottontail	X		X	
Order Rodentia						

Castoridae	<i>Castor canadensis</i>	Beaver		X		X
Cricetidae	<i>Peromyscus</i> spp.	Deer mouse	X			X
Sciuridae	<i>Otospermophilus variegatus</i>	Rock squirrel	X		X	
	<i>Sciurus nayaritensis</i>	Mexican fox squirrel	X		X	X

Table 2.3 Metrics of detection and diversity used to assess the performance of camera traps and environmental DNA samples for characterizing the community of mammals during the wet and dry season in the Cajon Bonito stream in northeastern Sonora, Mexico. We took two water samples from the stream per site in each of the 10 site locations. The number of events with environmental DNA refers to the total number of species detected in all of the 20 samples taken per season. The number of events with the camera traps refers to the number of species detected during a 31-day period considering a 24-hour independence window. When a species was detected at any given site using environmental DNA, we measured the number of days to the last detection of that species from the camera trap at the same location. When a species was detected at any given site using environmental DNA, we measured the distance where the same species was detected with camera traps, but we only considered upstream sites. If the species were detected at the same site, the distance would be 0.

Metric	Wet season	Dry season
Total number of species detected	19	19
Species detected with camera traps	18	17
Species detected with environmental DNA	5	4
Number of events with a positive detection with environmental DNA samples	36	9
Number of events with a positive detection with camera traps	379	293
Days to the last detection from the camera trap at the same location	Mean = 10.54 days SD = 8.44	Mean = 11.53 days SD = 10.07
Distance to closest detection with camera traps upstream	Mean = 3.17 km SD = 2.47	Mean = 3.02 km SD = 2.44

Table 2.4 Effect of environmental and detection covariates from camera traps over the detection of mammals using environmental DNA samples at the Cajon Bonito stream, Sonora, Mexico.

Variable	Estimate	Std. error	Z	P-value
Intercept	-2.48	1.186	-2.09	0.035
Season	0.19	1.532	0.13	0.896
Days with detection	-0.03	0.187	-0.18	0.851
Days to last detection	0.01	0.044	0.32	0.748
Distance to closest detection upstream	-0.04	0.196	-0.24	0.805
Season × Days with detection	0.07	0.206	0.36	0.713
Season × Days to last detection	-0.08	0.080	-1.10	0.271
Season × Distance to closest detection upstream	0.18	0.242	0.78	0.435

AIC = 116.4

BIC = 142.2

Deviance = 100.4

d.f. residual = 177

2.7 Figures

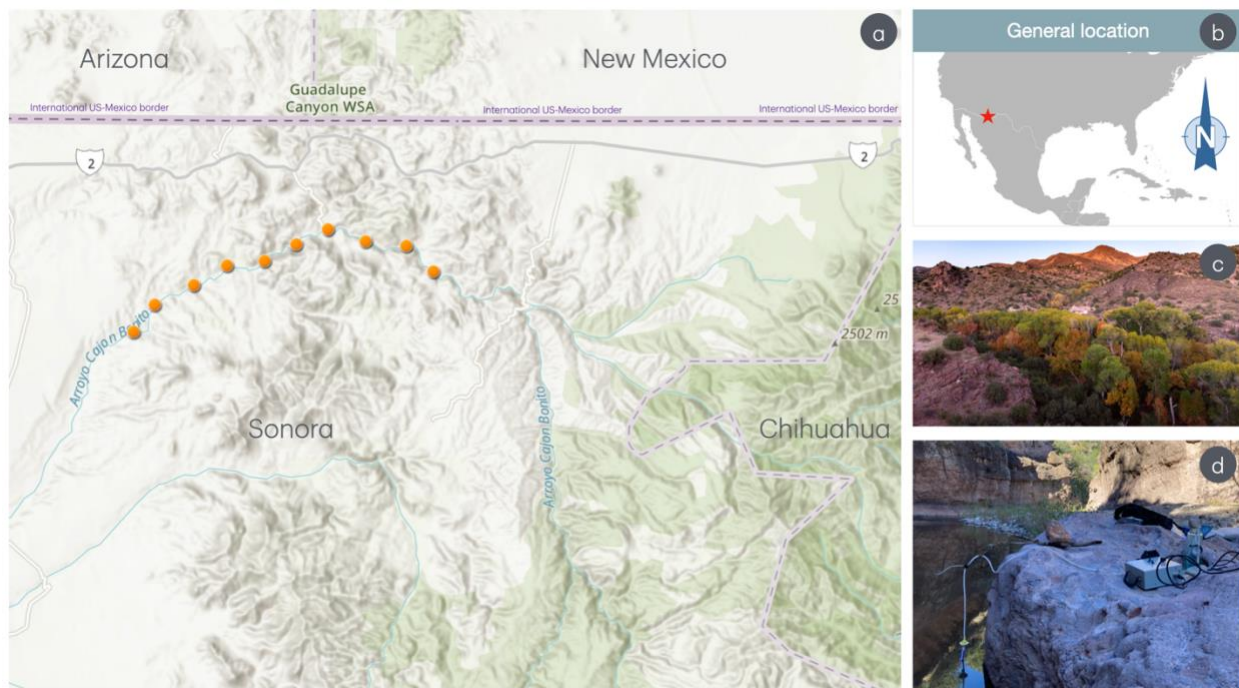


Figure 2.1 Sampling locations in the US-Mexico borderlands at Cajon Bonito stream in Sonora, Mexico. a) Location of the ten sampling points where environmental DNA and the camera traps were set along the Cajon Bonito stream. b) General location of the borderlands between Mexico and the United States. c) The Cajon Bonito stream is one of the few water sources in the arid landscape. d) Environmental DNA sampling at the stream using the self-preserving filters at the field.

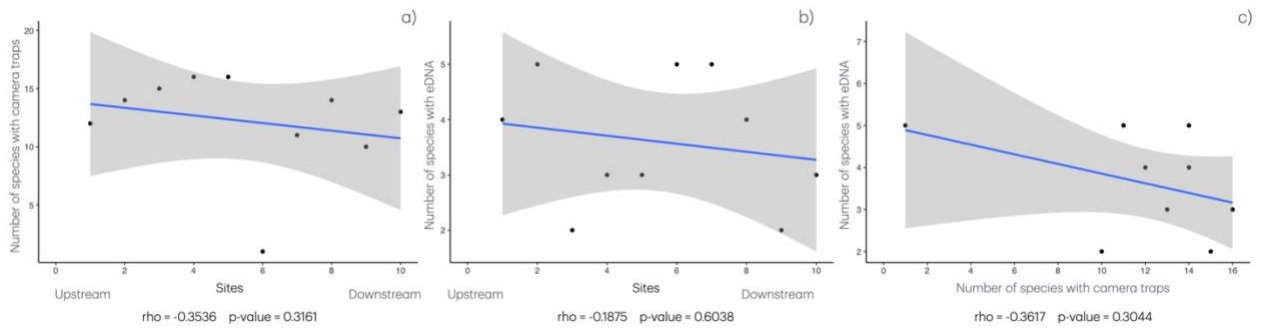


Figure 2.2 Correlations between the species richness detected with a) camera traps and the sites ordered from upstream to downstream, b) environmental DNA and sites, and c) camera traps and environmental DNA. All the surveys were along the Cajon Bonito stream, Sonora, Mexico.

Chapter 3. Spatiotemporal overlap of three apex predators, the black bear (*Ursus americanus*), puma (*Puma concolor*), and jaguar (*Panthera onca*), and their effect on two prey species in the US-Mexico borderlands

3.1 Abstract

Worldwide, many predator populations are on the brink of extinction. However, some species are expanding their range and recolonizing areas from which they were extirpated in the last century. We investigated the spatiotemporal ecology of black bears (*Ursus americanus*), pumas (*Puma concolor*), and jaguars (*Panthera onca*) in the US-Mexico borderlands. We used a 22-month camera trapping dataset, employing 85 motion-activated cameras placed along a riparian corridor and in a grid parallel to the international border. We focused on (i) spatial overlap, (ii) seasonal activity patterns, (iii) daily activity patterns, (iv) interspecific activity overlap, and (v) the effect of the presence of predators over two prey species, the white-tailed deer (*Odocoileus virginianus*) and the collared peccary (*Dicotyles tajacu*). We found spatial overlap between the three species of predators in riparian forests, and black bears and pumas in pine-oak forests, but pumas were typically the only apex predator in the scrublands and grasslands. We found distinct seasonal activity patterns among the three predators, with black bears showing peak activity in June, pumas exhibiting consistent activity throughout the year, and jaguars demonstrating peak activity from August to January. Daily activity was predominantly diurnal for bears and did not overlap with the two felids. Puma and jaguar activity overlapped, but puma activity peaked at dusk and jaguars during the night. The habitat use of both prey species responded positively to the presence of black bears but not to the felids. We suggest that given the dominance of black bears over both felids, prey species might be using those sites as a refuge from their other predators, exploiting

avoidance of bears by the felids that describe the complexity of spatiotemporal partitioning.

