Elusive felids of lowland Amazonia: Assessing the effects of human disturbance across an unprotected landscape

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Abstract

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Rapid human population growth and land conversion in the Amazon rainforest have caused extensive habitat fragmentation and defaunation, affecting threatened mammals, yet their response remains understudied. To bridge this gap, I assessed the impact of human disturbances on terrestrial mammals in an unprotected area of Madre de Dios, Peru. Over eight years (2015-2022), I conducted a camera trap study on 17 terrestrial mammal species, including predators and prey, with 14,849 captures across 293 sites. Using occupancy models, I gauged the influence of ecological and anthropogenic factors on species occupancy and detection. Human disturbances notably affected mammal species, particularly persecuted ones such as jaguars (*Panthera onca*), tapirs (*Tapirus terrestris*), brocket deer (*Mazama spp.*), collared peccaries (*Pecari tajacu*), and agoutis (*Dasyprocta variegata*). These species displayed significant changes in occupancy probability based on proximity to settlements, agriculture, and land use type. Additionally, white-lipped peccaries (*Tayassu pecari*) remained undetected for seven years. I also studied the spatiotemporal overlap of five sympatric felid species: jaguars, pumas (*Puma concolor*), ocelots (*Leopardus pardalis*), jaguarundis (*Herpailurus yagouaroundi*), and margays (*Leopardus wiedii*). Temporal overlap was high due to nocturnal activity, except for the diurnal jaguarundi. Increased human activity led to reduced temporal overlap. Conditional occupancy models revealed that felid co-occurrence was influenced by dominant species, size differences, distance from settlements, rivers, and prey index/habitat quality. While intact Amazon rainforests support fine-scale niche differentiation among felid guilds, heightened disturbances could disrupt resource availability, affecting intraguild interactions, ecosystem structure, and function. Additionally, I explored the impact of human activity on ocelot density and temporal activity. Density remained unchanged across the mixed-use and protected areas, however, there was a significant difference in the overlap estimates of ocelot and human activity between the two areas. In conclusion, my findings underscore the vital importance of conserving intact forests in lowland Peruvian Amazonia. Targeted conservation measures like expanded protected forest buffers along rivers are essential to mitigate the negative effects of human activities in the Amazon rainforest. Given ongoing anthropogenic disturbance in the neotropics, further research is imperative to grasp the demographic dynamics of vulnerable mammals in human-modified areas.

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DEDICATION

For Bruce, Khan and Loki, who will forever be with me.

I promise to keep learning, improving, and making a difference every day.

Chapter 1. MODERATE LEVELS OF HUMAN DISTURBANCE IMPACT PERSECUTED TERRESTRIAL MAMMALS IN THE PERUVIAN AMAZON RAINFOREST

1.1 INTRODUCTION

In tropical regions, a notable surge in human population growth has given rise to unparalleled levels of deforestation, driven by the economies of many developing nations that heavily rely on natural resources (Beaudrot et al., 2016). This conversion of land is predominantly instigated by extractive pursuits, the expansion of agriculture, and the creation of road networks. Collectively, these factors contribute to the fragmentation of habitats, extraction of resources, and an escalation in hunting activities (Espinosa et al., 2014; Gil-Sánchez et al., 2021). Particularly pronounced is the extensive transformation of land use and land cover within the rainforests of western Brazil and southeastern Peru. This transformation is most notable in close proximity to newly established road networks stemming from the Interoceanic Highway (IOH) (Chávez Michaelsen et al., 2013).

The impact of human activities on wildlife extends beyond habitat destruction and fragmentation. Humans can directly increase mortality rates via hunting and car strikes, for example, but they can also disrupt important cues used by species to assess predation risk, such as light and noise, affecting their overall landscape of fear (Mendes et al., 2020). Consequently, species are often forced to modify their foraging patterns and temporal activity in response to human disturbances, which can have significant implications for their fitness and overall population dynamics. Moreover, it has been observed that wildlife abundance is more closely related to patterns of hunting rather than traditional ecological variables like habitat area or forest type (Benítez-López et al., 2017); which highlights the crucial role of hunting and other human activities in shaping mammal populations. Higher landscape accessibility to hunters has been linked to lower occurrence and biomass of game species as well as apex predators. For instance, jaguar (*Panthera onca*) density was found to be up to 18 times higher in a more remote site compared to the most accessible site within a biosphere reserve in the rainforests of Ecuador (Espinosa et al., 2018). Additionally, a major contributor to the decline of predators is the decline of prey availability (Boron et al., 2019; Fuller & Sievert, 2001), mainly through anthropogenic habitat loss and hunting. Studies have found that the fine-scale habitat use of jaguar and puma (*Puma concolor*) was best explained by prey availability (Palomares et al., 2016; Santos et al., 2019); moreover, larger-bodied prey and prey with higher fecundity determine the carrying capacity of top predators in these tropical systems (Terborgh & Estes, 2010). Prey availability as a factor of habitat quality therefore plays a critical role in the occupancy and persistence of predators. Only by incorporating the diverse geographic, ecological, and anthropogenic dynamics at play can we holistically predict trends in the spatial patterns of wildlife.

As a consequence of multifarious anthropogenic activities, defaunation—the loss of animal populations ranging from local declines to species extinctions—has become most pronounced in tropical ecosystems, leading to an alarming projected loss of biodiversity (Beaudrot et al., 2016). Notably, mammal abundance has declined by 83% across tropical regions (Benítez-López et al., 2017). These declines can be traced back to the historical impact of human hunters, which have persisted over time and resulted in population declines and near-extinctions of large-bodied mammal species, primarily in tropical ecosystems (Benítez-López et al., 2017; Jorge et al., 2013). The consequences of defaunation can have far-reaching effects on the structure and functioning of entire ecosystems, including disruptions in dispersal mutualisms and declines in total biomass (Benítez-López et al., 2017; Gil-Sánchez et al., 2021).

Despite the ecological significance of highly persecuted felid and game species, the impact of less visible activities such as hunting and wildlife extraction remain poorly studied, and the majority of population dynamics research occurs inside protected areas (Espinosa et al., 2014, 2018). Wildlife abundance tends to be higher within protected areas, highlighting the importance of these designated regions in supporting diverse and thriving populations (Benítez-López et al., 2017) but also the importance of monitoring wildlife populations in human-modified landscapes. Despite efforts to protect larger, relatively undisturbed areas, ecological processes within these protected regions are gradually eroding, often without apparent signs (Jorge et al., 2013). Assessing the intactness of natural areas becomes crucial, and indicator species play a vital role in signifying the presence or absence of these ecological interactions. By focusing on these flagship species, conservation efforts can prioritize areas for protection and implement targeted strategies to mitigate further biodiversity declines.

Indicator species are generally large carnivores and herbivores that possess unique ecological roles, are easily detectable, and their status can represent the overall health and integrity of ecosystems (Caro, 2010; Jorge et al., 2013). Large mammal assemblages have been defined as rare evolutionary and ecological phenomena and one of the most crucial layers of conservation to optimize global biodiversity protection and stabilize the climate (Dinerstein et al., 2020). Large mammals are often long-lived, slow to reproduce, and have wide-ranging habitat requirements, making them more susceptible to human disturbances (Ripple et al., 2014); therefore, the decline or disappearance of these species can signal significant ecological disruptions, including changes in trophic interactions, seed dispersal patterns, and habitat quality (D’Cruze et al., 2021; Jorge et al., 2013). For example, a decline in key seed dispersers has been shown to decrease populations of plants, insects like dung beetles, amphibians, and insectivorous birds (Jorge et al., 2013). Expectedly, species that serve as indicators for biodiversity are generally the most highly persecuted species for similar reasons (Di Minin et al., 2016; Morrison et al., 2007); they are large/ easily detected, serve as resources competitors for humans, and are profitable for their meat, parts, or as pets (D’Cruze et al., 2021; Jorge et al., 2013; Morrison et al., 2007). Since indicator species and those most highly persecuted are the first to vanish from fragmented and hunted forests (D’Cruze et al., 2021; Jorge et al., 2013), they serve as strong indicators of species richness and ecosystem health.

In addition to traditional bushmeat subsistence hunting, Peru has emerged as a hotspot for the wildlife trade in Latin America, with widespread exploitation and poorly regulated exportation of live wild animals and parts (D’Cruze et al., 2021). Among the most commercially valuable bushmeat species in Peru are the white-lipped peccary (*Tayassu pecari*), collared peccary (*Pecari tajacu*), brocket deer (*Mazama spp.*), the lowland tapir (*Tapirus terrestris*), paca (*Cuniculus paca*), and agouti (*Dasyprocta spp.*) (Espinosa et al., 2014). In forests without hunting, white-lipped peccaries in particular account for the highest biomass of neotropical ungulates; 200-peccary herds can have a biomass greater than 4.8 tons (Peres, 1996). The sale of wildlife is primarily driven by the demand for wild meat, followed by the pet trade, posing further threats to these species (D’Cruze et al., 2021). The declining abundance of these herbivores, particularly terrestrial seed predators and dispersers, has far-reaching repercussions, including a decline in plant and amphibian diversity, the reduction of dung beetle diversity, the decrease in insect fauna associated with litter, and the loss of insectivorous birds (Jorge et al., 2013). Wild cats such as the jaguar and the ocelot (*Leopardus pardalis*) are also impacted by illicit trafficking, which exploits both live animals and their body parts, including their skins. Pre-CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) jaguars and ocelots were overexploited with 228,376 jaguar skins and 17,301 ocelot skins harvested across their ranges, which decimated populations (Mena et al., 2021). Felid declines have consequences not only for the population dynamics of their prey, but the subsequent decline or alteration in ecosystem structure and function (Mena et al., 2021).

Our study focused on understanding the occupancy and site use probability of 17 mammal species, including the felid guild and their prey, within an unprotected landscape in Peru. We included ecological and anthropogenic covariates and considered landscape accessibility to hunters by incorporating distances between camera stations and settlements and agricultural areas. Though the Las Piedras region is experiencing moderate levels of deforestation and habitat conversion compared to other areas within Madre de Dios (MDD) and Peruvian Amazonia, we hypothesized that mammal occupancy would still be shaped by anthropogenic threats and activities in our study area. We predicted that the highly persecuted species, including the two most persecuted cats (jaguar and ocelot) and the six prey species of the highest market value (lowland tapir, white-lipped peccary, brocket deer, collared peccary, paca, and agouti), would exhibit the most significant responses to human disturbances. Our goal was to assess whether moderate levels of human impact are intensifying defaunation in a biodiversity hotspot, potentially affecting ecosystem interactions across human-modified landscapes within the Amazon rainforest.

1.2 METHODS

1.2.1 *Study Area*

The southern part of the Peruvian Amazon lies within the department of MDD, one of the largest unprotected and intact tropical rainforests in Peru, which has the second largest extent of rainforest in the Amazon, and still consists of largely contiguous forests (Asner et al., 2010). The area contains four national protected areas of over one million hectares each, including the Manu National Park, the Alto Purus National Park, the MDD Territorial Reserve, and the Tambopata/Bahuaja Sonene National Reserve, as well as several large Indigenous reserves, conservation concessions, and private protected lands (Fig. 1). The region is known for its diversity and abundance of fauna; however, it is also a mosaic of concessions with registered activities that often do not reflect actual land use and continues to face increasing pressures of logging and clear-cut agriculture. The study was carried out at the Hoja Nueva research center (-12.127, -69.476) along the Las Piedras River, 70 km northwest of Puerto Maldonado. The four study areas included approximately 450 km^2 of lowland rainforest representative of diverse land cover and land use (Fig. 1).

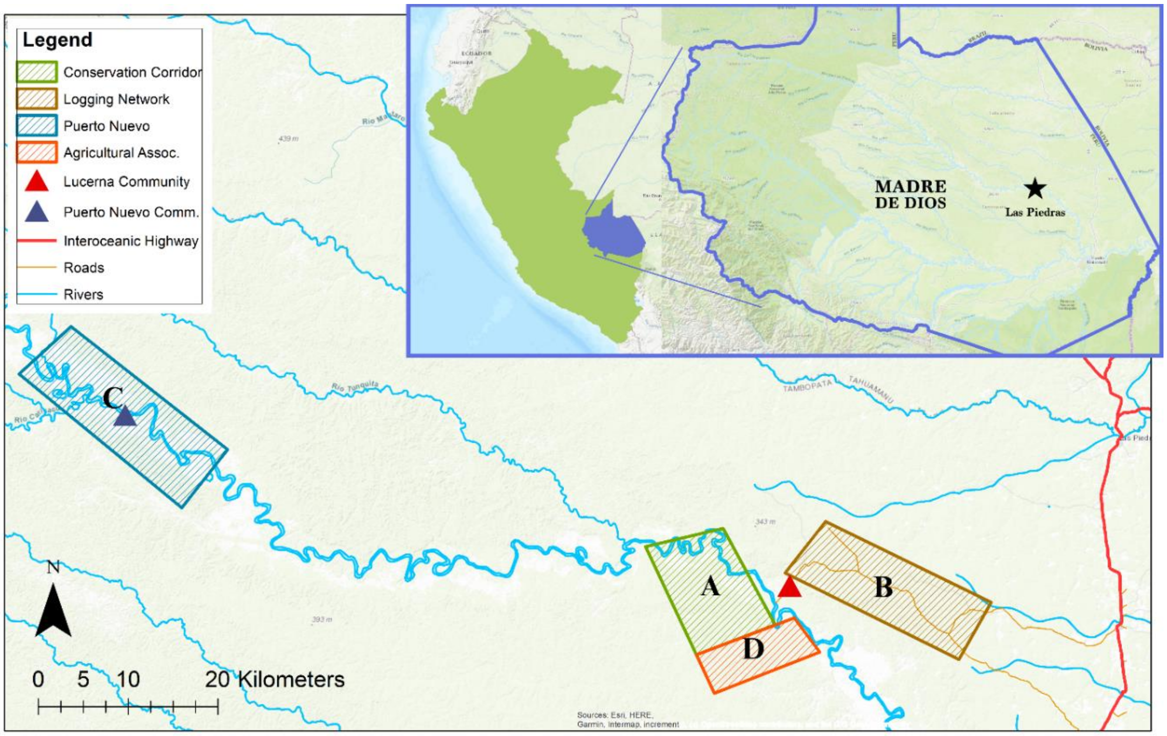

Fig. 1 Four different study areas (A, B, C, D) were surveyed between the years 2015 and 2022 along the Las Piedras River using eight camera trap grids, within the department of MDD, Peru (Southern Hemisphere UTM Zone 19, Easting: 408473, Northing: 8665291). Two settlements are indicated with triangles: Puerto Nuevo, an Indigenous subsistence hunting settlement, and Lucerna, a migrant agricultural settlement. The four study areas included the Las Piedras Conservation Corridor (A), logging networks between the IOH and Lucerna (B), the remote settlement of Puerto Nuevo (C), and a cacao agricultural association (D). Area A was surveyed five times, and areas B, C, and D were all surveyed once.