3.2 Introduction

Large predators face the highest extinction rates and population declines of all the wild mammals on Earth (Estes et al., 2011; Ripple et al., 2014). In an era of habitat degradation, loss of wilderness areas, and widespread landscape fragmentation, conserving large predators is challenging because of the vast areas and resources their body size requires to survive (Ceballos et al., 2017; Dirzo et al., 2014; Smith et al., 2016). The rarity and elusive nature of predators also makes monitoring their populations expensive, time-consuming, and more difficult to manage, especially when handling is required (Ordiz et al., 2013; Prugh and Sivy, 2020). Furthermore, predators can be in conflict with humans when they hunt wild and domestic species of economic and cultural interest for humans, making human-predator coexistence a constant struggle (Laliberte and Ripple, 2004; Oriol-Cotterill et al., 2015; Seddon et al., 2014; Sergio et al., 2006; Wallach et al., 2015). Top-down interactions mediated by predators are beyond the consumption of prey species, as they interact in the ecosystems and modify the structure of the landscape by controlling the community of mesopredators, regulating the length of the food chain, determining the intensity of the spatial use of resources by different guilds, and impacting biogeochemical cycles (Dorresteijn et al., 2015; Estes et al., 2011; Prugh et al., 2009; Ripple et al., 2014). The recolonization or reintroduction of predators into unoccupied regions of their historical distributions can shift the use of time and space of wildlife populations and restore ecological interactions lost with their extirpation (Wolf and Ripple, 2017). However, to restore the cascade of effects that the presence of predators provides to ecosystems, it is necessary not only to bring back the predators but also to achieve an effective population size that sustains the ecological roles they play in the community (Ripple et al., 2022).

In North America, during the 19th and 20th centuries, the United States conducted an extensive and effective campaign to eradicate wild predators (Brown, 1996; Brown and López-González, 2000; Feldpausch-Parker et al., 2017; Serfass et al., 2018). The US Forest Service and US Biological Survey began poisoning predators in 1913 (Hawthorne, 2004), and in 1945, the use of compound 1080 aimed at coyote control expanded the use of poisoning stations across the Southwest, killing around 60,000 and 100,000 coyotes a year (Dunlap, 1986) until a ban was established in 1972 (Hawthorne, 2004). The local decline of carnivore populations was coupled with increased ungulate populations that shifted ecosystem interactions and the baseline of what we currently understand as functional landscapes (Bradshaw et al., 2021; Laliberte and Ripple, 2004). The predator removal campaigns permeated the US-Mexico border and were adopted by institutions and landowners in Mexico and many other countries in Latin America (Ceballos et al., 1998; Medellín et al., 2005). With the cattle boom in the American Southwest at the end of the 19th century, the eradication campaigns were enhanced, and the United States and northern Mexico lost populations of the Mexican wolf (*Canis lupus baileyi*), brown bears (*Ursus arctos horribilis*), and the jaguar (*Panthera onca*; Lute and Carter, 2020). Other carnivore species, which were secondary targets, like pumas (*Puma concolor*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*), were heavily impacted but not wholly eradicated in the region (Bergstrom, 2017; Brown, 1996; Gallo-Reynoso et al., 2008; Lichwa-Schneringer et al., 2024; Martínez-Meyer et al., 2021).

With the reduction of cattle grazing in the Southwest, the shift of rural communities into urban cities, and the installation of legislation that protected endangered species in the United States in 1973 and Mexico in 1994 (Rabinowitz, 1999), the remaining populations of predators that persisted in remote locations expanded and recolonized several locations in the US-Mexico borderlands (Murphy and Macdonald, 2010; Onorato et al., 2007). This is the case with the black bear (*Ursus americanus*), pumas, and jaguars (Chappell, 2011; Gantchoff and Belant, 2017; Medellín et al., 2005; Murphy and Macdonald, 2010; Sanderson et al., 2021; Wilmers et al., 2013). Black bears have benefited from protection as

an endangered species in Mexico since 1986 (Medellín et al., 2005), and private landowners in northern Mexico spearheaded their conservation through cattle practices that mitigate the conflict with bears and the reduction of illegal hunting (Doan-Crider and Hellgren, 1996; Onorato et al., 2007). Puma populations in the Southwest have been expanding due to better hunting regulations and decreased eradication activities by predator control agencies (Bergstrom, 2017; Slagle et al., 2017). Killing jaguars was banned in 1969 in Arizona (Brown and López-González, 2000), and with no jaguar detections from 1986 to 1996 and a renewed interest in the status of the population of jaguars in the borderlands, the species was included in the Endangered Species Act in 1997 by the United States Fish and Wildlife Service (McCain and Childs, 2008; Rabinowitz, 1999). In Mexico, jaguars were protected in 1994 by publishing the first endangered species list (Diario Oficial de la Federación, 1994). Since the resighting of jaguars in 1996 in the Peloncillo Mountains, jaguars have been detected with increased frequency in the US-Mexico border (Babb et al., 2022).

Because large carnivores often compete for similar prey and habitat, intraspecific competition can trigger spatial and temporal mechanisms to avoid niche overlap and minimize conflict (Chamberlain and Leopold, 2005; Elbroch et al., 2016; Gustave et al., 2017; Koehler and Hornocker, 1991; Lonsinger et al., 2017), but our knowledge about these ecological interactions is limited because many populations were reduced or eliminated before we could study their populations in the wild (Beckmann and Berger, 2003; Berger, 2007, 1999; Seddon et al., 2014). However, recent reintroductions and natural recolonization by predators, have provided new insights into their roles when they are incorporated into the ecosystem (Alston et al., 2019; Duquette et al., 2017; Gasparini-Morato et al., 2021; Palomares and Caro, 1999; Seddon et al., 2014). For example, little information exists about interactions between bears, pumas and jaguars in northern Mexico (Gonzalez-Borrajo et al., 2017), although the temporal patterns of these species have been studied separately (Gutiérrez-González and López-González, 2017; Lara-Díaz et al., 2018; McCain and Childs, 2008; Rabinowitz, 1999). With the expansion of jaguars into the borderlands and the continuous

records of jaguars in the western US-Mexico borderlands (Babb et al., 2022; Ragan et al., 2021), there exists a unique opportunity to gain insight into activity patterns when all three species are present. In this study, we quantified spatial overlap among different vegetation cover types, temporal activity patterns of each species, and interspecific overlap among black bears, pumas, and jaguars. We also assessed the spatial responses of the two most abundant prey species to the site abundance of each predator species.

3.3 Methods

3.3.1 Study site

The study was conducted in northeastern Sonora, Mexico (Figure 3.1). The area is at the western slope of the northernmost section of the Sierra Madre Occidental in Mexico (González-Elizondo et al., 2012). The camera traps were installed in the properties owned and managed by the non-profit Cuenca de Los Ojos A.C., which is bounded to the north by the states of Arizona and New Mexico in the United States and on the east by the Janos Biosphere Reserve, Chihuahua, Mexico. CLO lands cover 52,000 ha, from which 25,000 ha have been voluntarily dedicated for conservation since 2018 (CONANP 2018). The main superficial water source of the region is the Cajon Bonito stream, which flows perennially in a 20 km section in our study area. The landscape is rugged and the elevation we surveyed was from 1,140 to 1,814 m asl. Desert grasslands and scrublands are found at lower elevations (<1,400 m asl), and a transition to oak (*Quercus* spp.) and pinyon-juniper (*Pinus discolor-Juniperus arizonica*) forest occurs around 1,600 m asl. Oak and pine forests, mostly *Pinus ponderosa*, are found at higher elevations (1,700-2,300 m asl). The mean annual temperature is 17.2°C, and the mean annual precipitation is 241.1 mm, during the monsoon in July-September (CONAGUA, 2024).

3.3.2 Camera trap monitoring

We used a total of 85 motion-activated cameras with infrared flash (Bushnell core DS, Utah, USA) to detect medium and large mammal species. We set 80 cameras in a grid arrangement (20×4), parallel to the international border between Mexico and the United States. Each camera was separated by ca. 2 km (Figure 3.1). However, because of theft and wildfires, we lost 15 camera traps, and for this study, we used 65 sites from the grid arrangement. Additionally, we set 20 camera traps along the Cajon Bonito stream that bisects the study area, each separated by 2 km. All cameras were positioned at a height of ca. 40 cm above the ground on trees close to trails, dirt roads, or where evidence of wildlife movement was evident, and we did not use any bait or lure. The cameras were programmed to take 10-s videos when motion and movement were detected with a 5-minute delay between consecutive detections (O'Connell et al., 2011). The analysis period was from 1 October 2020 to 31 July 2022. The total effort was 43,519 camera trap days. Because of malfunctions and theft, the time a camera trap worked at each location varies. The average monthly effort was 1,973.5 camera trap days (SD = 315.48 days) across the 85 locations. During the 22 months of monitoring, the average effort per location was 501.8 camera trap days (SD = 145.68). For each species, we considered detections independent events if they were separated by at least 60 minutes at the same location. When multiple detections occurred during the 60-minute window, we used the date and time of the event that was first recorded for the analyses. To document spatial overlap, we counted the number of events in which each apex predator was detected per site and reported naïve occupancy (the proportion of sites where each species was detected considering a total of 85 sites) for each vegetation type.

3.3.3 Seasonal activity

Given that all three species have large home ranges, are highly mobile, and are similarly detectable (Sollmann et al., 2013; Tanwar et al., 2021), we calculated each species' relative abundance index (RAI) by dividing the independent number

of events between the camera trap effort per month (O'Connell et al., 2011). The seasons we considered were the pre-monsoon dry season (April-June), monsoon season (July-September), post-monsoon dry season (October-December), and winter wet season (January-March; CONAGUA, 2024). To visualize the differences between months, we calculated a moving average window of two months and plotted the trendline.

3.3.4 Daily activity patterns

We calculated the daily activity patterns using the independent events for each species during the 22-month period. To consider variation in sunrise and sunset times throughout the year, for each event, we obtained the time of sunrise and sunset when the event was recorded using the central location of the camera trap array (31.27844, -109.00143) and the time zone GMT-7 using the package *activity* version 1.3.4 in R (R Core team, 2023). Then, each event was classified based on the difference in minutes from the time of the event to dawn or dusk. We divided the day into six categories: late night (midnight to 2-h before the sunrise); dawn (2-h before and after the sunrise); morning (2-h after the sunrise to noon); afternoon (noon to 2-h before the sunset); dusk (2-h before and after the sunset); and early night (2-h after the sunset to midnight). Using this method, dawn and dusk comprise exactly 4 hours, but the other categories slightly vary depending on the length of day/night throughout the year.

3.3.5 Interspecific overlap of daily activity

We were interested in estimating the interspecific overlap of the daily activity of the three species. For this analysis, the time of each event was converted to a decimal fraction, considering a day as the unit, and then to radians. We estimated the distribution of the daily activity of each species using the time-of-day data of the events to fit kernel densities with a bandwidth value of 1 (Vallejo-Vargas et al., 2022). To obtain 95% confidence intervals, the distribution was bootstrapped 1,000 times using the data for resampling (Ridout and Linkie, 2009). We

estimated the overlap for every pair of species combination by fitting the data to the approximate true density function and then comparing the kernel density estimates of both species (Ridout and Linkie, 2009). Because we had more than 50 events for all species, we used a non-parametric overlap index estimator (Δ_4) proposed by Schmidt and Schmidt (2006). This coefficient considers that two distributions that do not overlap have a value of 0, while identical distributions have a value of 1. We also compared the pairwise distributions by generating a randomized null distribution using data from both distributions. Then, we compared the overlap index (Δ_4) from the observed overlap against the null distribution, assuming that both distributions were the same. We did a permutation test of equality and a bootstrap 1,000 times to obtain a 95% confidence interval and a *P*-value to compare the null hypothesis that the observed distribution could arise by chance (Ridout and Linkie, 2009), using the *overlap* package version 0.3.9 in R (R Core team, 2023).

3.3.6 Effect of apex predators on the habitat use of two prey species

We tested the influence of each apex predator on the habitat use by the two most abundant prey species in our study site described previously by Marín et al. (*in prep.*), the white-tailed deer (*Odocoileus virginianus*) and the collared peccary (*Dicotyles tajacu*). We used the latent abundance mixture model to estimate the change in the abundance of the prey species at each site in response to the presence of predators (Royle and Nichols, 2003). Because we set the camera traps at 2 km from each other, we can not assume that each site is independent of the other, considering that the average home range of the two prey species and the predators includes at least two sites (Royle and Nichols, 2003). Instead of abundance and detection probability, our estimations, therefore, measure the intensity of use and the probability of detection at each site (Suraci et al., 2020).

We used the habitat-use models described by Marín et al. (*in prep.*) for the prey species. The covariates that influenced habitat use by white-tailed deer were the different vegetation types (grassland, scrubland, oak forest, pine-oak forest, and riparian forest), distance to the border wall, and the presence of cattle for

detectability. For the collared peccary, vegetation type was the only covariate that affected abundance, and no covariate influenced detectability. In accordance with the models presented by Marín et al. (*in prep.*) and to ensure the population closure assumption of the abundance mixture model, we only modeled the data for 40 weeks (November 1, 2021, to August 1, 2022). We considered 1 week as the unit for temporal repetition of the model, during which we counted the number of independent events that occurred during each week (i.e., detections at a site more than 60 minutes apart). We incorporated the standardized total number of independent events of each predator species to account for the presence of the predators at each site as a covariate. We constructed eight models for each prey species using the R package *unmarked* version 1.3.2 (Kellner et al. 2023), incorporating the original habitat use model described by Marín et al. (*in prep.*) as a null model. In the other seven models, as a covariate of the abundance, we included the abundance per site of each apex predator without interaction between the covariates. One model included the abundance of the three apex predators as independent covariates; three models consisted of the two-predator combinations (black bear and puma, black bear and jaguar, jaguar, and puma), and three models had only one predator species as a covariate. We ranked the beta estimates considering the Akaike Information Criteria (AIC) and obtained the conditional average of all eight models. We considered relevant those covariates whose confidence intervals did not include zero (Bauder et al., 2018).

3.4 Results

The total sampling effort during the 22-month period was 43,419 camera trap days. In total, we obtained 846 videos and 797 independent events of black bears at 47 different sites (Table 3.1; Figure 3.2), 731 videos and 688 independent events of pumas at 59 different sites (Figure 3.2), and 66 videos and independent events of jaguars at 21 different sites (Figure 3.2). All three species were found across the elevational range we surveyed, from 1,140 to 1,814 m asl. The average

elevation of detections was 1,407.8 m asl. for black bears (SD = 179.94), 1,400.6 m asl. for pumas (SD = 161.80), and 1,355.5 m asl. for jaguars (SD = 186.04).

Using the rosette patterns on jaguar pelages, we identified three individuals across the 66 jaguar events (Figure 3.3). “Valerio”, a male, was detected on 42 events at 16 different sites from January 2021 to July 2022 (Figure 3.3). “Bonito”, a male, was detected on 22 events at 15 different sites from November 2020 to June 2022 (Figure 3.3). “Adela”, a female, was detected on two events at different sites (Figure 3.3). On February 23, 2022, Valerio was detected with another jaguar in the same video, but due to the distance, it was not possible to identify the second individual. Adela, the female, was recorded vocalizing one month before by a camera trap located less than 2 km from this site and then one month later. The other male, Bonito, was not detected in any camera trap from November 2021 to May 2022. We, therefore, suspect the second jaguar in this video was Adela.