1.2.2 *Focal Species*

Our study focused on five felid species and 12 prey species, many of which are either data deficient or threatened with extinction locally and/or globally (Table 1). The five sympatric felid species in our region include the jaguar, puma, ocelot, jaguarundi (*Herpailurus yagouaroundi*), and the margay (*Leopardus wiedii*). The 12 terrestrial prey species we included in our study included the lowland tapir, giant armadillo (*Priodontes maximus*), giant anteater (*Myrmecophaga tridactyla*), white-lipped peccary, brocket deer, collared peccary, *Dasypus* armadillos, paca, agouti, common opossum (*Didelphis marsupialis*), green acouchi (*Myoprocta pratti*), and the Brazilian rabbit (*Sylvilagus brasiliensis*).

Table 1. Data for all 17 focal species including their weight range, ecological role, IUCN red list status, and Peru Red Book status. Cells shaded with orange represent the most highly persecuted species in this system that we predicted would respond significantly to human disturbances.

Species	Weight Range (kg)	Ecological Role	IUCN Status	Peru Red Book Status	Citations
Jaguar (*Panthera onca*)	30 - 120	Hypercarnivore / Apex Predator	Near Threatened	Near Threatened	(Emmons & Feer, 1999; IUCN, 2022; SERFOR, 2018)
Puma (*Puma concolor*)	22 - 80	Hypercarnivore / Apex Predator	Least Concern	Near Threatened	(IUCN, 2022; Moreno et al., 2006; SERFOR, 2018)
Ocelot (*Leopardus pardalis*)	8 - 18	Hypercarnivore / Mesopredator	Least Concern	Unlisted	(IUCN, 2022; Moreno et al., 2006)
Jaguarundi (*Herpailurus yagouaroundi*)	4.5 - 9	Hypercarnivore / Mesopredator	Least Concern	Unlisted	(IUCN, 2022; Santos et al., 2019)
Margay (*Leopardus wiedii*)	3 - 8	Hypercarnivore / Mesopredator	Least Concern	Data Deficient	(IUCN, 2022; Santos et al., 2019; SERFOR, 2018)
Lowland Tapir (*Tapirus terrestris*)	150 - 250	Herbivore / Seed Disperser	Vulnerable	Near Threatened	(IUCN, 2022; Padilla & Dowler, 1994; SERFOR, 2018)
Giant Armadillo (*Priodontes maximus*)	28 - 44	Insectivore / Ecosystem Engineer	Vulnerable	Vulnerable	(IUCN, 2022; SERFOR, 2018; Silveira et al., 2009)
Giant Anteater (*Myrmecophaga tridactyla*)	27 - 39	Insectivore	Vulnerable	Vulnerable	(IUCN, 2022; Medri & Mourão, 2005; SERFOR, 2018)
White-Lipped Peccary (*Tayassu pecari*)	25 - 35	Omnivore / Seed Predator / Ecosystem Engineer	Near Threatened	Near Threatened	(Kiltie & Terborgh, 1983)
Brocket Deer (*Mazama spp.*)	11.4 - 30	Herbivore / Seedling Predator	Data Deficient	Data Deficient	(Emmons & Feer, 1999; IUCN, 2022; Richard-Hansen et al., 1999; SERFOR, 2018)
Collared Peccary (*Pecari tajacu*)	15 - 25	Herbivore / Seed Predator / Ecosystem Engineer	Least Concern	Unlisted	(IUCN, 2022; Kiltie & Terborgh, 1983)
Armadillo (*Dasypus spp.*)	3 - 13	Insectivore / Ecosystem Engineer	Data Deficient	Unlisted	(IUCN, 2022; Richard-Hansen et al., 1999)
Paca (*Cuniculus paca*)	5.2 - 9.5	Herbivore / Seed Predator	Least Concern	Unlisted	(IUCN, 2022; Richard-Hansen et al., 1999)

Agouti (*Dasyprocta variegata*)	3 - 5.8	Herbivore / Seed Predator	Least Concern	Unlisted	(IUCN, 2022; Richard-Hansen et al., 1999)
Common Opossum (*Didelphis marsupialis*)	0.6 - 2	Omnivore / Scavenger	Least Concern	Unlisted	(IUCN, 2022; Richard-Hansen et al., 1999)
Green Acouchi (*Myoprocta pratti*)	0.6 - 1.8	Herbivore / Seed Predator	Least Concern	Unlisted	(IUCN, 2022; Richard-Hansen et al., 1999)
Brazilian Rabbit (*Sylvilagus brasiliensis*)	0.7 - 1	Herbivore	Least Concern	Unlisted	(IUCN, 2022; Richard-Hansen et al., 1999)

1.2.3 *Camera Trapping*

Within each study area, we placed 1-5 camera trap arrays between 2015-2022, resulting in eight sampling grids and a total of 293 camera stations. Cameras were spaced equidistantly for each grid, with an average distance between stations of 1.22 km. We based the spacing of six of the sample grids (2015-2022) on the ocelot, which has an average home range of 38.8 km^2 for males and 17.4 km^2 for females (Crawshaw, 1995). In 2022, we used smaller camera trap spacing in the remaining two sample grids to increase the detection of the margay. All grids except the two from 2022 accommodated at least one home range of our largest focal species, the jaguar, which is known to have a home range of 128.61 ± 49.5 km^2 across Central and South America; however, jaguar home range size is known to be markedly reduced in lowland rainforest (Gonzalez-Borrajo et al., 2017).

One of the four study areas surveyed consistently was the Las Piedras Conservation Corridor (LPCC) in the years 2018, 2019, 2021, and twice in 2022 for a total of 167 camera stations (see Area A in Fig. 1). The three remaining study areas were unprotected and included a variety of human disturbances typical to the Las Piedras region. Firstly, a network of logging roads between the IOH and the Las Piedras River was surveyed in 2015 (30 stations; Area B). A remote Indigenous settlement of subsistence hunters was surveyed in 2017 (46 stations; Area C). Lastly, a cacao agricultural association south of the LPCC was surveyed in 2021 (50 stations; Area D). All areas were sampled for approximately 90 days in the dry or dry-wet transition seasons between the months of July and December, minimizing the possibility that camera traps would be lost in the wet season due to failure from weather. The two macro-habitat types that were surveyed included terra firme (upland) forest and floodplain forest; the latter is a forest that is seasonally inundated during the wet season (November – April).

First, existing trail and road networks were located and mapped in each sample area, followed by overlaying a grid to select camera trap sites after selecting the first camera site at random. Where accessible, wildlife trails were used at grid points if a road or trail could not be found within 100 m. For example, the grids in 2015 (logging road networks) and 2017 (remote Indigenous settlement) were more elongated with larger gaps due to a lack of human trails and roads, so more cameras were placed on wildlife trails in these areas. Throughout the study areas, 153 camera stations were placed on human trails or roads, and 140 were placed on wildlife trails. We used Browning Strike Force trail cameras (BTC-5 and BTC-6 models), which trigger with movement at 20 m with an open view. Camera stations were made up of one or two cameras placed facing a trail, road, or wildlife trail, approximately 40-50 cm off the ground, set to capture videos.

1.2.4 *Covariates*

To investigate the effects of both 'bottom-up' ecological variables and human disturbance on mammal occupancy, we incorporated a suite of eight ecological and anthropogenic covariates (see Table 2 for details). These covariates were selected to capture various aspects of the landscape, including macrohabitat, indices representing small and large prey availability, enhanced vegetation index (EVI), distance from the Las Piedras River, distance from the nearest settlement, proximity to agriculture, and land use. The indices of large and small prey were specifically used as proxies for prey availability and habitat quality and were considered when modeling predator occupancy. Additionally, to account for landscape accessibility to hunters, we incorporated covariates mirrored from the work of Espinosa et al. (2018), such as distances between survey stations and both settlements agricultural areas. We included trail type (roads, human trails, or wildlife trails) as a covariate on detection probability (Harmsen et al., 2010).

Table 2. Descriptions of the covariates placed on detection and occupancy for the 17 mammal species across the four study areas, including two covariates on detection and eight covariates on occupancy.

	Covariate	**Description**
Detection	Trail Type	Trails were divided into two types based on their size and use by humans and wildlife: human trails/roads and wildlife trails.
	Trap Nights Operable	The number of nights operable for each camera site.
Occupancy	Macrohabitat	Macrohabitat refers to the general biome of each site and is defined by one of two categories: floodplain forest or terra firme forest. Floodplain forest represents seasonally inundated forests, usually in closer proximity to rivers, while terra firme forest represents upland forest. A Digital Elevation Model (DEM) was obtained from the local forestry department in Puerto Maldonado in 2015 to identify these two macrohabitats using elevation and a detailed map of the transition zones in each survey area.
	Small Prey Index	The index was calculated as the number of captures of prey < 5 kilos divided by the total number of trap nights per site.
	Large Prey Index	The index was calculated as the number of captures of prey > 5 kilos divided by the total number of trap nights per site.

	Enhanced Vegetation Index	Enhanced Vegetation Index (EVI) was obtained from the U.S. Geological Survey's EarthExplorer website (earthexplorer.usgs.gov) using the MOD13A1 Version 6 product (Didan, 2015). Imagery was downloaded for the week before each sample grid was surveyed. An EVI scale of 500m was used to quantify vegetation greenness around each site.
	Distance from River	The Las Piedras River was tracked via handheld GPS three times to get an accurate river layer. The distance between each camera trap station and the river was then measured using the "near" tool in ArcMap 10.4's Proximity toolset (ESRI, Redlands, USA).
	Distance from Settlement	GPS coordinates were taken in the center of both Lucerna and Puerto Nuevo. Distance between each camera trap station and the nearest settlement was measured using the "near" tool in ArcMap 10.4's Proximity toolset (ESRI, Redlands, USA).
	Proximity to Agriculture	All surrounding farmland was mapped manually using a handheld GPS when active farms were located within/near the study area. Proximity to agriculture was recorded as a category: whether a camera trap station was located within 500 meters of a farm greater than 4 hectares in size or not.
	Land-Use	We created an index of human land-use activity categorized as Low or High. Low land-use areas included conservation lands protected by conservation and eco-tourism NGOs within the LPCC. High-land use included settlements, agriculture areas, and Brazil nut harvesting concessions outside of the LPCC, including a number of sites where vehicles, hunting, and timber extraction were recorded.

We examined correlations between all continuous variables, and none were high enough to preclude independent inclusion in the subsequent occupancy analyses (all r < |0.7|). All continuous covariates (5 total) were standardized to have a mean of 0 and a standard deviation of 1 for analysis, and all categorical variables were listed as factors. The most common classification within each of the three categorical variables (e.g., "conservation" within land use) was set to be the default category (i.e., included in the intercept).

1.2.5 *Data Analysis*

Out of a total of 14,849 detections of these 17 mammals, the most highly photo-captured mammals were brocket deer (3016 captures) and agouti (2998 captures) whereas the least captured mammals were white-lipped peccary (34 captures) and jaguarundi (35 captures) (Table 3). Mean probability of detection ranged between 0.055 and 0.397, and the mean probability of occupancy ranged between 0.182 and 0.931. Distance from the river, land use, and macro-habitat were the most frequent covariates amongst the top models. Both trail type and trap nights operable were common in the top models, explaining the detection probability of 71% of studied species (Table 3).

Table 3. Single-species occupancy results for the 17 focal species including total captures from camera traps, individual sample occasions from detection histories, naïve occupancy, covariates for detection and occupancy in each top model, and the resulting probabilities of both detection and occupancy driven by the model covariates. Cells shaded with orange represent the species whose occupancy probability was significantly lower in areas with higher human disturbance.

Species	**Total Captures**	**Sample Occasion (Days)**	**Naïve Occupancy**	**Top Model**		**Mean Probability of Detection**	**Mean Probability of Occupancy**
				Detection	**Occupancy**		
Jaguar (*Panthera onca*)	231	5	0.358	Trail + Operable	Habitat + Agriculture + Land Use	0.065	0.611
Puma (*Puma concolor*)	471	5	0.461	Trail	Prey + River	0.130	0.638
Ocelot (*Leopardus pardalis*)	1181	5	0.700	Trail	Habitat + Agriculture	0.211	0.824
Jaguarundi (*Herpailurus yagouaroundi*)	35	10	0.085	-	Prey + Small Prey	0.080	0.228
Margay (*Leopardus wiedii*)	139	5	0.273	-	EVI + River	0.063	0.441
Lowland Tapir (*Tapirus terrestris*)	1412	5	0.761	Trail + Operable	EVI + Habitat + Agriculture	0.257	0.787
Giant Armadillo (*Priodontes maximus*)	92	10	0.208	-	River + Settlement	0.059	0.600
Giant Anteater (*Myrmecophaga tridactyla*)	117	10	0.249	-	EVI + River + Settlement	0.087	0.532
White-Lipped Peccary (*Tayassu pecari*)	34	10	0.072	Trail + Operable	-	0.055	0.278
Brocket Deer (*Mazama spp.*)	3016	5	0.918	Trail	Habitat + Land Use	0.395	0.931
Collared Peccary (*Pecari tajacu*)	1726	5	0.826	Trail + Operable	River + Settlement + Land Use	0.346	0.848
Armadillo (*Dasypus spp.*)	439	5	0.375	-	EVI + Habitat + River	0.144	0.430
Paca (*Cuniculus paca*)	1348	5	0.594	Trail	-	0.274	0.613
Agouti (*Dasyprocta variegata*)	2998	5	0.812	Trail	Settlement + Land Use	0.397	0.825
Common Opossum	945	5	0.549	Trail	Habitat + River +	0.218	0.586

(*Didelphis marsupialis*)					Agriculture + Land Use		
Green Acouchi (*Myoprocta pratti*)	446	5	0.294	Operable	Land Use	0.158	0.337
Brazilian Rabbit (*Sylvilagus brasiliensis*)	219	5	0.116	Trail	EVI + River + Land Use	0.148	0.182

We found substantial support for our prediction that the most persecuted species would respond to anthropogenic pressures; five of the eight species expected to be most sensitive to human disturbance experienced significant changes in occupancy probability in response to a covariate that reflected either direct or indirect human impact including the jaguar, lowland tapir, brocket deer, collared peccary, and the agouti. Of the nine species that are less persecuted within the study area, only two responded negatively to any of the covariates reflecting human disturbance. Overall, we observed that covariates characterizing habitat area/ forest type and resources, such as macro-habitat, EVI, distance to river, and the two prey indices, affected the occupancy probability of 65% of our focal species. Supporting our hypothesis, covariates reflective of deforestation and human impacts described the occupancy patterns of 47% of our focal species.

No consistent patterns emerged across the felid guild (Table 4). Jaguars and ocelots had proximity to agriculture in their top models, supporting our prediction that they would have a more heightened response to human disturbance than pumas, jaguarundis, and margays. While jaguar site use probability was lower in areas closer to agriculture, results for ocelots were not significant. Additionally, jaguar site use probability increased in mixed-use areas. Ocelot occupancy probability increased in floodplain forest compared to terra firme forest, and puma probability of use decreased with distance from the river. Interestingly, jaguarundi probability of occupancy increased in areas where both the small and large prey indices were higher, and margay occupancy increased at sites with a high EVI.

Table 4. Resulting estimates and standard errors from the top models of the five felid species, organized by the relative size of the species. Cells with a dash represent covariates that were not present in the top model. Orange shaded cells represent a persecuted species with a significant negative response to human disturbance. Detection intercept includes off-trail (wildlife trails) for trail type. Occupancy intercept includes floodplain for macro-habitat, >500m for proximity to agriculture, and low land use. All estimates are shown on the logit-scale. Significance: * p < 0.1.