3.4.1 Spatial overlap of apex predators

We detected at least one apex predator at 63 (74%) of the 85 sites we surveyed (Table 3.1). The black bear and the puma were co-detected at 40% of sites, and all three species were detected at 30% of sites (Figure 3.4). The puma and the jaguar were co-detected at only one site (2%). The sites where all three species were detected and where black bears and pumas were co-detected were distributed along all five types of vegetation (Figure 3.4). The puma and the jaguar were co-detected at only one location in the grassland (Table 3.1). The black bear was the only apex predator detected at two grassland sites and one pine-oak forest site (Table 3.1). The puma was the only apex predator detected at 14 sites in all vegetation types except the pine-oak forest (Figure 3.4). The jaguar was exclusively detected at only one site in the scrubland (Table 3.1).

3.4.2 Seasonal activity

Black bears showed peak activity at the end of the pre-monsoon dry season and minimal activity during the wet winter season (Figure 3.5). Only ten of 797 events

were recorded during winter, with no detections in February. After hibernation, black bears' activity increased monthly until they reached their peak activity during the month of June (RAI = 0.0656). From July to November, activity remained stable, and during December (RAI = 0.0037), activity was only ca. 20% of that of November (RAI = 0.0186). Pumas showed homogeneous activity across the year, except during the months of July and August when activity was reduced almost by half (Figure 3.5). The jaguar had lower activity from February to July and peak activity from August to January (Figure 3.5).

3.4.3 Intraspecific daily activity patterns

Each species showed a characteristic activity pattern (Figure 3.6). Black bears were most active between dawn and dusk (82%), and their activity peaked at dusk (27%). Pumas were most active between dusk and dawn (82%), with a peak at dusk (27%) and a smaller peak at dawn (18%). The activity of pumas during the morning and the afternoon was low and represented 10% and 7%, respectively (Figure 3.6). Jaguars were most active between dusk and dawn (88%), and their activity peaked at early night (30%) and then decreased during late night and dawn. The activity of jaguars during the morning and the afternoon was minimal and represented 2% and 10%, respectively (Figure 3.6).

3.4.4 Interspecific overlap of daily activity

The estimated overlap index of the black bear activity differed from that of pumas ($\Delta_4 = 0.83$, 95% CI = 0.778 - 0.864) and jaguars ($\Delta_4 = 0.74$, 95% CI = 0.650 - 0.842) (Table 3.2; Figure 3.7). Puma and jaguar activity patterns were similar ($\Delta_4 = 0.85$, 95% CI = 0.834 - 0.995), and the permutation test of equality suggested their distributions were not different (P -value = 0.5680).

3.4.5 Effect of apex predators on the habitat use of two prey species

The conditional averaged model of white-tailed deer showed that habitat use was positively affected by grassland and oak forest, distance to the border, and the

abundance of black bears but negatively affected by scrubland and pine-oak forest. The presence of cattle did not have an effect on detectability (Table 3.3). The conditional averaged model of collared peccary showed a relevant response for two covariates with a negative effect on the habitat use by the pine-oak forest, but a positive response to the abundance of black bears (Table 3.4).

3.5 Discussion

Our study leverages a rare opportunity to document the activity patterns of three coexisting apex predators while one species, the jaguar, is recolonizing the borderlands between Mexico and the United States. Because jaguars' rosettes are unique to each individual, we determined that three individuals were using the area during our survey, including one female who likely interacted with one of the males on one occasion (Figure 3.3). This is the first record of a female jaguar in the borderlands in decades: the last one was killed in 1949 in Arizona, 12 km north of the border in the Cerro Colorado mountains, Arivaca area, Santa Cruz County (Babb et al., 2022), and the most recent northernmost record of a female in Mexico was shot in 1998 ca. 170 km south of the border in Moctezuma, Sonora (Warshall, 2013). Given that females tend to disperse shorter distances and remain closer to their mother's home range than males (González-Borrajo et al., 2017; Seymour, 1989), and the northernmost report of a reproductive population of jaguars is 200 km south of the border at the protected area Reserva Jaguar del Norte (Amador-Alcalá et al., 2024), our records suggest that females may be expanding northward and successful reproduction may be occurring closer to the international border than is currently believed. We also documented one of the male jaguars rubbing his neck into a fallen log (Figure 3.3), a typical scent-marking behavior of felids that denotes they are establishing a territory (Smith et al., 1989). Macho B, a jaguar residing in Arizona from 2004 to 2007, was also recorded doing this behavior (McCain and Childs, 2008). Although we only have data on a few individual jaguars and no evidence or knowledge of where the closest reproductive population is. Future monitoring efforts should be focused

on documenting the current status of the northernmost jaguar population, surveying the mountain corridors that connect the 170-km gap between the Reserva Jaguar del Norte and our study site to confirm where females are reproducing.

3.5.1 Spatial overlap

The presence of three and two focal apex predators was distributed across all vegetation types. Still, half of these sites were at riparian and pine-oak forest vegetation types, suggesting that these areas provide valuable resources for apex predators with different diets. Access to water in arid landscapes is a limiting resource exploited by predators in search of prey (Sánchez-Montoya et al., 2022). In our study site, adult black bears are not hunted by other apex predators and have not been hunted by humans in the area for at least two decades. When black bears and pumas interact, in most cases, bears dominate (Elbroch and Kusler, 2018). However, when both species are present, pumas hunt more frequently to compensate for losses caused by kleptoparasitism by bears and do not spatially avoid bears (Elbroch et al., 2015). Evidence on the interaction of pumas and jaguars at the northernmost breeding population of jaguars showed that both species overlap spatially in most of the sites and that jaguars are not dominant over pumas (Gutiérrez-González and López-González, 2017). The use of the riparian forest by black bears, a larger apex predator that is dominant but does not rely on hunting as their primary source of food, might provide the opportunity for pumas and jaguars to use the space at different times than bears for hunting or moving across the landscape.

Pumas were the most ubiquitous predator in the landscape, and their ecological role has been associated with their interaction with prey species and the provision of food by leaving carrion to smaller carnivores (Allen et al., 2014; Elbroch and Wittmer, 2012; Perrig et al., 2017). At our study site, pumas were the species distributed most evenly across the different vegetation types, but considering that pumas were the only apex predator present at several sites where the grassland and scrubland are the dominant types of vegetation, their

ecological role might be essential to maintaining the population of scavengers and controlling mesopredator populations of coyotes and bobcats (Jachowski et al., 2020; Newsome et al., 2017), in these vegetation types.

3.5.2 Seasonal activity patterns

Regarding seasonal activity, we found that black bears, pumas, and jaguars have different patterns at our study site that suggest some spatiotemporal separation. The seasonal activity pattern of black bears that we documented was consistent with those reported in central Arizona, where females went into hibernation on average from November 10 to April 26 and males from November 24 to March 20 (LeCount, 1983), but longer than the denning period in northeastern Mexico, where females hibernated on average from December 22 to April 25 (Doan-Crider and Hellgren, 1996). Activity by pumas was constant throughout the year, except in the summer period when black bears were more active. This trend has been reported in other studies and attributed to kleptoparasitism by black bears over puma kills (Allen et al., 2014). Despite using a relativized index based on effort, the abundance trends for July and August are preliminary, given that we only surveyed one year due to the loss of camera traps and inaccessibility to the locations during the monsoon. In the case of jaguars, we found that jaguars are more active from August to January. This peak of activity after the monsoon coincides with previous reports in the United States, where almost half of the records occurred from November to January (McCain and Childs, 2008; Rabinowitz, 1999) and with the closest southern population, which had activity peak during November and December (Amador-Alcalá et al., 2024). Jaguars and pumas have similar body sizes and diets in this region (Cassaigne et al., 2016, 2021). However, the hiatus of jaguar activity during the hottest months of the year suggests that they may be using the Sierra Madre Occidental mountains, which reach ca. 2,400 m asl. and extend south from our study site, to find refuge from the heat, even with the presence of the Cajon Bonito, a perennial stream that serves as a corridor for wildlife during the summer (Ragan et al., 2022). In fact, the jaguars we documented used areas where pumas were abundant all year,

and where the activity of black bears was high during the monsoon season, disregarding potential interspecific competition with pumas or black bears.

3.5.3 Daily activity patterns

We found characteristic daily patterns for each apex predator. The black bears were more diurnal, and pumas had a bimodal distribution around dawn and dusk. Despite the overlap of the two felids in their daily activities, jaguars were more nocturnal, and pumas' peak activity was at dusk and dawn. The crepuscular and nocturnal pattern reduces the metabolic cost of temperature regulation (Donadio and Buskirk, 2006) and corresponds with the preferred hunting times of pumas and jaguars, when prey is more vulnerable (Allen et al., 2014; Seymour, 1989; Tucker et al., 2014). Bear activity patterns were similar on average to those described in other studies across the region (Lara-Díaz et al., 2018; Lara-Díaz et al., 2021; Onorato et al., 2003), but we found that the bears in our study site were more diurnal. Evidence suggests that black bears increase their activity at sites where more humans are present at low levels (Suraci et al., 2021), and this could be attributed to the search for food, which can increase negative interaction with humans in the long term, or bears dealing with the increased use of humans in remote areas for recreation (Suraci et al., 2021), or the dependence of bears to human subsidized food in areas where bears are hunted (Kirby et al., 2017). Because our study site is privately owned and managed for the conservation of wildlife with low human presence in the landscape, we suspect the higher diurnal activity of bears we found compared to other locations in the region, might be due low human activity. Another factor that impacts the daily temporal patterns is the strong seasonal changes in the bear activity patterns throughout the year. For example, we found that black bears are more active during the hotter months of the year, at the end of the spring and the beginning of summer. In contrast, during autumn, when several trees are masting, they might expand their foraging activities during the day with a lower energetic cost for thermoregulating (Doan-Crider and Hellgren, 1996; Hellgren, 1993; Lara-Díaz et al., 2018) and are more prone to seasonal migrations (Noyce and Garshelis, 2011).

Jaguar and puma activity patterns were consistent with other reports in the American Southwest. For example, based on 69 records with camera traps in the US borderlands, mainly by a single individual (Macho B = 65 records), researchers found that 87% of the records occurred during dusk and night, 16:31–04:30 (McCain and Childs, 2008). Our results are similar to previous data where pumas and jaguars coexist (Gutiérrez-González and López-González, 2017), as we found the same pattern of high crepuscular activity of pumas and nocturnal activity of jaguars. Regarding the dietary overlap among the three carnivores, the diet of jaguars in northern Mexico is less dependent on larger prey, and they persist on medium-sized prey, compared to subtropical latitudes, where they depend on larger prey (López-González and Miller, 2002). A study in central Sonora showed that peccary and deer are the main prey for both species, but other species were also detected, such as lagomorphs (genus *Lepus* and *Sylvilagus*), coatis (*Nasua narica*), coyotes (*Canis latrans*), opossums (*Didelphis virginiana*), grey foxes (*Urocyon cinereoargenteus*), rock squirrels (*Otospermophilus variegatus*), skunks (*Mephitis* spp.), and desert tortoises (*Gopherus morafkai*) (Cassaigne et al., 2021). Pumas, which have a diet more restricted to deer and collared peccaries in this portion of their range and are subordinate predators to black bears (Elbroch et al., 2015; Allen et al., 2014), are more susceptible to negative interactions with black bears, such as kleptoparasitism and loss of kittens (Elbroch and Kusler, 2018).

3.5.4 Effect of apex predators on the habitat use of two prey species

In northern Mexico, pumas' and jaguars' main prey consists of white-tailed deer and collared peccary (Cassaigne et al., 2021). Our results show evidence that both prey species use sites where bears are more abundant but did not show any response to the abundance of pumas or jaguars (Tables 3.3 and 3.4). Given the documented dominance of black bears over both felids (Elbroch and Kusler, 2018), prey species might be using those sites as a refuge from jaguars and pumas, exploiting avoidance of the most behaviorally dominant predator, the black bear, that is less focused on hunting and is often categorized as an

omnivore (Larivière, 2001). The absence of a negative spatial response to pumas and jaguars might indicate that temporal mechanisms to reduce predation might be occurring and shaping the landscape of fear between the prey and predator species we analyzed. Studies on predator-prey dynamics across both time and space have shown that when both species overlap in the use of space, prey temporal patterns are adjusted to minimize overlap and reduce the risk of predation (Kohl et al. 2018). A previous study found that the peak of activity of white-tailed deer and collared peccary is higher during the day (Gutiérrez-González and López-González, 2017), which is when the black bears at our study site are more active.

The effects of the interactions that we documented are from a community where only the black bear and pumas have been exerting their ecosystemic roles for decades, and the habitat use of prey species is adapted to their spatiotemporal patterns. With more jaguars in the region, the current prey-predator spatiotemporal dynamics might change. However, we suspect that if healthy prey populations are maintained and human influence is limited to the currently low levels, the prey population will remain stable given the high spatial and temporal overlap of jaguars with pumas and the dominant effect of the presence of black bears where the three apex predators are present.

3.5.5 Implications for conservation

Our study is one of the first to document the comeback of the jaguar in the US-Mexico borderlands and its interactions with other large carnivores and their prey. This region has already been recognized as a potential corridor for endangered jaguars and bears (Landau et al., 2022; Lara-Díaz et al., 2021), but the expansion of the border wall is likely to limit movement by these three species across the US-Mexico border (Harrity et al., 2024). At our study site, the establishment of natural protected areas, conservation easements, and ranches with positive attitudes towards human-predator coexistence provides a space where these apex predators cohabit in the same area. However, on a broader scale, cattle and agriculture operations in the adjacent grasslands are expanding

and limiting the movement paths of predators and other vagile species (Coronel-Arellano et al., 2018; Sierra-Corona et al., 2015). Our study highlights that the uniqueness of riparian and forested ecosystems resides in their provision of resources such as water and shade for wildlife populations, but also in sustaining the interaction of the large-bodied carnivores and the ecosystemic roles they play in these arid ecosystems. However, in grasslands and scrublands, where the presence of the apex predators is limited to the presence of one species, the top-down community interactions are less redundant and diverse, hence ensuring the presence of a functional population of pumas to exert their ecological role is crucial for maintaining the integrity of these ecosystems. More detailed information on the movement patterns of apex predators could be coupled with our results to inform how predators' movement and novel interactions shape wildlife populations and how they respond to human barriers. Finally, updating the status and distance to the border of the northernmost reproductive populations of jaguars in Sonora will fill knowledge gaps on the effects of rewilding the community predators in the borderlands, the current rates of expansion, and what we can do to protect the permanence and connectivity of their populations.

3.6 Tables

Table 3.1 Number of sites per vegetation type where apex predators, black bears (*Ursus americanus*), pumas (*Puma concolor*), and jaguars (*Panthera onca*), were co-detected or exclusively detected in northeastern Sonora, Mexico. The detections were obtained from 85 sites where a single camera trap was set without bait from October 1, 2020, to July 31, 2022.

Type of vegetation	Sites with apex predators	Only black bear	Only puma	Only jaguar	Black bear and puma	Black bear and jaguar	Puma and jaguar	Black bear, puma and jaguar
Riparian	13		1		4			8
Pine-oak forest	11	1			7			3
Oak forest	7		3		3			1
Scrubland	8		3	1	2			2
Grassland	24	2	7		9		1	5
Total	63	3	14	1	25	0	1	19

Table 3.2 Pairwise intraspecific overlap of the daily activity of three apex predators in the US-Mexico borderlands, the black bear (*Ursus americanus*), puma (*Puma concolor*), and jaguar (*Panthera onca*). We used two methods to compare the overlap in the activity. The estimated overlap index Δ_4 is obtained by comparing the kernel density distribution of each species and estimating the overlapped density under the curve. The second method calculates the observed overlap index for both species. Then, it creates a null overlap index representing a hypothetically random distribution from each pair of distributions, assuming that both have the same origin. By bootstrapping 1,000 times, the probability that the observed overlap arose by chance is determined with a *P*-value threshold of 0.05. For both methods, the overlap index value of 0 represents completely different distributions, and values of 1 represent a complete overlap. *P*-values < 0.1 are bolded.