Species	**Detection Intercept**	**Trail (On)**	**Trap Nights Operable**	**Occupancy Intercept**	**Terra Firme Macro-Habitat**	**Big Prey Index**	**Small Prey Index**	**EVI**	**Distance from River**	**Agriculture < 500 m**	**Mixed Land Use**
Jaguar (*Panthera onca*)	-337(0.18)*	0.95(0.19)*	0.26(0.11)*	0.499(0.41)	-0.77(0.50)	-	-	-	-	-2.23(1.33)*	2.62(1.3)*
Puma (*Puma concolor*)	-3.09(0.17)*	1.76(0.18)*	-	0.58(0.18)*	-	0.26(0.18)	-	-	-0.33(0.17)*	-	-
Ocelot (*Leopardus pardalis*)	-2.26(0.10)*	1.50(0.11)*	-	2.56(0.46)*	-1.32(0.49)***	-	-	-	-	-0.82(0.53)	-
Jaguarundi (*Herpailurus yagouaroundi*)	-2.44(0.34)*	-	-	-1.61(0.40)*	-	0.50(0.28)*	0.45(0.24)*	-	-	-	-
Margay (*Leopardus wiedii*)	-2.69(0.14)*	-	-	-0.25(0.23)	-	-	-	0.31(0.18)*	0.26(0.17)	-	-

The four prey species that are both highly persecuted and had a significant response to human impact variables included tapir, brocket deer, collared peccary, and agouti, and land use was the most common anthropogenic variable in prey top models (Table 5). The occupancy probability of acouchi, brocket deer, collared peccary, and common opossum significantly decreased in mixed-use areas outside of the protected conservation corridor; only the occupancy probability of Brazilian rabbits increased in this matrix habitat compared with low land use by humans. One species, the common opossum, had a higher probability of occupancy near agricultural areas, whilst the occupancy of the lowland tapir decreased significantly at sites within 500 m of agriculture. Only agouti had a significant increase in occupancy in response to an increasing distance from settlements. The occupancy probability of the following five species significantly decreased with distance from the river: giant anteater, Brazilian rabbit, collared peccary, common opossum, and *Dasypus* armadillos. While the occupancy probability of brocket deer and *Dasypus* armadillos increased in terra firme (upland) forest, the lowland tapir had higher occupancy in seasonally flooded forest. Lastly, increased greenness (EVI) had a significant positive effect on the occupancy probability of the giant anteater and lowland tapir.

Table 5. Coefficient estimates and standard errors from the top models of the 12 prey species, organized by the relative size of the species. Dashed cells represent covariates that were not present in the top model. Orange shaded cells represent a persecuted species with a significant negative response to human disturbance. Detection intercept is for wildlife trails for the trail type. Occupancy intercept includes floodplain for macro-habitat, >500m for proximity to agriculture, and low land use (conservation corridor). All estimates are shown on the logit-scale. Significance: * p < 0.1.

Species	Detection Intercept	Trail (On)	Trap Nights Operable	Occupancy Intercept	Terra Firme Macro-Habitat	EVI	Distance from River	Dist. from Comm.	Agriculture < 500 m	Mixed Land Use
Lowland Tapir (*Tapirus terrestris*)	-1.20(0.06)*	0.25(0.08)*	-0.18(0.05)*	2.47(0.38)*	-1.49(0.41)*	0.35(0.16)*	-	-	-1.02(0.44)*	-
Giant Armadillo (*Priodontes maximus*)	-3.05(0.20)	-	-	2.37(2.18)	-	-	-3.13(2.24)	2.07(1.57)	-	-
Giant Anteater (*Myrmecophaga tridactyla*)	-2.35(0.19)*	-	-	0.16(0.40)	-	0.81(0.27)*	-0.73(0.34)*	0.48(0.31)	-	-
White-Lipped Peccary (*Tayassu pecari*)	-2.43(0.45)*	-1.81(0.59)*	-0.56(0.29)*	-0.96(0.53)*	-	-	-	-	-	-
Brocket Deer (*Mazama spp.*)	-0.28(0.05)*	-0.29(0.07)*	-	3.39(0.70)*	1.27(0.53)*	-	-	-	-	-2.08(0.73)*
Collared Peccary (*Pecari tajacu*)	-0.71(0.06)*	0.13(0.08)	-0.16(0.05)*	2.25(0.30)*	-	-	-0.57(0.24)*	0.42(0.26)	-	-0.83(0.38)*
Armadillo (*Dasypus spp.*)	-1.79(0.08)*	-	-	-0.73(0.26)*	0.71(0.35)*	0.22(0.14)	-0.58(0.21)*	-	-	-
Paca (*Cuniculus paca*)	-0.82(0.07)*	-0.30(0.09)*	-	0.46(0.12)*	-	-	-	-	-	-
Agouti (*Dasyprocta variegata*)	-0.65(0.06)*	0.43(0.07)*	-	1.38(0.21)*	-	-	-	0.33(0.19)*	-	0.49(0.33)
Common Opossum (*Didelphis marsupialis*)	-1.41(0.09)*	0.25(0.10)*	-	0.44(0.28)	0.49(0.33)	-	-0.37(0.18)*	-	0.82(0.44)*	-1.0(0.29)*
Green Acouchi (*Myoprocta pratti*)	-1.69(0.11)*	0.23(0.11)*	-	-0.31(0.18)*	-	-	-	-	-	-0.86(0.29)*
Brazilian Rabbit (*Sylvilagus brasiliensis*)	-3.56(0.42)*	2.50(0.43)*	-	-2.61(0.40)*	-	-0.35(0.23)	-1.12(0.40)*	-	-	1.40(0.45)*

In terms of detection probability, we found that three prey species – the lowland tapir and both peccary species – had a negative relationship with the number of trap nights. However, more trap nights significantly increased the detection probability of the jaguar and the green acouchi. Although brocket deer, paca, and white-lipped peccary had higher detection probability on wildlife trails, the following mammals generally had significantly higher detection on human trails and roads than on wildlife trails: lowland tapir, common opossum, agouti, Brazilian rabbit, jaguar, puma, and ocelot.

1.3 RESULTS

Out of a total of 14,849 detections of these 17 mammals, the most highly photo-captured mammals were brocket deer (3016 captures) and agouti (2998 captures) whereas the least captured mammals were white-lipped peccary (34 captures) and jaguarundi (35 captures) (Table 3). Mean probability of detection ranged between 0.055 and 0.397, and the mean probability of occupancy ranged between 0.182 and 0.931. Distance from the river, land use, and macro-habitat were the most frequent covariates amongst the top models. Both trail type and trap nights operable were common in the top models, explaining the detection probability of 71% of studied species (Table 3).

We found substantial support for our prediction that the most persecuted species would respond to anthropogenic pressures; five of the eight species expected to be most sensitive to human disturbance experienced significant changes in occupancy probability in response to a covariate that reflected either direct or indirect human impact including the jaguar, lowland tapir, brocket deer, collared peccary, and the agouti. Of the nine species that are less persecuted within the study area, only two responded negatively to any of the covariates reflecting human disturbance. Overall, we observed that covariates characterizing habitat area/ forest type and resources, such as macro-habitat, EVI, distance to river, and the two prey indices, affected the occupancy probability of 65% of our focal species. Supporting our hypothesis, covariates reflective of deforestation and human impacts described the occupancy patterns of 47% of our focal species.

No consistent patterns emerged across the felid guild (Table 4). Jaguars and ocelots had proximity to agriculture in their top models, supporting our prediction that they would have a more heightened response to human disturbance than pumas, jaguarundis, and margays. While jaguar site use probability was lower in areas closer to agriculture, results for ocelots were not significant. Additionally, jaguar site use probability increased in mixed-use areas. Ocelot occupancy probability increased in floodplain forest compared to terra firme forest, and puma probability of use decreased with distance from the river. Interestingly, jaguarundi probability of occupancy increased in areas where both the small and large prey indices were higher, and margay occupancy increased at sites with a high EVI.

The four prey species that are both highly persecuted and had a significant response to human impact variables included tapir, brocket deer, collared peccary, and agouti, and land use was the most common anthropogenic variable in prey top models (Table 5). The occupancy probability of acouchi, brocket deer, collared peccary, and common opossum significantly decreased in mixed-use areas outside of the protected conservation corridor; only the occupancy probability of Brazilian rabbits increased in this matrix habitat compared with low land use by humans. One species, the common opossum, had a higher probability of occupancy near agricultural areas, whilst the occupancy of the lowland tapir decreased significantly at sites within 500 m of agriculture. Only agouti had a significant increase in occupancy in response to an increasing distance from settlements. The occupancy probability of the following five species significantly decreased with distance from the river: giant anteater, Brazilian rabbit, collared peccary, common opossum, and *Dasypus* armadillos. While the occupancy probability of brocket deer and *Dasypus* armadillos increased in terra firme (upland) forest, the lowland tapir had higher occupancy in seasonally flooded forest. Lastly, increased greenness (EVI) had a significant positive effect on the occupancy probability of the giant anteater and lowland tapir.

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1.4 DISCUSSION

Our study yielded new insights into the influence of various ecological and anthropogenic variables on a community of felid predators and their prey in the Amazon rainforest. Responses to human impacts were strongest for the most highly persecuted mammals – both predators and game species – but were also very species-specific within the predator and prey guilds. In addition, mammals with less hunting pressure did not spatially avoid the more disturbed sites within our study area.

We did not observe any anthropogenic effects on one of the most persecuted species, white-lipped peccary (hereafter “white-lips”), because we did not capture them for seven years consecutively. Their absence is concerning given their ecological role, vulnerable status according to the IUCN, and near-threatened designation in Peru by SERFOR (IUCN, 2022;

SERFOR, 2018). In contrast to the usual abundance of white-lips compared to collared peccary in Amazonian ecosystems, our study observed an abundance of collared peccary and no white-lips until 2022. White-lips typically dominate over collared peccaries, leading to lower occupancy probability for the latter at sites occupied by white-lips (Ferreguetti et al., 2017). They serve as ecosystem engineers, seed predators/ dispersers, and important prey for top predators like puma and jaguar (Ferreguetti et al., 2017; Kiltie & Terborgh, 1983). The disappearance of white-lips from large regions like MDD for over ten years initially led to the hypothesis of migration; however, a 15-year study in northern Brazil debunked this, showing that population declines were caused by disease outbreaks rather than migration (Fragoso, 2004). Disease outbreaks resulted in high mortality, with hunting further reducing the remaining individuals, while areas without hunting allowed for repopulation (Fragoso, 2004). Recolonization of herds from distant locations explains the 10–15-year process observed across the Amazon rainforest. The development of remote areas in the Las Piedras region, including road construction, settlement formation, and agriculture, has led to increased habitat fragmentation, hunting, and disease, likely contributing to the disappearance of white-lips. Our camera traps did not capture white-lips from 2014 to 2021, suggesting an epidemic after urbanization and the introduction of agriculture/livestock in the early 2000s. However, small groups were observed in person between 2017 and 2020 (D. J. Singer, personal communication, May 20, 2023), indicating that a few groups remained to repopulate the area; we then obtained our 35 records of white-lips on camera within the confines of the protected corridor in 2022. Encouragingly, in May 2023, our team witnessed a group of over 100 individuals, indicating population stabilization within the conservation corridor but unknown status outside of this privately protected area.

After white-lips, the most sought after bushmeat species include agouti, collared peccary, brocket deer, and lowland tapir, which all had significant responses to our anthropogenic covariates: distance from the closest settlement, proximity to agriculture, and land use type. Although agoutis are thought to be more adaptable to human-modified areas (Naughton-Treves et al., 2003), their negative relationship with settlements indicates a direct response to human presence and likely hunting pressure. Brocket deer and collared peccary both decreased in occupancy probability in mixed-use areas, which aligns with results from previous studies, confirming their heightened sensitivity to human disturbance (Nagy-Reis et al., 2017). Tapirs likely responded to agriculture in particular for several reasons: the presence of hunting, a decrease in food availability, and reduced access to water. Given that permanent households are prominent among the cacao and papaya farms and these households are isolated from both the closest settlement and the city, families rely upon the combination of their local crops and bushmeat to subsist. Tapirs are hunted with relative ease due to their heaviness and a method called "spotlighting" where their large eyeshine is spotted using flashlights at night. Additionally, clearcutting for agriculture has drastic, immediate effects on the floristic composition and vegetation structure at the forest edge and well into the remaining forest interior (Williams-Linera, 1990), decreasing interior species of the herbaceous layer that are vital to the tapir's diet. Tapirs are semiaquatic and need consistent access to water bodies for various reasons including thermoregulation, to facilitate movement, and to escape predators (Burs et al., 2023). Drier and hotter forest edges cause increased forest desiccation and the disappearance of water bodies; canopy water loss has been known to extend over one kilometer into the forest in a landscape that has only been moderately fragmented (Briant et al., 2010). Matrix habitat or mixed-land use areas likely did not affect tapir occupancy because food and water availability remain high in these areas compared to landscapes of agriculture and forest fragments.

Due to their large home ranges and requirement for substantial contiguous areas to survive, jaguars are especially vulnerable to fragmentation and human development (Michalski & Peres, 2005; Zeilhofer et al., 2014). Our research shows that jaguars in the Las Piedras are using areas of mixed land-use outside of protected areas, but specifically avoiding cacao farms within the agricultural association that borders the LPCC. The agricultural association is predominantly made up of 5–20-hectare areas clearcut for cacao production, but oftentimes there are permanent households where domestic animals such as dogs, pigs, and chickens reside without fencing. One of several reasons that jaguar site use decreases in proximity to agriculture could be the higher likelihood of retaliation for livestock kills in these areas (Amador et al., 2013). Additionally, cacao farms likely do not provide sufficient vegetation cover and have lower occupancy of the jaguar's main prey species, the lowland tapir. Mixed-use areas, which we defined as matrix habitat outside the protected LPCC, increased the site use probability of jaguars in our study area. Vehicles, hunting, and timber extraction were recorded at these sites, which were in closer proximity to human settlements, logging camps, and Brazil nut concessions. An increase in jaguar site use probability in these areas could be due to several factors: the extensive daily distance traveled by jaguars (McBride & Thompson, 2018), the use of habitual travel routes and paths of least resistance (Karanth & Nichols, 1998), their documented tolerance of human disturbance (e.g. ability to become more nocturnal in human-occupied areas) (Foster et al., 2010; Monette et al., 2020), and the relatively low level of human impact in these areas comparatively. Although these sites were outside of the protected corridor, the forest is generally intact and connected, and human activity is limited; therefore, jaguars still use these areas for navigation, at least to get from one zone of their range to another.

While most of our persecuted predator and game species showed a significant response to human impacts, the ocelot and the paca did not. Due to the extent to which ocelots are hunted (Valsecchi et al., 2023), usually in retaliation for livestock killings (Mena et al., 2021), we expected similar results to the jaguar with either distance from settlements or agriculture proving significant in affecting ocelot occupancy. Our results could indicate that ocelots are more capable of adapting to human disturbance; however, it could also be due to a lack of data from agricultural areas, as sites within 500 m of cacao or papaya agriculture only represented 12% of our total sites (in part due to camera theft near agricultural locations). This reduced sample size is likely causing us to miss patterns in species occupancy in relation to proximity to agriculture for not just ocelots but all of the species. Although the paca did not have a negative response to any human impact covariates, their significantly lower detection probability on human trails could represent an avoidance of humans at finer scales in response to hunting or could indicate they prefer smaller mammal trails. Additionally, paca are known to be a riverine species, and past studies have deployed camera traps within 100 m of a water source to effectively study their ecology (Figueroa-de-León et al., 2017). Therefore, the design of our study may be impeding our ability to detect patterns in the occupancy of paca given their habitat requirements and space use.