Species comparison	Estimated overlap index Δ_4 (95% CI)	Observed overlap index	Null overlap index (SE)	<i>P</i> -value
Black bear <i>versus</i> puma	0.83 (0.778 – 0.864)	0.82	0.95 (0.012)	< 0.0001
Black bear <i>versus</i> jaguar	0.74 (0.650 – 0.842)	0.74	0.87 (0.032)	< 0.0001
Puma <i>versus</i> jaguar	0.85 (0.834 – 0.995)	0.88	0.87 (0.031)	0.5680

Table 3.3 Response of one of the most abundant and larger prey species in the US-Mexico borderlands, the white-tailed deer (*Odocoileus virginianus*), to the abundance of black bear (*Ursus americanus*), puma (*Puma concolor*), and jaguar (*Panthera onca*) in northeastern Sonora, Mexico. *P*-values < 0.1 are bolded.

Covariate	Estimate	Std. error	Z	<i>P</i> -value
Vegetation: grassland	0.77	0.186	4.13	<0.0001
Vegetation: scrubland	-0.66	0.341	1.93	0.0537
Vegetation: oak forest	0.53	0.269	1.96	0.0504
Vegetation: pine-oak forest	-1.33	0.612	2.17	0.0298
Vegetation: riparian	0.42	0.331	1.27	0.2055
Distance to the border	0.33	0.170	1.92	0.0554
Black bear abundance	0.26	0.153	1.70	0.0894
Puma abundance	-0.18	0.130	1.36	0.1735
Jaguar abundance	-0.14	0.118	1.17	0.2408
Detectability	-2.25	0.107	21.03	<0.0001
Detectability (Cattle)	-0.04	0.032	1.38	0.1674

Table 3.4 Response of one of the most abundant prey species in the US-Mexico borderlands, the collared peccary (*Dicotyles tajacu*), to the abundance of black bear (*Ursus americanus*), puma (*Puma concolor*), and jaguar (*Panthera onca*). *P*-values < 0.1 are bolded.

Covariate	Estimate	Std. error	Z	P-value
Vegetation: grassland	0.24	0.265	0.91	0.3654
Vegetation: scrubland	0.47	0.319	1.49	0.1369
Vegetation: oak forest	-0.00	0.437	0.01	0.9950
Vegetation: pine-oak forest	-2.80	1.062	2.64	0.0083
Vegetation: riparian	0.13	0.541	0.24	0.8090
Black bear abundance	0.53	0.228	2.33	0.0201
Puma abundance	0.16	0.117	1.40	0.1611
Jaguar abundance	-0.10	0.124	0.78	0.4337
Detectability	-2.76	0.150	18.42	<0.0001

3.7 Figures

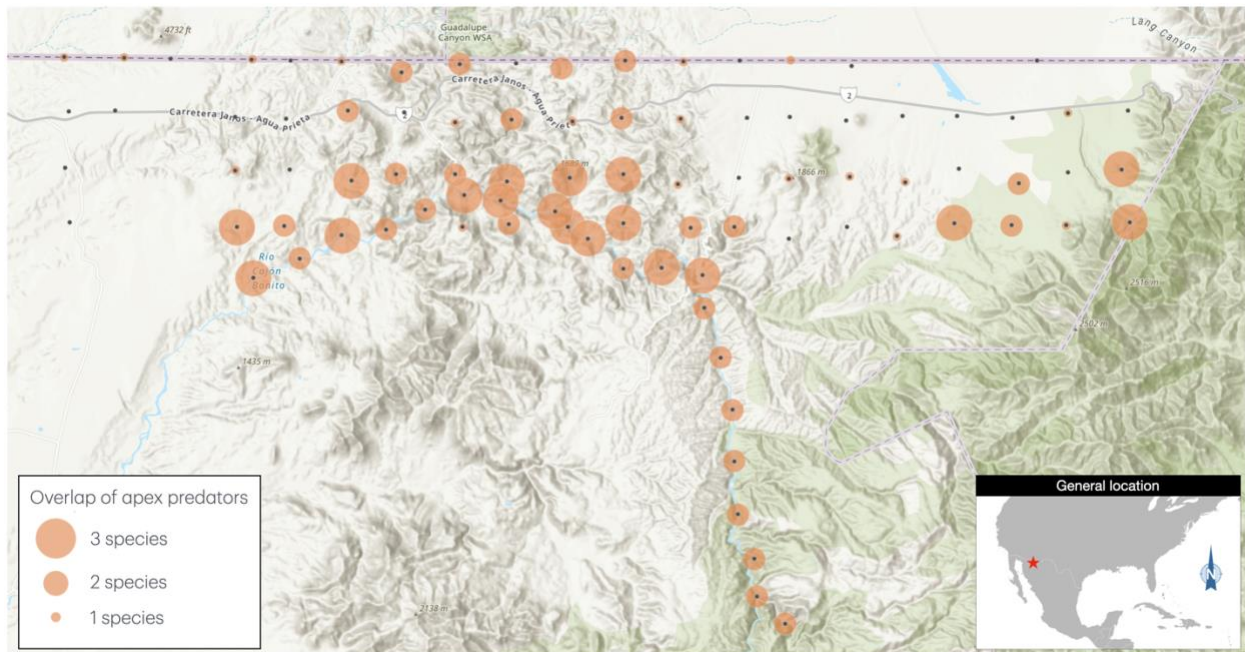


Figure 3.1 Spatial overlap of three apex predators in the site location in Mexico-US borderlands in Sonora, Mexico. The black dots indicate the location of the 85 motion-activated cameras during a 22-month period. Sixty-five cameras were set in a 2×2 km grid arrangement parallel to the international border. Additionally, 20 cameras were set along the Cajon Bonito stream, separated by 2 km following the stream course. The three apex predators were the black bear (*Ursus americanus*), puma (*Puma concolor*), and jaguar (*Panthera onca*).