The Las Piedras River was a significant predictor of mammal occupancy across our study area. Distance from the closest river and vicinity to fresh water have been recorded to increase species occupancy in similar systems, within both the predator and prey guilds (Boron et al., 2019; Dias et al., 2019; Rich et al., 2017). The river and floodplain forest are crucial as mammal habitat; however, riverine habitat is also used by humans for the establishment of settlements and agriculture. The combination of abundant natural resources, transportation opportunities, and fertile soils make riverine habitats a primary choice for colonization in the Amazon rainforest (Lentz, 2000; Moran, 2007). Consequently, subsistence hunting is concentrated around farms and settlements and near the margins of rivers; distance from rivers has been used as a covariate to predict hunting intensity given it is a common access point for hunters (Espinosa et al., 2018; Whitworth et al., 2019). Riverine concessions in MDD should therefore receive prioritized protection in the face of further colonization due to the importance of rivers for mammal habitat.

Only two of the nine relatively non-persecuted mammals spatially avoided disturbed sites including the common opossum and green acouchi; in addition, the common opossum and Brazilian rabbit benefited from matrix habitat in our study area. The common opossum, although not persecuted for its meat, parts, or as a pet, has been known to be frequently killed by humans and dogs across its geographic range, which could explain its avoidance of areas with high land use (Vaughan & Hawkins, 1999). Common opossums also had a positive relationship with agricultural sites, likely due to the abundance of food (fruit, vegetables, and small domestic animals/ eggs), so their response to human disturbance varied. The green acouchi also avoided areas of high land use, which could be in response to human pressures like hunting; however, it could also be attributable to changes in community structure and interspecific competition. Populations of generalist rodents likely surged in matrix habitat (Suzán et al., 2008), increasing competition for food resources in human-modified areas, and pushing out the acouchi. The Brazilian rabbit increased in occupancy in areas of high land use and avoided intact forest within the private protected area; although there is little research on this particular species, rabbits in general are known to better cope with human disturbance and benefit from human infrastructure and resources (Bock et al., 2009).

The probability of occupancy for two vulnerable, large-bodied mammals with low reproductive rates—the lowland tapir and the giant anteater—showed a notable increase in correlation with higher levels of greenness (EVI). To ensure the accuracy of EVI values in capturing seasonal variations, systematic updates were applied prior to each grid, mitigating the influence of known fluctuations. Beyond being a mere indicator of greenness, EVI emerges as a versatile tool in ecological monitoring for species diversity and composition, gross primary production (GPP), forest degradation, and canopy dynamics (Hasanah et al., 2020; Maeda et al., 2014). Our results indicate a correlation between large prey occupancy and high GPP, dense canopy, and low forest degradation. By increasing the enforcement of deforestation policies and advocating for sustainable land management practices that prioritize canopy preservation, such as agroforestry initiatives, the integrity of canopy dynamics can be effectively maintained.

Our research sheds light on the impacts of human activities and their consequences for wildlife populations using occupancy models and analyzing various ecological and anthropogenic covariates. Additionally, the methods developed in our study provide a means to detect the often subtle and overlooked process of defaunation, even in rapidly changing ecosystems like those in South America, by incorporating potential hunting access points (proximity to agriculture and settlements) into occupancy models. Our findings highlight the urgency of addressing deforestation and defaunation to prevent further ecosystem degradation. In some cases, like white-lipped peccary, we had no detections in areas with moderate levels human impact, indicating that even some amount of habitat destruction and hunting are fostering defaunation and the loss of ecological processes within the Las Piedras region. However, it is important to note that there are still opportunities for action and conservation interventions to mitigate defaunation in many areas as found that protected areas had higher occupancy probabilities for a number of prey species in our study. Protected areas, especially those bordering or utilized by human communities, can act important refugia for wildlife species from habitat loss and hunting (Boron et al., 2022; Lyra-Jorge et al., 2008). By identifying key indicator species and understanding their responses to human pressures, targeted conservation efforts can be implemented to ensure the long-term stability and functionality of these vital rainforest ecosystems across the globe.

Chapter 2. SPATIOTEMPORAL PARTITIONING OF FIVE SYMPATRIC FELIDS IS DETERMINED BY FINE-SCALE HABITAT DIFFERENCES AND HUMAN ACTIVITIES IN LOWLAND AMAZONIA

2.1 INTRODUCTION

Carnivores are vital for stabilizing ecosystems, especially in Neotropical regions where they significantly impact community and forest dynamics (Blake & Loiselle, 2018; Davis et al., 2011; Terborgh & Estes, 2010). Interactions among carnivores play a key role in shaping their guild composition and, as a result, can influence ecosystem dynamics. For example, 'mesopredator release' after the loss of large carnivores can lead to the decline or extinction of prey species (Caro & Stoner, 2003; Crooks & Soulé, 1999; Karanth et al., 2017). Thus, guilds of top predator species are often used to test hypotheses about and reveal the evolutionary or ecological outcomes of their relationships (Schoener, 1974).

Human-induced changes, both bottom-up (e.g., land use change) and top-down (e.g., hunting), can lead to varied behavioral and demographic responses in carnivores, ultimately affecting interspecific competition and niche partitioning (Dorresteijn et al., 2015). For example, human activities such as agricultural expansion, road construction, and urbanization in remote rainforests have led to reduced niche partitioning among felids across the tropics (Boron et al., 2019; Tobler et al., 2013). The resulting matrix and mixed-use landscapes outside protected areas can significantly alter the spatiotemporal patterns of these species, as well as their patterns of coexistence (Dorresteijn et al., 2015). Therefore, understanding how anthropogenic disturbances impact neotropical felids and their communities is crucial for predicting population trends and viability of these predators (Boron et al., 2019).

In tropical forests, intraguild competition is a critical factor restricting felid species' population sizes and spatiotemporal distributions (Di Bitetti et al., 2010). The competitive exclusion principle states that two species cannot occupy the same ecological niche without negative impacts on one or the other (Di Bitetti et al., 2009). Interspecific competition manifests in different ways, such as exploitative competition, interference competition, and intraguild predation (Sitvarin & Rypstra, 2014; Vance-Chalcraft et al., 2007), all of which influence the number of species and individuals an ecosystem can support (Di Bitetti et al., 2010). Apex predators, like jaguars (*Panthera onca*), can control mesopredators both through direct killing and by instilling fear, leading to changes in behavior and habitat use that limit mesopredator distribution and abundance (Ritchie & Johnson, 2009). Nonetheless, species with similar niches can coexist when they partition time, space, or resources, and human activities can influence this partitioning positively or negatively (Rodriguez Curras et al., 2022).

For felid communities in the neotropics, where the distributions of five focal species - jaguars, pumas (*Puma concolor*), ocelots (*Leopardus pardalis*), jaguarundis (*Herpailurus yagouaroundi)*, and margays (*Leopardus wiedii*) - extensively overlap, understanding coevolutionary processes is essential for unraveling how species sharing the same habitat adapt and interact over time, influencing resource partitioning, predator-prey dynamics, and ecosystem stability. (Di Bitetti et al., 2010; Sunquist & Sunquist, 2002). This knowledge enhances our grasp of complex ecological relationships and aids in maintaining the equilibrium of natural systems. Size differences between sympatric neotropical felids significantly impact their relative niches (Kiltie

& Terborgh, 1983). Intraguild predation intensity is highest when the larger species is 2.0 – 5.4 times larger than the smaller, and food competition is most pronounced when the larger species is less than twice the size of the smaller (Donadio & Buskirk, 2006). Based on this theory, interspecific killing should be highest in the following dyads: jaguar:ocelot, puma:ocelot, ocelot:jaguarundi, and ocelot:margay; food competition should be highest for jaguar:puma and jaguarundi:margay. A size chart showing the relative body weight relationships between felids can be found in Fig. 2. Predictions about their coexistence have mainly focused on morphological differences, but behavioral differences like spatiotemporal partitioning can also play a vital role in shaping the dynamics of these intraguild interactions and influencing the equilibrium of these predator species within their shared ecosystems (Santos et al., 2019).

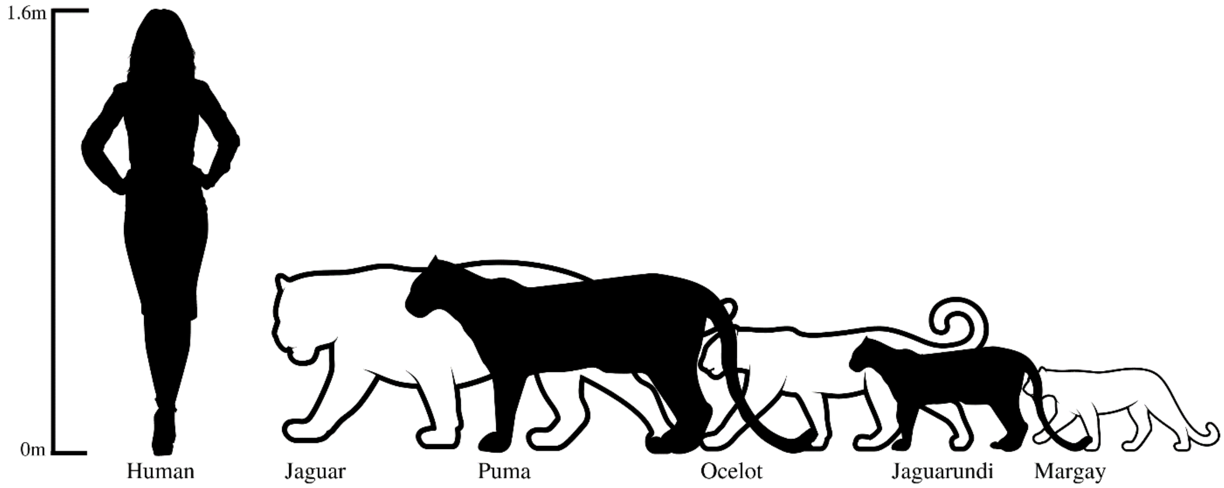

Fig. 2 A size chart showing the relative body weight relationships between the five local felids to Las Piedras, Madre de Dios, Peru, and an average human female of 1.6 meters.

Spatiotemporal segregation, which occurs along various axes such as habitat use, activity patterns, and resource utilization, is proposed as a mechanism that reduces intraguild competition and killing among competing carnivores (D. M. Dias et al., 2019; Santos et al., 2019; Shores, 2020). Subordinate species employ this evolutionary tactic to avoid encounters with dominant competitors (Palomares & Caro, 1999). For instance, the ocelot primarily exhibits nocturnal behavior, while the smaller jaguarundi tends to be more diurnal or crepuscular (Sunquist & Sunquist, 2002). Habitat preferences, with the jaguar favoring forests and the puma showing a broader habitat tolerance (Craighead et al., 2022; Figel et al., 2021), contribute to spatial partitioning as different felids utilize distinct habitat types, reducing competition for resources. Moreover, dietary specialization, such as the jaguarundi's specialization for birds, the margay's preference for non-volant small mammals, and the ocelot's specialization for small mammals and reptiles (Bianchi et al., 2011; E. Wang, 2002) further facilitates coexistence among sympatric felids.

In the context of human disturbance, comprehending interactions among neotropical felids becomes a crucial knowledge gap, given the growing human population and its impact on ecosystems. While assessing various dimensions of competition aids our understanding of carnivore coexistence, delving into these interactions within human-modified landscapes is equally imperative. As human activity alters natural balances in ecosystems, it is essential to investigate where similar felid species diverge in their needs and behaviors. This exploration provides invaluable insights into the extent and nature of interspecific competition in these communities, thus playing a pivotal role in the conservation and management of neotropical felids amidst escalating human influences (Davis et al., 2011). Understanding the spatiotemporal partitioning within felid communities is essential for grasping ecological processes and upholding ecosystem equilibrium, particularly given the profound impact of human activities on these interactions. When factoring in elements like size disparities, interspecific competition, habitat preferences, and anthropogenic effects, we gain intricate insights into the mechanisms enabling felid coexistence in the neotropics. By delving into these ecological intricacies, we pave the way for more informed conservation strategies that safeguard both these vulnerable species and the intricate ecosystems they inhabit.

In this study, we used conditional occupancy models and kernel circular density functions of overlap to investigate spatiotemporal partitioning within the felid community of Las Piedras, Madre de Dios, Peru, and its implications for coexistence dynamics in the context of human-induced landscape changes. Overall, we hypothesized that we would observe changes in the spatiotemporal patterns of felid dyads in response to both ecological variables and human activities, and that these changes would vary in both directionality and intensity per dyad. Based on the theories of interspecific predation intensity and food competition, we predicted that our conditional occupancy models would best describe the spatial interactions in dyads where the dominant species was less than 5.4 times larger than the subordinate species. For example, we did not expect to see significant interactions between one of the two smallest felids (jaguarundis or margays) and one of the two largest felids (jaguars or pumas), owing to their greater than 5.4 difference in size. However, interactions among carnivores are unlikely to be based solely on size, but rather a combination of size, risk, resource availability, and human activities. Thus, based on previous literature, we predicted that smaller predators would both respond behaviorally to risk (i.e. “landscape of fear”; (Gaynor et al., 2019) and evade direct lethal encounters with larger predators, using a combination of spatial and temporal avoidance (Haswell et al., 2017; Ritchie & Johnson, 2009). Our conditional occupancy models using terrestrial camera traps likely do not fully encapsulate the spatiotemporal patterns of margays given their arboreal nature and the importance of both horizontal and vertical habitat separation for niche partitioning (Schoener, 1974); as such, we predicted less of a response in their respective models. Additionally, previous studies detail the largely diurnal activity of the jaguarundi and the predominantly nocturnal activity of the remaining four felids (Santos et al., 2019), which we expected to observe in our study area as well. Lastly, because competitive interactions are more heightened and conspicuous in top predators and these species have a disproportionate effect on ecosystems (Di Bitetti et al., 2010; Schoener, 1974), we predicted that our spatiotemporal covariates would describe the most significant interactions between the three largest felids: jaguars, pumas, and ocelots. Our aim for this study was to use ecological and anthropogenic predictors to tease apart the multifaceted interactions between five felids to inform conservation methods in human-modified landscapes.

2.2 METHODS

Madre de Dios (MdD) represents the southern region of the Peruvian Amazon and consists of largely contiguous forest within four national protected areas and three jaguar conservation units (JCUs) that overlap with these protected areas (Asner et al., 2010; Rabinowitz & Zeller, 2010). The region of Las Piedras within MdD is one of the largest remaining intact forests in Peru that remains unprotected (see Fig. 3). Las Piedras consists of a mosaic of concessions that face anthropogenic threats like selective logging, clear-cut agriculture, and hunting, despite being a critical part of the Tropical Andes Biodiversity Hotspot (Myers et al., 2000).