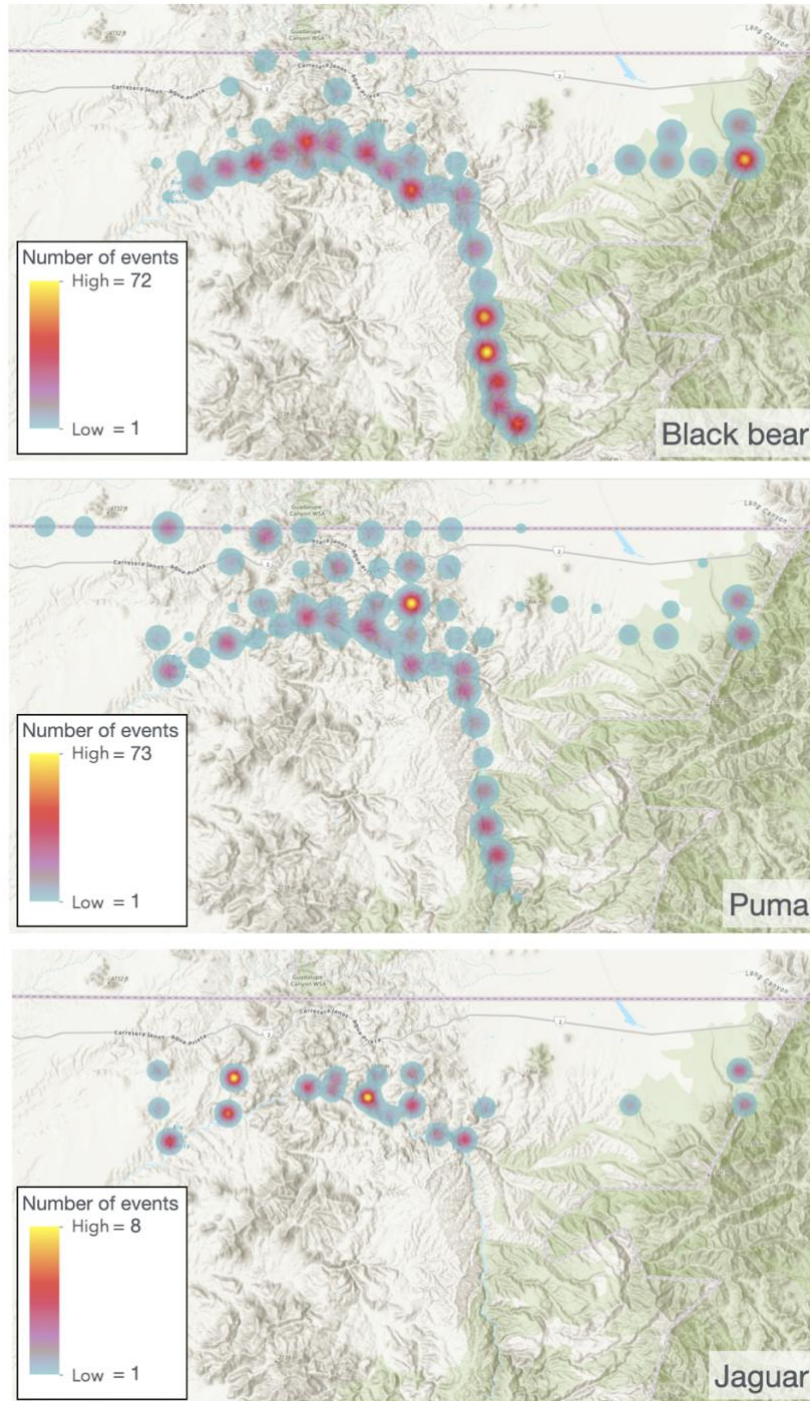


Figure 3.2 Heat map of the number of events and locations where three apex predators were detected in northeastern Sonora, Mexico. The predator species are black bear (*Ursus americanus*), puma (*Puma concolor*), and jaguar (*Panthera onca*).



Figure 3.3 Three different jaguars were identified at the private protected area of Cuenca Los Ojos in northeast Sonora, Mexico. a) Valerio, a male individual marking a tree. b) Bonito, a male jaguar. c) a female jaguar, Adela, was recorded less than 5 km from the US-Mexico international border.

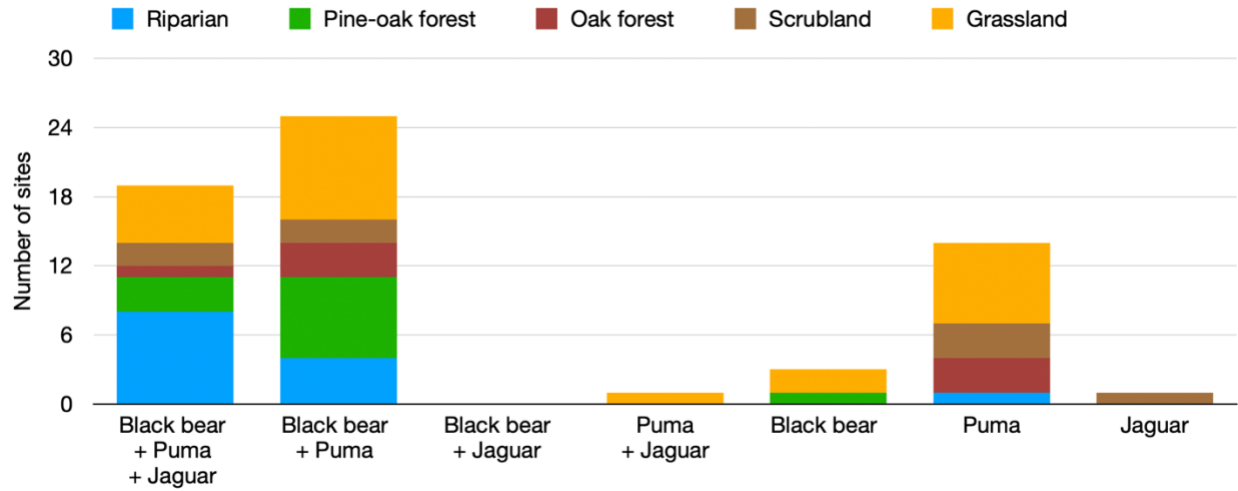


Figure 3.4 Number of sites and distribution along the different vegetation types where three apex predators co-occurred in northeastern Sonora, Mexico. The predators were the black bear (*Ursus americanus*), puma (*Puma concolor*), and jaguar (*Panthera onca*).

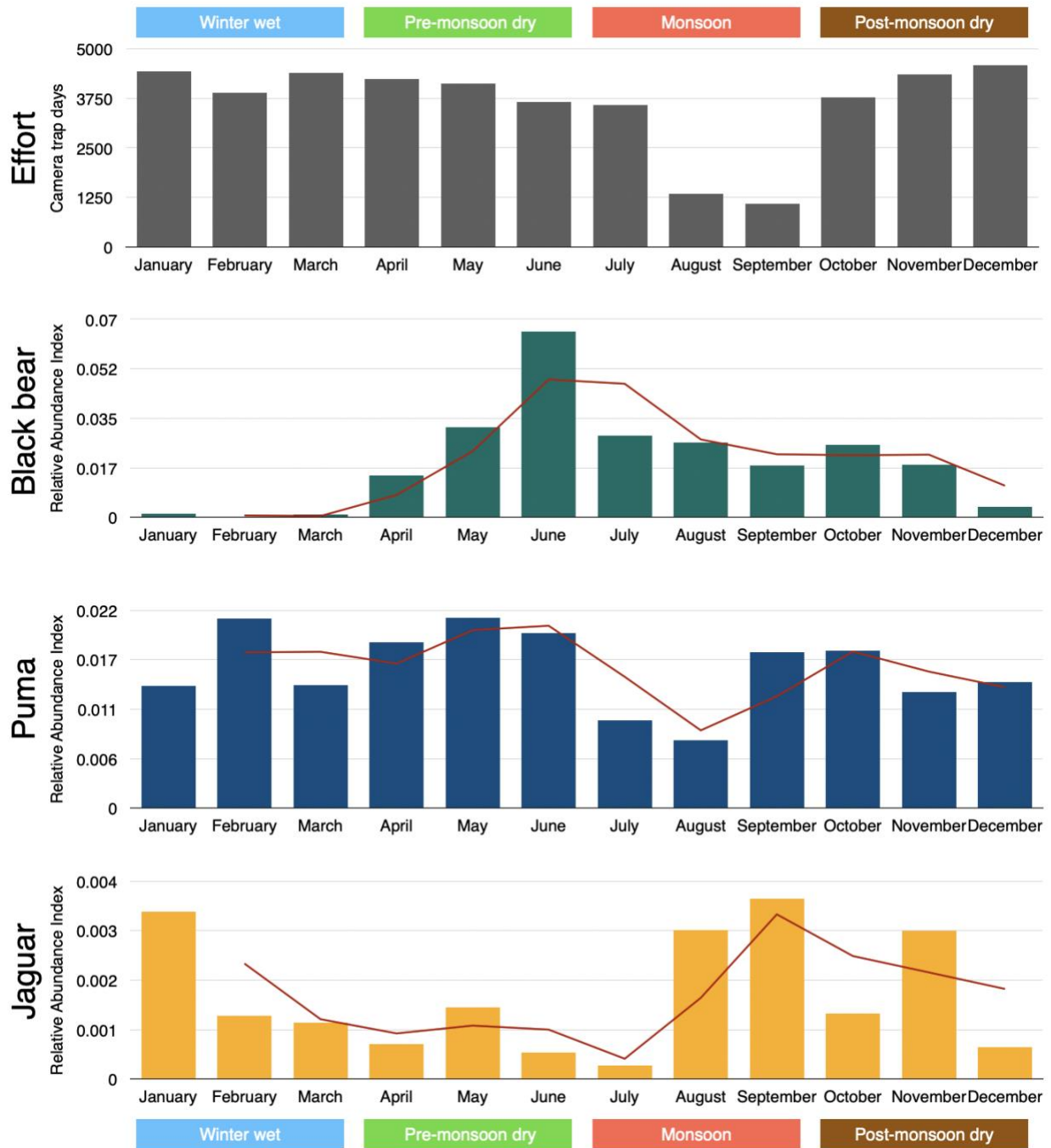


Figure 3.5 Monthly relative abundance index of the three apex predators, the black bear (*Ursus americanus*), puma (*Puma concolor*), and jaguar (*Panthera onca*), from 2020-2022 in northeastern Sonora, Mexico.