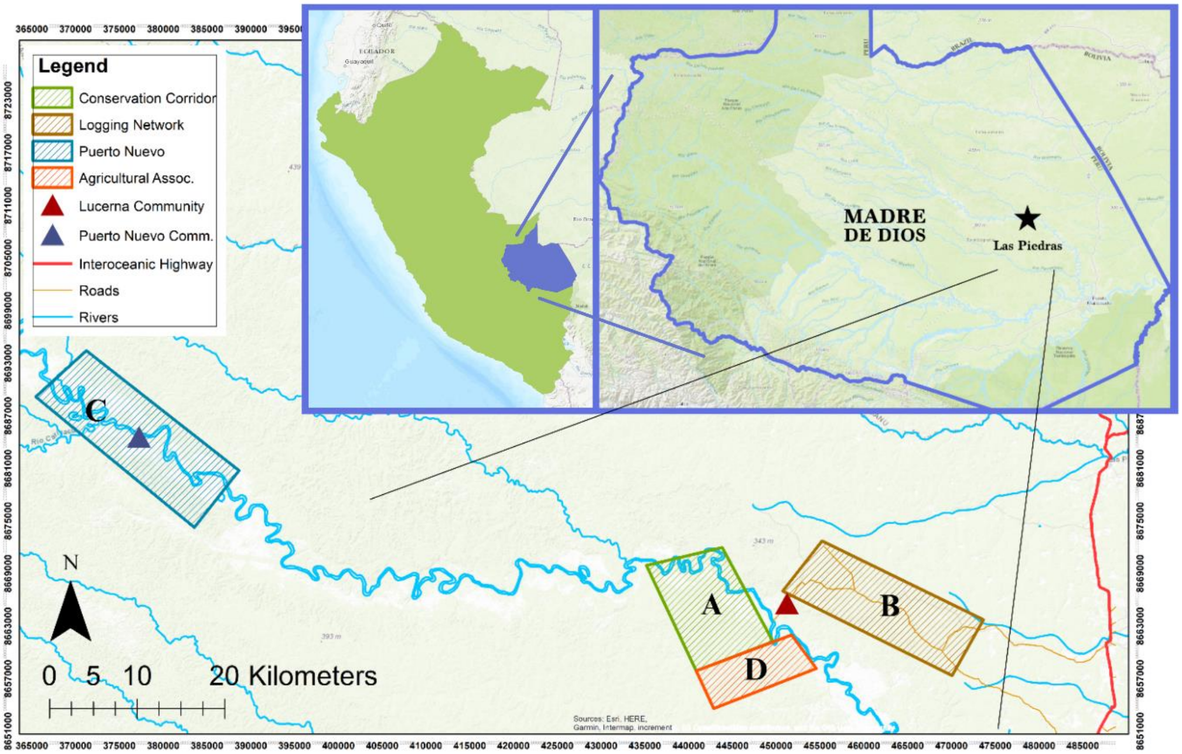

Fig. 3 Pictured are the four areas sampled between the years 2015 and 2022, all located within the Las Piedras region of the department of MdD in Peru. *Sample area A, the Las Piedras Conservation Corridor, was surveyed five times in 2018, 2019, 2021, and twice in 2022. Sample area B was a network of logging roads sampled in 2015. Sample area C was the indigenous community of Puerto Nuevo, surveyed in 2017. Lastly, sample area D was the agricultural association of Lucerna, surveyed in 2021.*

The study area was located 70km north of Puerto Maldonado along the Las Piedras River based out of the Hoja Nueva research center (-12.1265 S, -69.4760 W). We deployed camera traps into eight grids within four areas (see Fig. 3); the areas covered approximately 450 km² of lowland rainforest with diverse land cover and land use activities. Grid sizes were informed by the average recorded home range of the ocelot - approximately 38.8 square km for males and 17.4 square km for females - given its status as the median in size among the five felids and additionally because, among the five felids it is most captured on camera traps (Crawshaw, 1995). In 2022, we reduced the camera trap spacing aimed at better detecting the two smallest felids, jaguarundis and margays, which were informed by the estimated home range of the margay.

We systematically selected camera sites, favoring roads and trails within 50m of a grid point to maximize felid captures (Ahumada et al., 2013). When roads or trails were not present within 50m of a grid point, cameras were placed on wildlife trails. Across the 293 total stations, 153 were placed on roads or trails and 140 were placed on wildlife trails. Sample areas included the 167 camera stations inside the protected lands of the Las Piedras Conservation Corridor (LPCC; Area A), 30 stations within a network of logging roads between the IOH and the Las Piedras River (Area B), 46 stations around a remote indigenous community of Puerto Nuevo (Area C), and 50 stations within the Lucerna agricultural association south of the LPCC (Area D; see Fig. 3). Camera stations were set in two macro-habitat types, floodplain (seasonally inundated) forest and terra firme (upland) forest, for approximately three months between July and December. Browning Strike Force trail cameras (BTC-5 and BTC-6 models) were used. Each station consisted of one or two cameras placed on a tree 50 cm off the ground. The average survey length of each station was 81 camera trap nights or just under three months. For this study, each camera trap station represented a unique site (n = 293).

2.3 DATA ANALYSIS

2.3.1 *Spatial Partitioning*

To explore the effects of both humans and a dominant species on each subordinate felid species, we fit two-species single season occupancy models (MacKenzie et al., 2005; Richmond et al.,

2010) using the ‘wiqid’ package (Juat et al., 2022) in RStudio using R Version 4.1.1 (R Core Team, 2022). These conditional occupancy models account for false absences and can infer the potential influence of competition based on patterns in species occupancy between a dominant species A and a subordinate species B. We used these models to not only determine how the presence/absence of a dominant felid affects the occupancy of a subordinate felid, but also if the subordinate felids are responding to anthropogenic factors conditional upon the occupancy of the dominant felid. We estimated the probability of detection and occupancy of each species within the pair, where the probabilities of the subordinate felid B are conditional upon those of dominant felid A. Given there were five species, ten pairs were tested where each model contained $S = 2$ species and the dominant species A was determined *a priori* by body weight. Detection histories were created by grouping five consecutive trap nights into one sampling occasion for all felids, resulting in a species being either present (1) or absent (0).

We ran an initial null model for each pair without interactions or covariates, followed by a model with co-occurrence but without covariates. Then, we ran eight more models with an interaction between each felid pair and covariates on both detection and occupancy, each with an ecological or anthropogenic covariate placed on the co-occurrence parameters ψBa and ψBA. The human disturbance covariates included the following: proximity to agriculture, distance from the closest community, overall land use type, and human activity. Ecological covariates included enhanced vegetation index (EVI), macro-habitat, distance from the river, and prey index. Descriptions of the covariates for detection and occupancy can be found in Table 6. Due to the limited number of captures of some felid species like the jaguarundi and the large number of potential combinations of model parameters, we simplified the size of the *a priori* candidate model set. We used a multistep modeling approach by first performing single-species, single-season occupancy models with covariates for each felid species and selected the top model for each species by lowest AIC value (Richmond et al., 2010; Wang et al., 2015). The resulting detection covariates from these top models were placed on the detection of the dominant species (pA) as well as the subordinate (pB) and the resulting occupancy covariates were placed on the occupancy of the dominant species (ψA) in their respective co-occurrence models. Only one ecological or anthropogenic covariate was placed on the co-occurrence parameters, ψBa and ψBA, at a time for model convergence, resulting in eight separate models. We used Akaike's information criterion (AIC) (Akaike, 1973) to compare the ten total models per dyad and to determine the top models per felid pair based on Δ2 AIC. We then proceeded to examine the chosen top model per dyad and reported the significant estimates per model based on their 95% confidence intervals (CIs).

Table 6. Descriptions of the covariates chosen a priori to be placed on the detection of each species (pA and pB), as well as the eight ecological and anthropogenic covariates that were placed on the interaction/no interaction parameters (ψBa and ψBA) as well as ψA.

	Covariate	**Description**
Detection	Trail Type	Trails were divided into two types based on their size and use by humans and wildlife: human trails/roads and wildlife trails.
	Trap Nights Operable	The number of nights operable for each camera site.
Occupancy	Enhanced Vegetation Index	EVI was obtained from the United States Geological Survey's EarthExplorer website (earthexplorer.usgs.gov) using the MOD13A1 Version 6 product (Didan, 2015). Imagery at the 500m scale was downloaded corresponding to the sample period of each grid.
	Macro-Habitat	A binary covariate with two categories: floodplain forest or terra firme forest. Floodplain forest represents seasonally inundated forests in closer proximity to rivers and streams. Terra firme forest represents upland forest. A Digital Elevation Model was obtained from the local forestry department in Puerto Maldonado in 2015 to identify these two macrohabitats.
	Prey Index	The number of captures of prey > 5 kilos divided by the total number of trap nights per site and used as a proxy for overall habitat quality.
	Distance from River	The Las Piedras River was tracked via handheld GPS. The distance between each camera station and the river was then measured using the "near" tool in ArcMap 10.4's Proximity toolset (Redlands, 2011).
	Distance from Settlement	GPS coordinates were taken in the center of each riverine settlement close to the sample grids. The distance between each camera station and the nearest settlement was measured using the "near" tool in ArcMap 10.4's Proximity toolset (Redlands, 2011).
	Proximity to Agriculture	Farmland was mapped manually using a handheld GPS unit. Proximity to agriculture was recorded as a binary covariate: whether or not a camera station was located within 500m of a farm greater than 4 hectares in size.
	Land Use Type	A binary covariate categorized as low or high. Low land-use areas included conservation lands protected by conservation and eco-tourism NGOs within the LPCC. High land-use included settlements, agricultural areas, and Brazil nut harvesting concessions outside of the LPCC, including sites where vehicles, hunting, and timber extraction were recorded.
	Human Activity	A binary covariate categorized as low or high based on the number of photo captures of humans. Many stations had 0 human captures. Any stations above 10 human captures were considered high.

2.3.2 *Temporal Partitioning*

The activity patterns and temporal overlap of all five felids were estimated using the 'Overlap' package (Ridout & Linkie, 2009) in RStudio using R Version 4.1.1 (R Core Team, 2022). We extracted the time and date of all camera trap images for each species, and only one capture at most was recorded per hour of the same species. We used kernel density estimation (KDE) to estimate the daily activity pattern of each species We calculated the coefficient of overlap ($\overline{\Delta}$) between species, i.e., the proportion of the area where two kernel density curves overlap, to compare species overlap in areas with high and low human activity. The coefficient of overlap can range from 0 to 1, where 0 indicates no overlap in the activity curves and 1 indicates complete overlap.

We estimated the coefficient of overlap per species pair in areas of low human activity (248 sites) and overlap in areas of high human activity (45 sites). The same human activity covariate from the two-species conditional occupancy models was used (Table 6) to determine if sites had low or high human activity. We selected the coefficient of overlap metric (Δ1 or Δ4; (Ridout & Linkie, 2009) based on the minimum number of detections in each species pair within the habitat. Any time one species had less than 75 captures, we used the Δ1 estimator, which is more accurate when fewer data are available (Ridout & Linkie, 2009; Singh & Macdonald, 2017). Otherwise, we used the Δ4 estimator when both species had greater than 75 captures. The 95% CIs of the coefficient of overlap were calculated using 1,000 bootstrap samples and adjusted for bootstrap bias (Meredith & Ridout, 2017). We considered the overlap to be significantly different if the 95% CI from the high or low human activity did not include the mean of the opposite human activity level.

2.4 RESULTS

2.4.1 *Spatial Partitioning*

The resulting probabilities of both detection and occupancy per felid species can be found in Table 7. Models with covariates fit the data better for each felid pair than models without interaction or with interaction but without covariates. Distance from river as a covariate on interaction was the most influential covariate present in five top models (Δ2 AIC), followed by the prey index and the enhanced vegetation index, which were both present in three top models. Distance from settlement and human activity each appeared in one top model (Table 7).

Table 7. Covariates present in the top models (Δ2 AIC) of the conditional occupancy per felid pair (where subordinate felids are shaded in green). Orange-shaded cells represent the covariates in the top models that had significant effects on co-occurrence based on 95%CIs.

	Jaguar	**Puma**	**Ocelot**	**Jaguarundi**
Puma	Settlement	-	-	-
Ocelot	River	Habitat River	-	-
Jaguarundi	Prey	Human Activity Prey	Prey	-
Margay	EVI River	EVI Habitat River	River	EVI

Based on 95% CIs, the subordinate species from six of the ten felid pairs shifted their probability of occupancy at a site based on the presence or absence of the dominant felid (see Table 8). Several covariates were significant in explaining shifts in felid interaction (ψBa and/or ψBA): 1) jaguar:puma (distance from settlement), 2) jaguar:ocelot (distance from river), 3) puma: ocelot (macro-habitat and distance from river), 4: puma:margay (macro-habitat), and 5: ocelot:jaguarundi (prey index).

Table 8. The resulting estimates, standard errors, and covariates from each felid pair's top model. Estimates are followed by standard errors in parentheses. Interactions are abbreviated: ψBa = occupancy of the subordinate species when the dominant species is absent, and ψBA = occupancy of the subordinate species with the dominant species is present. Covariates are abbreviated: SE = distance from settlement, RI = distance from river, PR = prey index, HA = macro-habitat (where FL = floodplain and TF = terra firme), and EV = enhanced vegetation index. Cells shaded orange represent significant estimates based on 95% CIs.

	ψBa Intercept	**ψBa**	**ψBA Intercept**	**ψBA**
Jaguar:Puma	-0.15(0.32)	0.45(0.38) SE	1.29(0.35)	-0.92(0.34) SE
Jaguar:Ocelot	0.65(0.32)	-0.31(0.60) RI	2.66(0.52)	-0.61(0.30) RI
Jaguar: Jaguarundi	-1.07(0.66)	0.77(0.60) PR	-1.40(0.54)	0.69(0.48) PR
Jaguar:Margay	-0.45(0.43)	0.97(0.66) RI	-0.10(0.30)	0.12(0.21) RI
Puma:Ocelot	1.33(0.54) HA:FL	-0.49(0.64) HA:TF	3.31(0.86) HA:FL	-1.89(0.92) HA:TF
Puma: Jaguarundi	-1.51(0.61)	0.50(0.46) PR	-1.12(0.54)	0.92(0.53) PR
Puma:Margay	-1.38(0.84) HA:FL	1.95(0.96) HA:TF	-0.06(0.40) HA:FL	-0.48(0.49) HA:TF
Ocelot: Jaguarundi	-1.10(0.84)	1.10(1.05) PR	-1.29(0.47)	0.69(0.36) PR
Ocelot:Margay	-1.66(0.65)	0.13(0.57) RI	0.03(0.26)	0.48(0.26) RI
Jaguarundi: Margay	-0.12(0.29)	0.66(0.30) EV	-0.47(0.61)	-0.67(0.64) EV

Margays had the fewest significant predictors of their conditional occupancy compared to the other four larger felids. Margays did not shift their occupancy in response to the presence or absence of jaguars. They did, however, increase in occupancy probability in areas of high EVI when jaguarundis were absent, and increase in occupancy probability in terra firme habitat when pumas were absent. Margay occupancy was higher at sites where ocelots were present.

Jaguarundis, the second smallest felid, manifested responses to the presence and absence of the three larger felids, despite being the least-detected species (n = 40). The probability of occupancy of jaguarundis decreased at sites where jaguars, pumas, or ocelots were present. Interestingly, when ocelots were present, jaguarundi occupancy increased as prey index increased but not in areas where ocelots were absent.

Ocelots were the most highly captured felid in this study (n = 1,239). Ocelot occupancy increased at sites where jaguars were present, but decreased with distance from the river when jaguars were present. When pumas were present, ocelot occupancy probability increased in floodplain forest but decreased in terre firma forest.

Opposed to our predictions, puma occupancy probability increased when jaguars were present. Puma occupancy probability decreased significantly with distance from settlements when jaguars were present. This was the only significant felid interaction directly linked to human activity and disturbance, indicating that pumas were more likely to occupy areas near humans when jaguars were present.

2.4.2 *Temporal Partitioning*

Detailed activity patterns of each felid species can be found in Appendix A. Apart from the jaguar:puma and jaguar:ocelot dyads, all overlap coefficients were lower in areas of high human activity than at sites with low human activity, contrary to our original predictions (see Table 9). The overlap of the remaining species pairs decreased between 6.1% and 24.5% at sites where humans were more active. Based on the bootstrapped 95%CIs we found that 7 of the 10 dyads had differences between high and low human activity that were significant or trending. Temporal overlap was highest for the jaguar: puma, puma: ocelot, and ocelot:margay interactions, whereas temporal segregation was highest for the ocelot: jaguarundi, jaguarundi:margay, and puma:jaguarundi dyads (Table 9).

Table 9. The overall percent temporal segregation per felid pair across the study area, as well as overlap coefficients per felid pair using one of two estimators (Δ1 or Δ4) and their 95% CIs for sites with low (248) and high (45) human activity. We considered the overlap to be significantly different between low and high human activity if both the means of each level didn't overlap with the 95%CIs of the other level (highlighted in orange). Results were considered trending if only one level's mean overlapped with the 95%CIs of the other level (highlighted in blue).

	Low Human Activity				**High Human Activity**			
	Δ1	**Δ4**	**95% CIs**		**Δ1**	**Δ4**	**95% CIs**	
Jaguar: Puma	-	0.815	0.743	0.888	-	0.869	0.783	0.956
Jaguar: Ocelot	-	0.726	0.652	0.801	-	0.729	0.642	0.816
Jaguar: Jaguarundi	0.528	-	0.402	0.654	0.352	-	0.197	0.506
Jaguar: Margay	0.772	-	0.684	0.859	0.661	-	0.534	0.788
Puma: Ocelot	-	0.877	0.838	0.918	-	0.816	0.740	0.892
Puma: Jaguarundi	0.378	-	0.271	0.485	0.280	-	0.124	0.436
Puma: Margay	0.924	-	0.873	0.985	0.738	-	0.609	0.867
Ocelot: Jaguarundi	0.290	-	0.193	0.387	0.131	-	0.013	0.249
Ocelot: Margay	0.906	-	0.858	0.955	0.839	-	0.721	0.958
Jaguarundi: Margay	0.350	-	0.234	0.466	0.105	-	-0.030	0.240

2.5 DISCUSSION

Our study provides a multidimensional view of felid coexistence using the combination of spatial co-occurrence and temporal overlap. In general, we observed that subordinate felids exhibited shifts in their occupancy in response to the presence or absence of a dominant felid species; as predicted, with the addition of ecological and anthropogenic covariates, these results were specific to each dyad and had no general pattern across the entire felid guild. Although the interactions between carnivores are complex and not solely based on size, using covariates we were able to factor in size, resource availability, human activities, and potential responses to both encounter and risk of encounter using spatiotemporal data. Spatial models significantly described dyad interactions where the difference in size was less than 5.4, with a few exceptions. We confirm that subordinate felids use a combination of spatial and temporal avoidance to decrease encounters with dominant felids; the only three dyads with no significant shift in occupancy all included the semi-arboreal margay, and we predicted less of a response in their respective models. Lastly, our overall prediction of temporal partitioning was supported given the diurnal activity of the jaguarundi and the predominantly nocturnal activity of the remaining four felids.

Mechanisms of niche partitioning were relatively unique for each species pair, apart from the effects of human disturbance on temporal partitioning and the patterns of temporal segregation in dyads that include the jaguarundi. Human activity increased temporal segregation between most felid species (70%), promoting coexistence, which contradicts what has generally been observed in meta-analytical studies of carnivore interactions (Gaynor et al., 2018; Palomo Munoz, 2021). We believe this is mostly due to shifts by the two smallest felids, jaguarundis and margays, in response to human activities. As predicted, the jaguarundi was diurnal in our study area whereas the remaining four felids were predominantly nocturnal, which is the consensus across other systems (Santos et al., 2019). Therefore, niche partitioning where it concerns the jaguarundi is namely achieved temporally; however, jaguarundis naturally overlap with the temporal activity of humans. Although we did not observe a significant shift to nocturnality by jaguarundis in response to human activity due to a lack of data, this should be a conservation concern in areas of human disturbance as it would increase encounters between the jaguarundi and the larger felid predators.

As predicted, our conditional occupancy models best described the spatial interactions in dyads where the dominant species was less than 5.4 times larger than the subordinate species. This was particularly apparent for jaguar:puma, jaguar:ocelot, puma:ocelot and ocelot:jagarundi, whose interactions were all significantly described by one of our covariates. This is potentially due to the fact that the dyads that are nearer in size have more complex relationships dictated more intricately by differing conditions due to increased niche overlap. Hypercarnivorous top predators like the jaguar and puma have a disproportionate effect on the entire carnivore guild as well as whole ecosystems (de Oliveira & Pereira, 2014; Di Bitetti et al., 2010; Schoener, 1974), and our results indicate they are most affected by humans, even in moderately impacted environments.

Jaguarundis had significantly lower occupancy probability when ocelots were present; however, jaguarundi occupancy probability increased as prey availability increased when ocelots were present. These results align with previous studies where jaguarundis have responded both spatially and in abundance to local ocelot populations (Dias et al., 2019; Kasper et al., 2016). Our results demonstrate that jaguarundis can generally coexist with other predators that share resources by hunting at a different time of day, but this coexistence is likely jeopardized when resources are degraded; e.g., when prey availability is diminished. In this context, human-modified areas experiencing defaunation or a decrease in resource availability threaten the coexistence of jaguarundis with their dominant competitor, the ocelot. Because the pressure of intraguild killing by ocelots is already prominent and well-documented (Di Bitetti et al., 2010; Oliveira et al., 2010), further niche overlap in disturbed areas could displace local jaguarundi populations.

Jaguars and pumas partitioned less by time (16%) and pumas were more likely to occur when jaguars were present. Conditional occupancy results also showed that distance from settlements was significant in predicting the occupancy of pumas when jaguars were present, which could be driven by several factors. Pumas are known to be more adaptable to fragmented habitats than jaguars and may be more likely to use smaller patches of suitable habitat closer to human settlements or tolerate human presence and activities (Figel et al., 2021). Human activities such as hunting or habitat modification near communities may create more favorable conditions for pumas to occur when coexisting with the larger jaguar. While the temporal overlap of jaguars and pumas was reduced in areas of human activity, pumas were more able to segregate spatially in closer to settlements, thereby avoiding jaguars across space instead of time. These results suggest that jaguars and pumas have complex interactions that are influenced by human activities and the spatial distribution of settlements and merit further exploration in areas with more frequent and/or larger settlements.

The spatiotemporal results for jaguar:ocelot and puma:ocelot demonstrate the importance of spatial and dietary partitioning in limiting competition, and specifically rivers as landscape features that shape their spatial interactions. This has important conservation implications given that riverine habitat is the first to be colonized by humans for agriculture and settlements; rivers are also used as access points to the jungle for subsistence hunting (Lentz, 2000; Moran, 2007; Whitworth et al., 2019). Given these larger felids' need for space to limit competition and for their ecological roles in the community, conservation efforts should focus on preserving riverine habitat and protecting large, intact forest habitat to maintain interactions and ecosystem stability in this biodiverse system.

Contrary to our predictions, our models did describe several interactions between dyads (jaguar:jaguarundi, puma:jaguarundi, and puma:margay) that we did not expect due to the large difference in size between the subordinate and dominant predators. Jaguarundi occupancy probability decreased at sites where pumas were absent and where jaguars were present. Jaguarundis and pumas could have a higher overlap of finer-scale habitat requirements and preferred prey. Very little is known about the diet of the jaguarundi, but one study used scat analysis to conclude that their diet consisted mostly of birds (occurred in 55% of the fecal samples) followed by small mammals (41%) and reptiles (17%) (Bianchi et al., 2011). Pumas have one of the most flexible diets of described felids, with at least 232 species listed as prey throughout their range and they are able to switch to smaller prey and birds when their primary prey are unavailable (Karandikar et al., 2022). This switch to smaller prey could potentially suppress mesopredators and other small predators that rely on small prey in areas of spatial overlap ((Karandikar et al., 2022). Jaguarundis and jaguars showed higher temporal overlap (52%) which could lead to increased spatial avoidance by jaguarundis to successfully coexist as we saw in our results. However, all of these results should be placed in the context that we had a small sample size of jaguarundi detections (n = 40).

There were no clear patterns across the conditional occupancy results for margays, and they had less significant dyadic interactions than any other subordinate felid. Given that they often seek refuge, rest, and hunt in trees, terrestrial camera traps likely do not fully encapsulate the spatiotemporal patterns of margays; when applicable, gathering data that includes both horizontal and vertical habitat separation is therefore crucial to better understand niche partitioning (Schoener, 1974). Margays likely do not compete with larger felids as much as the ground-dwelling species like jaguarundis because they are able to partition by strata (Hodge, 2014). Ocelots and margays have both been described as generalists in their diets, with a preference for non-volant mammals (Bianchi et al., 2011; E. Wang, 2002). Their generalist diet across their range reflects their dietary plasticity and ability to modify their prey base to local resource pools and may contribute to their niche partitioning.

We had several limitations to this study that likely kept us from fully understanding the effects of human disturbance on felid interactions. First, the last axis of niche segregation, diet, is crucial in maintaining coexistence within the carnivore guild (Ramesh et al., 2012), and human disturbance has proven to impact this niche dimension in carnivore communities (Sévêque et al., 2020). Although we can predict diet overlap based on previous literature, our conclusions about niche partitioning in felids would be stronger with the addition of local scat analysis and diet information. Second, human defaunation of felid prey via hunting is of concern in the region but was not included in the present study. In addition to decreasing prey abundance, human hunting can force prey to overlap more with their predators (i.e., become more nocturnal) (Shores, 2020); the inclusion of prey dynamics would be useful in future studies to better understand niche partitioning in felids. We suggest that further research aims to investigate similar axes of coexistence, incorporating biological/ ecological factors as well as anthropogenic variability into chosen models. Third, it is necessary to observe the spatial and temporal patterns of felids in areas with more intense human activities such as mining, large-scale agriculture, logging, and oil drilling, which are rampant throughout Amazonia but not yet present within the landscape of the Las Piedras. Finally, investigating margays using arboreal camera trap techniques would improve our understanding of their spatial patterns, contributing to a more holistic picture of their interactions with the four larger felids.

The landscape of the Las Piedras watershed has experienced increased selective logging and clearcut agricultural practices for almost 20 years, but the majority remains intact and connected in comparison to other areas of MdD and Amazonia in general (Finer & Peña, 2015). The human population in both MdD and throughout Peru is expected to grow rapidly over the next 20-40 years, with settlements primarily encroaching upon Peru's remaining natural areas (Resultados Definitivos Del Departamento de Madre de Dios, 2018). This urban expansion could shift how felids coexist by causing niche compression, intensifying negative interactions among competing species, and triggering the population release of mesocarnivores leading to subsequent effects on prey species and whole ecosystems. Similar to the decrease in avian biodiversity in response to the release of grey fox populations after the decline of coyotes (Crooks & Soulé, 1999), the loss of top predators like jaguars and pumas could cause ocelot populations to rise, thereby impacting small mammal and avian prey, as well as smaller mesopredators. Previous research has shown that after the local extinction of jaguars, pumas and ocelots exhibited unusual diets; pumas consumed a higher proportion of peccaries (*Pecari tajacu*) and ocelots consumed more medium-sized prey, indicating that competitive release can lead to prey shifts within the felid guild (Moreno et al., 2006).

Our study explores multiple niche axes and show the effects of human activity on felid interactions and community dynamics in the Amazon rainforest – information that is necessary to make predictions about the coexistence of predators across human modified landscapes globally (Rodriguez Curras et al., 2022). Our results show that the interactions between people, carnivores, and the environment are complex, and in general coexistence is species and species-pair specific. Human activity is changing the natural patterns of temporal overlap between many felid dyads, and implicating increased competition between jaguars, pumas and ocelots. If human activity were to cause the diurnal felid, the jaguarundi, to shift more crepuscular or nocturnal thereby increasing encounters with larger predators, this elusive species could become displaced. With regard to space use, local felids remain resilient in this ecosystem, which has yet to undergo more serious land use and land cover changes; however, indications of imminent, significant change can often be predicted from initially subtle responses (Frey et al., 2020). The protection and sustainable use of land within the Las Piedras, and all currently unprotected remaining frontier forests of the Amazon, is key to biodiversity conservation, especially because the unobserved and often cascading ecological effects of human disturbance remain poorly understood. We propose more species-specific research in niche overlap and intraguild competition within human modified landscapes to better understand species' survival and evolution in novel ecosystems (Teixeira-Santos et al., 2020) and the implications for communities of flora and fauna in an increasingly anthropogenic world.

Chapter 3. ADAPTATION OF REALIZED NICHE BY OCELOTS IN RESPONSE TO MODERATE LEVELS OF HUMAN IMPACT IN MADRE DE DIOS, PERU

3.1 INTRODUCTION

The Amazon rainforest, one of the most biodiverse regions on Earth, is facing alarming rates of habitat loss and fragmentation due to human activities such as logging, agriculture, and infrastructure development (Espinosa et al., 2014). These activities have significant implications for carnivores, such as decreased population connectivity and genetic diversity from population declines (Lorenzana et al., 2020; Wultsch et al., 2016), as well as cascading effects on mesocarnivores and prey species, prompting functional changes in whole ecosystems (Benítez-López et al., 2017; Rabinowitz & Zeller, 2010). Carnivores can play vital roles in maintaining ecosystem balance through regulating prey populations and shaping community dynamics (Jorge et al., 2013). Mesocarnivores, such as ocelots (*Leopardus pardalis*), are small- to medium-sized carnivores that occupy intermediate trophic levels and play critical roles in ecosystem processes (Di Bitetti et al., 2010; Smith et al., 2018). For example, mesocarnivores can have direct and indirect effects on predator-prey interactions and occupy distinct ecological niches as direct seed dispersers or predators of crucial seed dispersers (Peres & Palacios, 2007; Roemer et al., 2009). Because mesocarnivores serve as indicators of broader ecosystem health and resilience, studying the response of mesocarnivores to changing human pressure in the Amazon rainforest is crucial for informing conservation efforts and ensuring the preservation of intact and functional ecosystems.