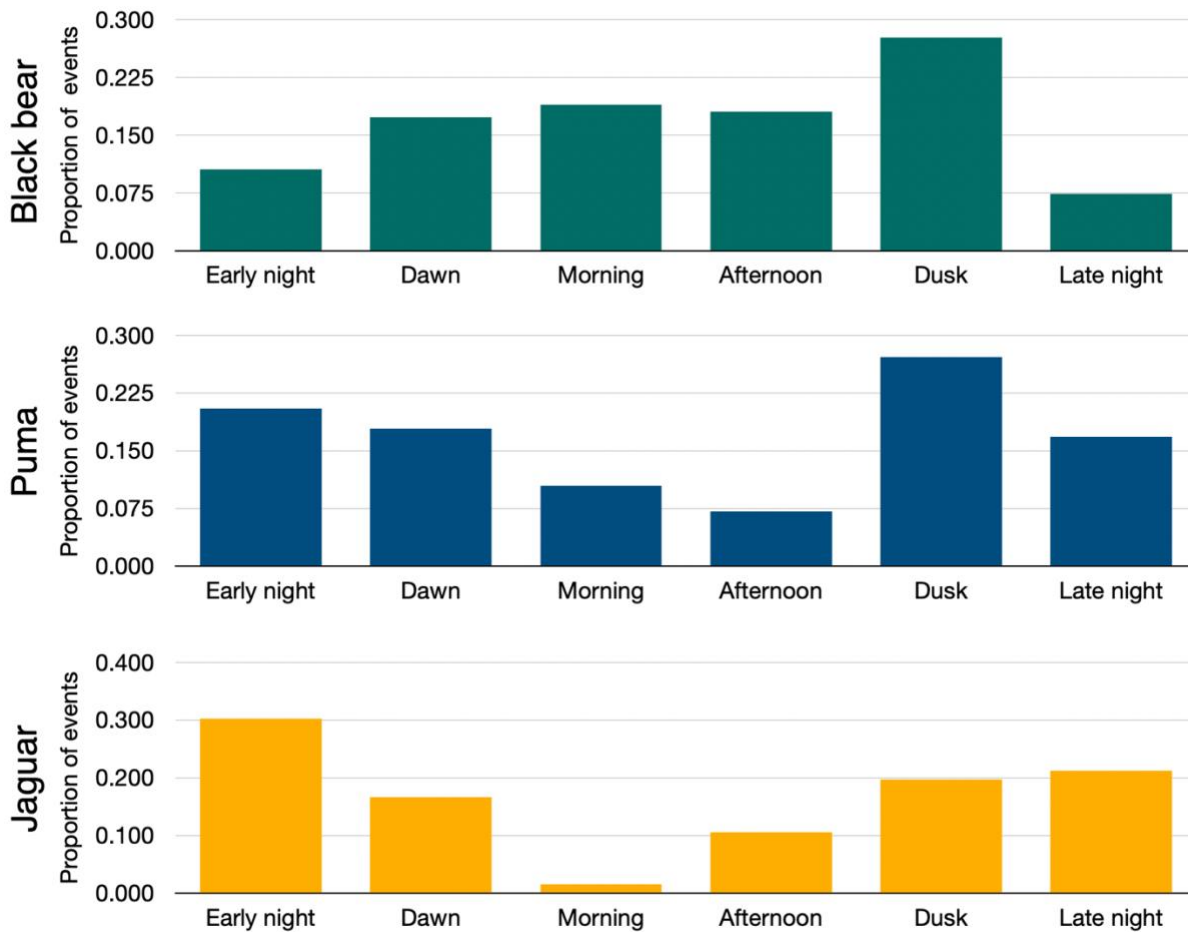


Figure 3.6 Daily activity patterns obtained with camera trap records of three apex predators in the US-Mexico borderlands: the black bear (*Ursus americanus*), puma (*Puma concolor*), and jaguar (*Panthera onca*). Each event was assigned to one of the six categories based on the difference in time from the event to the sunrise and sunset throughout the year. Late night: Midnight to 2-h before the sunrise; dawn: 2-h before and after the sunrise; morning: 2-h after the sunrise to noon; afternoon: noon to 2-h before the sunset; dusk 2-h before and after the sunset; early night: 2-h after the sunset to midnight.

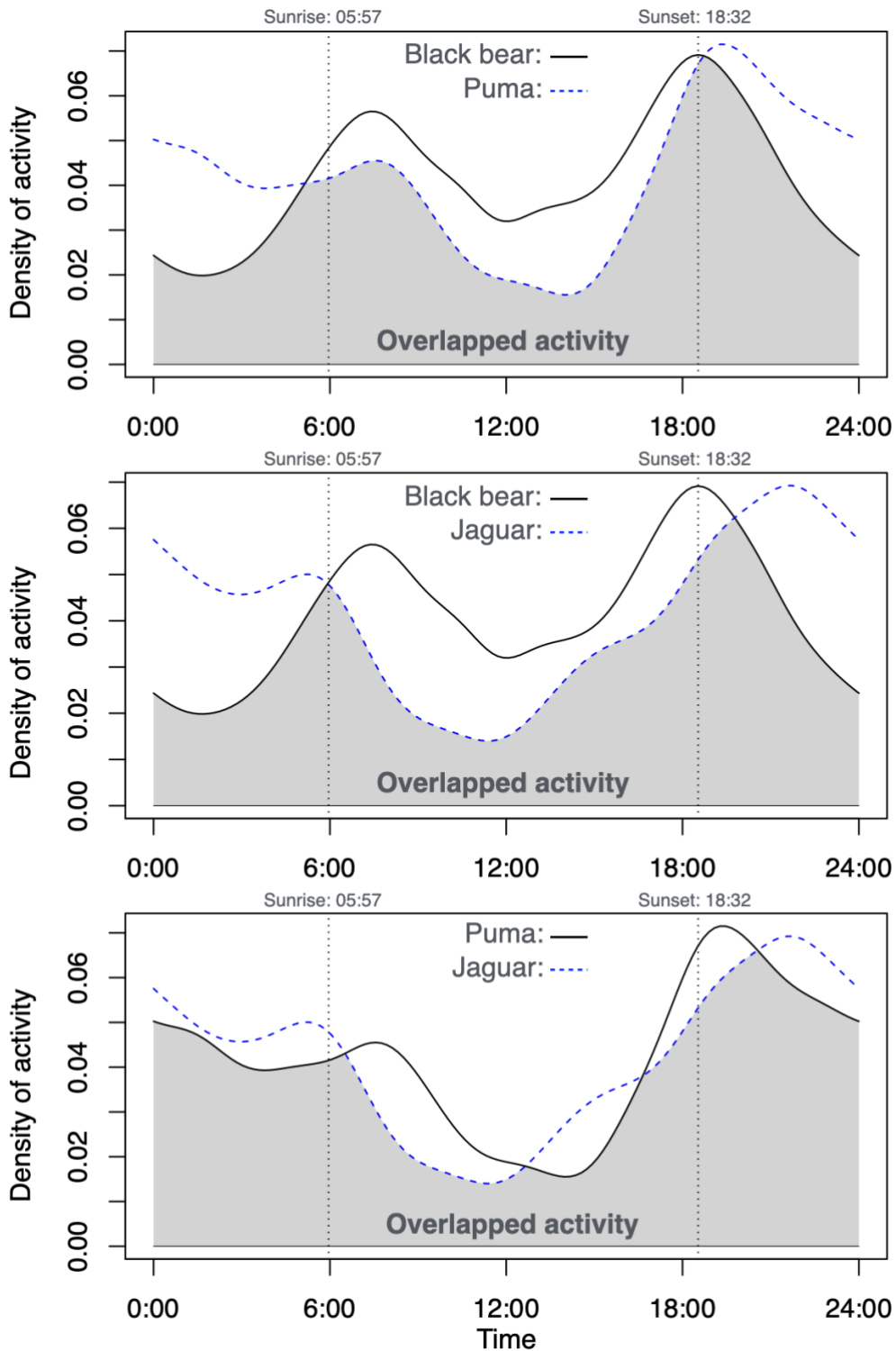


Figure 3.7 Overlap activity patterns between the three apex predators, the black bear (*Ursus americanus*), puma (*Puma concolor*), and jaguar (*Panthera onca*) in the northwestern US-Mexico borderlands. The sunrise and sunset times are just for reference and were obtained by averaging the time of sunrise and sunset of each event over the course of the year for the three species.

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