The ocelot is one of the most widespread felids in the Americas (Blake et al., 2016), inhabiting a variety of forest types and habitats spanning from the southern USA to northern Argentina (Di Bitetti et al., 2006). Ocelots are considered generalist predators, and they play an important role in maintaining ecological stability in relatively intact forests where they are common by influencing smaller carnivores and directly impacting prey populations and distributions (Boron et al., 2022; Emmons, 1987; Oliveira et al., 2010; Rocha et al., 2016). Like many mesocarnivores, ocelots can persist in areas of light to moderate human land use, particularly those that consist of only minor habitat degradation and disturbances restricted primarily to daytime hours, such as small-scale agriculture and cattle farming, road creation, and seismic exploration, specifically in areas connected to intact forests (Boron et al., 2022; Kolowski & Alonso, 2010; Massara et al., 2018). Although ocelots exhibit a high level of ecological plasticity (Massara et al., 2015), they have a strong preference for intact forest and natural vegetation (Wang et al., 2019) appear to avoid intense human land use and conversion (Di Bitetti et al., 2008; Kolowski & Alonso, 2010).

Given that the range of the ocelot is being rapidly fragmented and degraded by human expansion (Satter et al., 2019), it is important to understand the effects of different ecological and anthropogenic factors on the density, home range response, and activity patterns of this felid. Abiotic factors, such as rainfall and latitude, have been associated with ocelot occupancy on a continental scale (Boron et al., 2022; Di Bitetti et al., 2008). On a finer scale, ecological factors associated with ocelot habitat use are the amount and structure of intact forest, the presence of large cats (jaguars, pumas), and availability of specific prey types (Massara et al., 2015, 2018; Moreno-Sosa et al., 2022; Paolino et al., 2018; Wang et al., 2019). Additionally, factors identified as negatively influencing occupancy, habitat use, and spatiotemporal patterns include intense human land use and conversion, extensive habitat fragmentation, and elevated presence of free-ranging domestic dogs (Di Bitetti et al., 2006, 2008; Kolowski & Alonso, 2010; Massara et al., 2015). Ocelots were heavily poached prior to legislation banning their trade (Di Bitetti et al., 2006); however, illegal poaching still occurs, particularly in areas impacted by human development (Satter, Augustine, Harmsen, Foster, & Kelly, 2019).

Mesocarnivores in general have been known to adapt temporally to be more successful at spatially tolerating humans, specifically by decreasing their diurnal activity and/or increasing their nocturnal activity in areas of greater anthropic disturbance (Chen et al., 2023; Gálvez et al., 2021; Teixeira et al., 2023). Even species that are already considered nocturnal, like the güiña (*Leopardus guigna*), reduced their crepuscular activity in more disturbed areas (Gálvez et al., 2021). Similarly, ocelots are primarily nocturnal (Bolze et al., 2021; Cruz et al., 2018; Dillon & Kelly, 2007) and were observed to be less crepuscular in areas with higher human access or near human settlements (Cruz et al. 2018). However, Kolowski & Alonso (2010) found no significant effects on ocelot temporal patterns during times of oil drilling. Given the complex set of factors impacting ocelot populations and the different effects of human activity on ocelot activity and behavior, it is important to better understand how the steadily increasing matrix habitat and subsequent human activities influence their population dynamics.

Studies have reported varying ocelot densities in different parts of Central and South America, ranging from 2.9 to 84.8 individuals per 100 km^2 (Rocha et al., 2016). Ocelots are known to have relatively large home ranges, which can vary depending on factors such as sex, age, and habitat quality. Home range sizes reported in studies conducted in the Americas range from 1.8 to 38.8 km², and male home ranges are larger than those of females (Rocha et al., 2016). Ocelot populations generally exhibit a slightly skewed sex ratio, with slightly more females than males, although sex ratios can vary depending on the population and study area, with female-biased sex ratios reported in some studies (Di Bitetti et al., 2006). The large variation in ocelot density and home range sizes reported in different studies necessitates better understanding of local population demographics for effective conservation, particularly in the face of increasing deforestation and defaunation (Boron et al., 2022).

The objective of this study was to estimate the activity patterns, density, home range, and sex ratios of ocelots in the lowland Amazon rainforest of the Las Piedras region in Madre de Dios, Peru using data collected with an extensive camera trap grid across mixed used areas with agriculture and resource extraction and a privately protected area. We hypothesized that ocelots would adapt their realized niche temporally given the response of other similar mesocarnivores, like the leopard cat (*Prionailurus bengalensis*) and the güiña (*Leopardus guigna*), in their respective systems (Chen et al., 2023; Gálvez et al., 2021). We predicted that ocelots would therefore be more nocturnal in the mixed-use area where humans were detected more frequently. Given that human disturbance is moderate in the mixed-use area, we expected to see temporal differences before changes in density become more evident. We expected ocelot density to be high in the region of Las Piedras relative to other unprotected areas due to the existence of high-quality habitat within dispersed protected areas and unfrequented concessions. Consistent with their dimorphic ecology, we expected the home range size of males to be several times larger than female home ranges. Understanding the details of ocelot demography and behavior in matrix habitat could guide the establishment of corridors to connect protected areas and ensure landscape-level species conservation, which is becoming increasingly necessary as the western Amazon region is rapidly fragmented.

3.2 METHODS

3.2.1 *Study Area*

The study area was situated near the Hoja Nueva Research Center (-12.049, -69.533) along the Las Piedras River in Madre de Dios, Peru (Fig. 4). The 174 km^2 study area included a privately protected area and a mixed-use area to the east and south. The protected area comprised non-timber forest product, conservation, and eco-tourism concessions where human activities are limited to academic tourism, forest ranger patrols, and non-invasive wildlife research. The mixed-use area included cacao and papaya farms, seasonal logging networks where roads were constructed and used to extract large hardwoods, and patches of native forest; secondary activities like bushmeat hunting were present in the mixed-use area and not in the protected area. Floodplain forest (seasonally inundated, riverine) and terra firme forest (upland) were the two habitat types present throughout the study area.

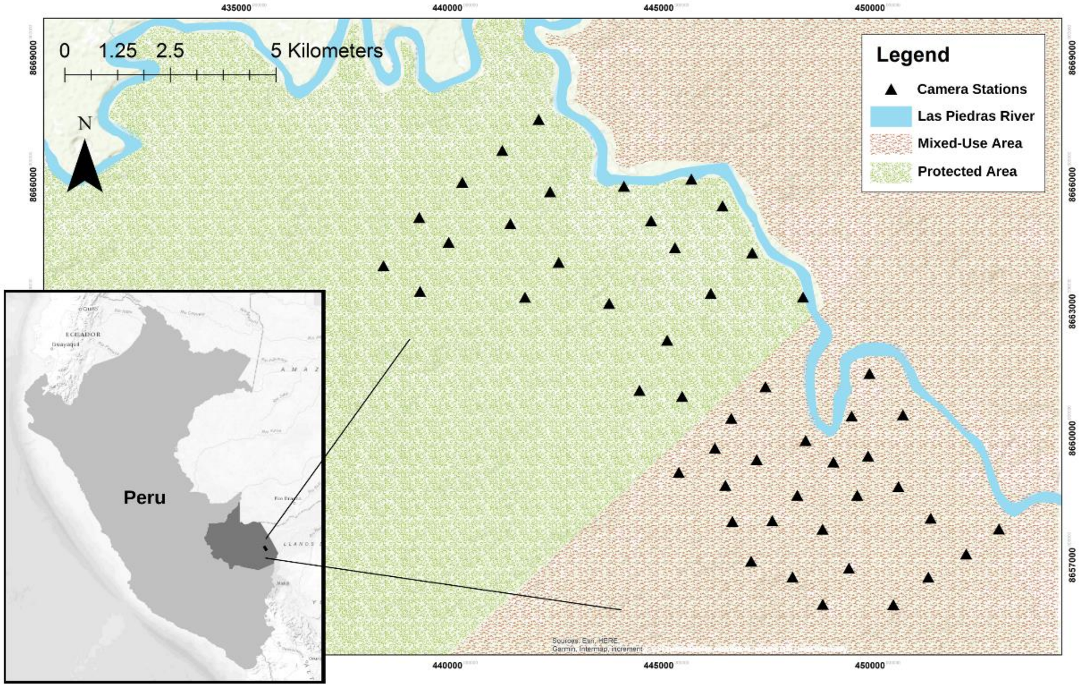

Fig. 4 Map of the study area showing the locations of camera trap stations along the Las Piedras River within the department of Madre de Dios in Peru, with the protected area in green and the mixed-use area in red at its southern border.

3.2.2 *Camera Trapping*

Paired camera traps were set at 50 sites between 21 May 2021 and 01 Nov 2021; 27 stations were installed in the mixed-use area and 23 in the protected area. Due to the estimated home range of both male and female ocelots (Dillon & Kelly, 2008; Goulart et al., 2009), camera stations were placed with a mean distance of 1,008 meters between sites to maximize recaptures of both males and females. Cameras were placed approximately 50cm off the ground, staggered on opposite sides of the trail and facing each other. When possible, we placed cameras on human trails and roads to maximize ocelot captures; 12 stations (~25%) were placed along mammal trails when a human trail or small road was unavailable. All cameras used were Browning Strike

Force trail cameras (BTC-5 or BTC-6 models), set to capture videos of ten seconds in length, with a one second trigger delay between captures.

Photo captures of ocelots were analyzed by two reviewers to identify individuals. The first reviewer identified individual ocelots by considering unique coat patterning from both sides of the animal using photos from the paired cameras (see Fig. 5). This step was done by visually investigating the footage and with the support of HotSpotter (Crall et al., 2013), a software package that allows selection of rectangular regions of interest (ROIs) to query and compare results across a labeled database for all the ocelots captured in our study. Photos where the coat pattern could not be seen clearly were removed. The first reviewer created ROIs for all captures, beginning the query process in one corner of the camera trap array and moving systematically to the opposite corner. This method was used knowing that recaptures would likely be highest per individual at the surrounding stations. After all ocelots were identified and sexed, the second reviewer went over the dataset to verify all identifications using both the original photos and verifying the queried results from HotSpotter. Individuals were sexed using the presence or absence of the scrotum in the photos.

Fig. 5 The right and left side of a young male ocelot captured on paired camera traps.

3.2.3 *Data Analysis*

To determine if density differed by between the two areas, we first fit spatial capture-recapture models using the 'secr' package in R (Efford, 2023; R Core Team, 2022). We created 5-day sampling occasions, resulting in 33 total occasions across the 165 trap nights. Because ocelots could be observed more than once at a camera station within a sampling occasion, we used a Poisson observation model and a hazard half-normal detection function. We used the secr package to give an initial estimate (623.58) of the scale parameter σ and then tested the sensitivity of the parameter estimates under different buffer sizes. Based on this initial comparison, we selected a 3000 m buffer with 300 m spacing, approximately half of σ, for all analyses.

To test for differences in density between the protected area and the mixed-use area, we created a "habitat" mask that divided the state space into two areas (Fig. 4). No significant difference in density between the protected and mixed-use areas would support our prediction that ocelots have yet to adapt spatially to the moderate levels of human impact present in the matrix habitat. In addition to calculating ocelot density within the two separate areas, we calculated the weighted averages of density by the number of mask points in each region (1694 in the protected area, 2308 in the mixed-use area) to obtain an average density in the state space. We expected that detection would vary by trail type due to felids using linear features as travel routes and human trails being wider than wildlife trails (Di Bitetti et al., 2010; Harmsen et al., 2010), so we included it as a covariate on the baseline detection rate (λ_0). Trail was defined as "on" if the site was on a human-made trail or road, and "off" if placed on a mammal trail. To test for differences in home range size between male and female ocelots, we allowed σ, the scale parameter of the detection function, to vary by sex.

We compared four models testing the effects sex on σ and both sex and trail type on λ_0 using 2-class finite mixture models: 1) sex on λ_0, 2) sex on σ, 3) sex on both λ_0 and σ, and 4) sex on σ and both sex and trail type on λ_0. We included habitat as a covariate on density in all models because our goal was to estimate density in both habitat types. We compared the models using Akaike information criterion (AIC: Akaike, 1973) and selected the top model for inference. Home range radii were calculated for both males and females based on σ and converted into a circular home range estimate.

Ocelot temporal overlap between the private protected area and the mixed land-use area as well as ocelot overlap with human activity in the two areas were estimated using the ‘Overlap’ package (Ridout & Linkie 2009) in RStudio using R Version 4.1.1 (R Core Team, 2022). We first extracted the time of all camera trap images taken of ocelots, and each time was converted to radians using the package ‘astroFns’ (Harris, 2022). Kernel circular density functions were then employed using the ‘Overlap’ package to determine ocelot activity patterns (Worton 1989). We produced three overlap coefficients: 1) the overlap of ocelot activity between the protected area and the mixed-use area, 2) the overlap of ocelot activity and human activity in the protected area, and 3) the overlap of ocelot activity and human activity in the mixed-use area. We use the Δ4 coefficient of overlap for all models because every sample had greater than 75 captures (Ramesh et al. 2017; Ridout & Linkie 2009). A significant difference in the estimates of activity overlap between humans and ocelots in the two areas would support our hypothesis that anthropogenic disturbance is disrupting natural patterns in ocelots and modifying their realized niche. The 95% confidence intervals (CIs) to test significance in the coefficients of overlap were calculated using 1,000 bootstrap samples, where estimates can vary between 0 (no overlap) to 1 (complete overlap).

3.3 RESULTS

A total of 39 individual ocelots were identified during the survey, including 21 females and 18 males. Ocelots were detected at 34 of the 50 sites. 18 (8 males, 10 females) ocelots were captured at 16 sites in the mixed-use area and 21 individuals were captured in the protected area (10 males, 11 females). Out of 293 photo captures of ocelots, we identified 272 photos to the individual; the remaining 21 captures were either too blurry or only partially captured a passing individual.

Based on AIC, the top model included region on density, sex on σ, and both sex and trail type on detection rate. The model with second-ranking AIC (region on density, sex on σ, and sex on encounter probability) had a Δ7.65, indicating that trail type is an important covariate for detection. All parameter estimates for the top model are shown in Table 10. Estimated density was 25.22 ocelots per 100 km² (SE 6.72) in the protected area and 37.69 ocelots per 100 km² (SE 6.72) in the mixed-use area, however, there was no significant difference in density based on CIs. Density averaged across the state space was 32.41 ocelots per 100 km² (SE 7.51). The estimated baseline detection rate off trail, λ_0, was 0.10 (SE 0.03) for males and 0.34 (SE 0.12) for females. Baseline detection rates increased for both males (0.29; SE 0.04) and females (0.95; SE 0.19) when on a trail. The estimated scale parameter, σ, was 953.60m (SE 65.17) for males and 466.11m (SE 28.03) for females, leading to home ranges of 17.12 km² and 4.09 km², respectively. The overall sex ratio was 0.46/0.54 (males/females).

Table 10. Mean parameter estimates, standard errors (SE), and 95% confidence intervals (CI) from the resulting top model that included habitat as a covariate for density, sex and on/off trail as covariates for baseline detection (λ_0), and sex as a covariate for σ. Estimates are shown on the logit scale for Proportion: Males and on the log scale for the remaining parameters. * = Significant based on 95%CIs not overlapping zero.

Parameter	**Mean**	**SE**	**Lower 95% CI**	**Upper 95% CI**
Density Intercept (Protected area)	-5.98	0.26	-6.50	-5.47
Density: Mixed-use area	0.40	0.34	-0.27	1.07
λ_0 **Intercept (Females, Off Trail)**	-1.09*	0.35	-1.78	-0.40
λ_0**: Males**	-1.20*	0.24	-1.66	-0.73
λ_0**: On Trail**	1.04*	0.33	0.40	1.68
σ **Intercept (Females)**	6.14*	0.06	6.03	6.26
σ**: Males**	0.72*	0.09	0.54	0.90
Proportion: Males	-0.15	0.32	-0.78	0.48

We found evidence to support our hypothesis that ocelots alter their temporal activity patterns more in the mixed-use area. Results from the kernel density functions of ocelot activity revealed shifts in temporal patterns between the private protected area and the mixed land use area, with an overlap of 0.85 (see Fig. 6). Peaks of activity in the protected area were at 3am and 7pm, with some diurnal activity between 9am and 3pm. In the mixed-use area, ocelots became most active from 9pm – 4am, and they decreased activity between 9am – 3pm to almost zero. Additionally, while the overlap of ocelot and human activity was overall low, it was significantly higher in the protected area (0.27; 95%CI 0.21-0.33) than in the mixed-use area (0.20; 95%CI 0.15-0.26), supporting our predictions.

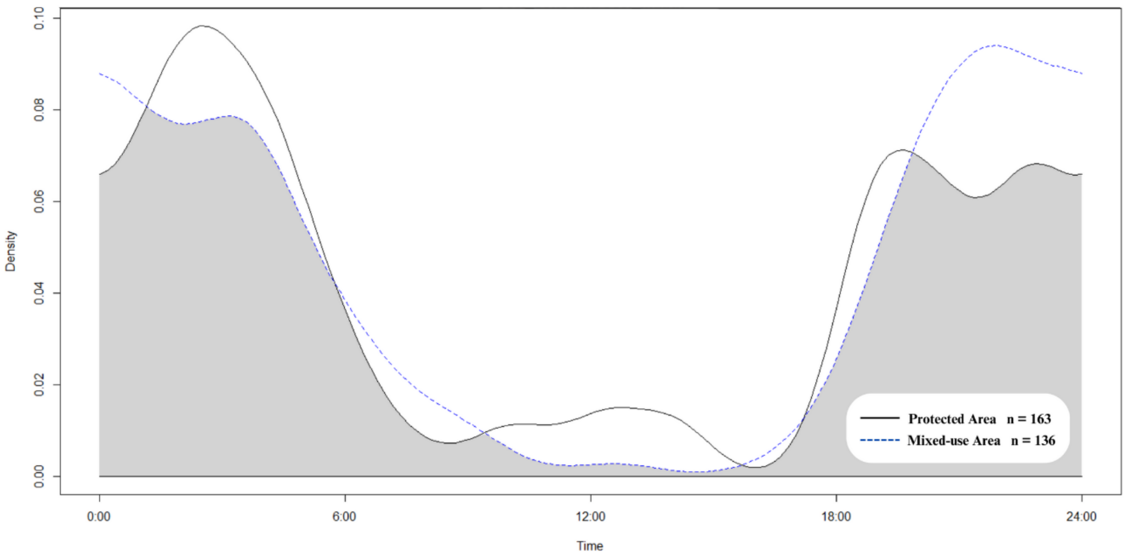

Fig. 6 Ocelot temporal activity in the protected area compared to the mixed-use area, where overlap between the two is shown in grey shading. The respective Δ4 coefficient for overlap was calculated as 85.62% using the package 'Overlap' in R.

3.4 Discussion

Our analyses supported our hypothesis that ocelots will temporally adapt their realized niche in response to human disturbance across our study area. The overlap of ocelot and human activity was significantly lower in the mixed-use area, supporting our prediction that ocelots would become more nocturnal in areas of increased human activity. Ocelot density did not vary significantly between the protected area of primary rainforest and the mixed-use area of matrix habitat. Our results did, however, support our prediction that male ocelots would have larger home ranges and movement parameters given the sexual dimorphism in the species, and that we would observe female-biased sex ratios.

Previous research has described ocelots as primarily nocturnal, with peaks in activity before dawn and between 8pm – 11pm (Blake et al., 2016; Bolze et al., 2021; Di Bitetti et al., 2006;

García-Restrepo et al., 2019). Our results suggest that in matrix habitat ocelots are adapting their realized niche by shifting to more nocturnal activity in areas of mixed land-use, likely to facilitate spatial coexistence with humans in these more disturbed areas. This is consistent with other research on ocelots which has shown they increase diurnal activity in areas with more human disturbance (Cruz et al., 2018; de la Torre et al., 2016) and are more likely to trails at during night than during the day (Bolze et al. 2021). This shift to more nocturnal activity has been seen in many species globally (Gaynor et al., 2018) and the consequences of these shifts, extend beyond species fitness and population persistence. With increased human pressures globally, species-specific shifts to greater nocturnality could have adverse effects on entire ecological communities, such as behavioral release in smaller mesocarnivores, changes in predator-prey dynamics, or a decline in seed dispersers (Frey et al., 2020; Roemer et al., 2009).

Ocelot density showed no significant difference between the protected area of primary rainforest and the mixed-use area of matrix habitat. The mixed land-use area, despite facing seasonal deforestation, agricultural activities, selective logging, and hunting, remained relatively intact, contributing to these results. However, the northeast sector of the survey area, with the highest human disturbance and subsequent camera theft issues, limited data gathering. The loss of three stations in the disturbed northeast sector left only seven stations to record ocelot presence near farmland. No ocelots were captured at those seven stations. By contrast, in the less disturbed western sector of the mixed-use area, seven camera stations captured 10 different individuals. Our study did not include areas of the highest human disturbance; instead, we focused on moderately disturbed areas near farms or logging, but not within them. Thus, it seems likely that ocelot density may vary more along a gradient of human disturbance than just by the binary term we were able to include in the analysis. Sampling more heavily impacted areas and determining more refined measures of human impact would allow for the patterns to be explored in more detail.

Interestingly, ocelots in the mixed-use area seemed to have potentially adapted to their environment and available resources. We did not capture any individuals in both areas, even though there was less than a 1 km buffer between the protected area and the mixed-use area. The persistence of ocelot populations in matrix habitats adjacent to protected areas has been observed at other study sites (Boron et al., 2022), but the population division observed in our study has not. In addition to temporal adaptations, the ocelot population in the mixed-use area could be acclimating to changes in resources caused by human activities, potentially leading to their isolation. Mesocarnivores can undergo rapid behavioral changes in response to altered resource pools and environmental modifications made by humans, even within a single generation (Verdade et al., 2011). Ocelots, and mesocarnivores in general, have high phenotypic plasticity and therefore high adaptability in their diet and space use, potentially enabling them to adjust to matrix habitats. The absence of top predators, which tend to decline in agricultural landscapes, may further enhance these traits (Verdade et al., 2011; Zeilhofer et al., 2014). Several potential mechanisms for isolation of ocelot populations between adjacent mixed-use and intact areas could cause mixed-use areas to become population sinks which could lead to negative effects on the overall population at larger scales. The potential for ocelot populations to become genetically fragmented in areas of moderate human disturbance warrants greater exploration.

Our estimate of 25.22 - 37.62 ocelots per 100 km² is comparable to the 24.84 ocelots per 100 km² reported by da Rocha et al. (2016) using secr models in the Amazon rainforest of Brazil. It is likely that other studies throughout the ocelot's range have overestimated density when using traditional capture recapture models. For example, (Di Bitetti et al., 2008) correlated abiotic continental factors to ocelot abundance using density estimates from 21 studies. Their resulting regression equations using latitude and rainfall overestimate ocelot density in our region of Madre de Dios by more than double. While larger-scale abiotic factors play an important role in the abundance and diversity of flora and fauna, overestimating local population densities can mislead local and global wildlife management initiatives and subsequent conservation actions. It is unclear if the biased predictions from Di Bitetti et al. (2008) are due to the initial studies overestimating ocelot densities or to natural variation that occurs in broad scale generalizations, but our study highlights the need for continuing to improve our understanding of local ocelot densities in the Amazon. Additionally, these results highlight the need to use similar methods across studies to allow for easier and more direct comparisons. Secr, which is widely used for estimating density and movement in wildlife populations (Royle et al., 2013), provides this functionality and we recommend future metanalyses focus on studies employing secr methods.

As expected, we found that males had a larger home range size than females. Previous studies in tropical forests observed that males had a home range at least 2.2 – 2.7 times larger than females (Crawshaw, 1995; Di Bitetti et al., 2006) and telemetry studies yielded an even greater difference of 3.3 – 3.9 (L. Emmons, 1988; Ludlow & Sunquist, 1987), the latter of which aligns with our results. Larger home ranges for males are likely related to differences in resource requirements, competition for territories, and having access to multiple potential mates (Rabinowitz &

Nottingham, 1986). By contrast, female ocelots tend to have smaller home ranges that are centered around their dens where they raise their young (Sunquist & Sunquist, 2002). This pattern of male carnivores having larger home ranges than females is not limited to ocelots; many other felids, including bobcats (*Lynx rufus*), pumas, and jaguars also exhibit this sexual dichotomy (Nuñez & Miller, 2019; Pesenti & Zimmermann, 2013). This difference is thought to be driven by similar factors, including competition for mates and differences in parental care responsibilities.

Our study found a sex ratio of 1:1.2 (males/females), though not statistically different from a 1:1 ratio. While we found an effectively even sex ratio, several studies have hypothesized that solitary carnivores, like ocelots, should have male-biased sex ratios (Tobler & Powell, 2013; Wearn et al., 2013). This could be because male carnivores generally travel longer distances and have a higher probability of detection (Anile & Devillard, 2018; Mohamad et al., 2015). For example, Petersen et al. (2020) found sex ratios of the mainland clouded leopard (*Neofelis nebulosa)* to be 1.2:1 (males/females) in core habitat and 3:1 in edge habitat. However, Pin et al. (2022) found higher sex ratios for female leopard cats (*Prionailurus bengalensis)* in three different study areas within Cambodia (1: 1.2-1.9 males/females). Similar to our study, ocelot sex ratios in Misiones, Argentina, which were higher for females at two sites (0.67:1 and 0.45:1 males/females) (Di Bitetti et al., 2006).

Overall, our results suggest that even moderate levels of human impact are shifting the realized niche of ocelots. In addition to adjusting their temporal patterns in response to human activity, we observed two separate groups of ocelots, suggesting a potential fragmentation of the ocelot population in the two areas. Ocelot populations may appear intact when only one axis affecting their density and activity patterns is examined; it is therefore crucial for future research to examine the effects of humans and intra-guild competitive relationships in addition to prey abundance and environmental productivity when evaluating their population dynamics. The success of ocelot persistence in mixed-use areas is likely to be contingent on several factors, namely the quality/size of remaining intact forest and the distance to a protected area or corridor. Severe habitat degradation, hunting of prey, and retaliation for livestock kills will further reduce their ability to persist in matrix habitat. Conservation efforts that focus on protecting and restoring habitat quality and connectivity in matrix habitats may be crucial for the persistence of ocelots in these landscapes, and for other mesocarnivores. Our results provide valuable insight into ocelot demographics along the frontlines of habitat conversion in western Amazonia, a critical area in the ongoing conservation needs of this species.

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APPENDIX A: FELID ACTIVITY PATTERNS

General activity patterns showed that four of the five species were mostly nocturnal, except the jaguarundi which had a diurnal activity pattern (see Fig. 7). Jaguars had peak activity between 6-10pm and were least active between 10am and 2pm. Pumas were more nocturnal than jaguars, with two peak ranges of activity between 6-10pm and 1am-5am. Pumas are the least active between 9am-3pm. Ocelots are active throughout the entire night (7pm-4am); their two high peaks of activity are from 7-8pm followed by 3am-4am. Ocelots are the least active between 7am-5pm. Jaguarundis are active diurnally between 5am-6pm, with peak activity between 6-8am. They have little to no activity between 7pm and 4am. Margays are the opposite; they are most active between 7pm-4am with a peak between 10-11pm. Margays exhibited little activity throughout the day and were the least active around 10am.

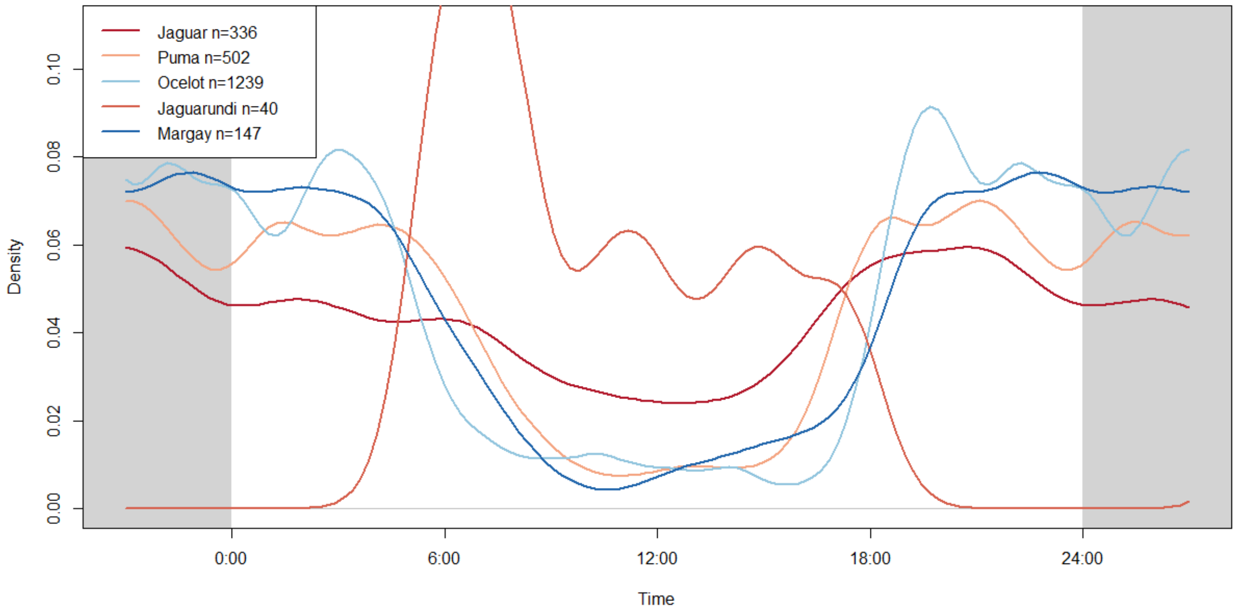

Fig. 7 Overlayed activity patterns of all five felid species in Las Piedras, Madre de Dios, Peru, on a 24-hour scale.

VITA

Samantha Zwicker (MS, PhD) is a tropical ecologist and wildlife rehabilitation specialist who recently received her doctorate from the University of Washington's Quantitative Ecology Lab. Sam is also the founder and co-director of Hoja Nueva, a leading conservation organization confronting the multifaceted threats to the biodiversity of the Peruvian Amazon through rewilding programs, ecological research, and applied conservation. She has also been a Panthera Small Cat Action Fund Grantee, a Wild Felid Legacy Scholar, and an NIH Global Health Fellow. In addition to spearheading Hoja Nueva's projects within the rainforests and communities of Madre de Dios, Peru, Sam is also investigating neotropical felid population dynamics, assessing the effects of human impact on threatened mammals using camera trapping, and describing interspecific competition and spatiotemporal overlap between sympatric carnivores.