



Drivers of jaguar (*Panthera onca*) and puma (*Puma concolor*) predation on endangered primates within a transformed landscape in southern Mexico

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Abstract

Human pressures have increasingly placed keystone species, such as large cats, under threat. Together with forest loss, prey depletion is one of the main threats to the survival of jaguars (*Panthera onca*) and pumas (*Puma concolor*) throughout the Neotropics. Generally, primates are not considered main prey for jaguar and puma, and their inclusion in the diet could be indicative of ongoing prey species decline. Here, we investigate the effect of habitat type and disturbance on primate predation by large cats. Surveys took place during the dry seasons (March to June) of 2010 and 2011, covering a total of 608.5 km across 24 localities in the Uxpanapa Valley, Mexico. We found 65 felid scat samples with the aid of a wildlife scat detection dog, and then examined them to identify predator species and classify the prey remains they contained. Primates represented the most frequent prey (35%) for both jaguar and puma in our study site and constituted approximately half of the biomass consumed by these felines in the area. Primate remains were more likely to be found in scats surrounded by the lowest percentage of conserved forest or in areas surrounded by more villages, showing the potential effects of human activities on these species' populations. The high proportion of primates found in scats within our study site could be an early indication that populations of ungulates and other "typical" prey are beginning to collapse, and urgent conservation interventions are needed for both large cats and primates before they become locally extinct.

Abstract in Spanish is available with online material.

KEYWORDS

diet, howler monkey, human impacts, large felids, spider monkey, Uxpanapa Valley

1 | INTRODUCTION

Large mammalian carnivores are vital for the maintenance of biodiversity and ecosystem function and serve as indicators of ecosystem

health (Ripple et al., 2014; Wolf & Ripple, 2016). However, human pressures in developing countries pose unprecedented threats to large carnivores (Alvarenga et al., 2021; Ceballos et al., 2021), predominantly through habitat transformation and prey loss (Sandom

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et al., 2017). Understanding the effects originating from these anthropogenic actions is essential for the conservation and management of large carnivore populations, particularly in areas undergoing intensive degradation.

In the Neotropics, populations of all wild felids are declining (ISEC, 2022) including jaguars (*Panthera onca*) and pumas (*Puma concolor*), the two largest felids that occur sympatrically (Ávila-Nájera et al., 2018). The IUCN lists the jaguar as Near Threatened (Quigley et al., 2017) and it is placed in Appendix I of CITES (CITES, 2022), while puma is listed as being species of Least Concern by the IUCN (Nielsen et al., 2015) and are included in Appendix II of CITES. In Mexico, jaguar is considered to be at risk of extinction (SEMARNAT, 2010). Overall, both species are displaying a general trend of population decline (Nielsen et al., 2015; Quigley et al., 2017), and their conservation status will probably worsen in the near future (Hayward et al., 2016; Zanin et al., 2016). Jaguar and puma are obligate carnivores and opportunistic hunters, highly dependent on a good prey base of medium to large sized mammals (Ávila-Nájera et al., 2018; Paviolo et al., 2018; Hernández-SaintMartín et al., 2015; Novack et al., 2005; Rubio-Rocha et al., 2023). Their prey use varies greatly depending on geographical location, but both have a similar primary prey base consisting of peccaries, large rodents, deer, and armadillos (Foster et al., 2010; Foster & Harmsen, 2022; Galindo-Aguilar et al., 2022; Piña-Covarrubias et al., 2023). However, human pressures, together with landscape transformation, can prompt changes in their predation behavior (Craighead, 2019). Jaguar and puma have both been known to switch to alternative prey when the abundance of their main prey has decreased under particular environmental pressures (Foster et al., 2016; Soria-Diaz et al., 2018).

The rarity of felid predation on primates is readily apparent in the Neotropics (Hart, 2007), with studies showing felids tend to significantly avoid carnivores and primates as prey, while all other broad taxonomic groups are usually killed in accordance with their abundance (Hayward et al., 2016; Rubio-Rocha et al., 2023) and vulnerability (Magioli & Paschoaletto, 2021). Predation rates on atelid primates, including howler (*Alouatta* spp.) and spider monkeys (*Ateles* spp.), are thought to be low, possibly due to their behavioral characteristics, which include sociality and arboreal locomotion (Bidner, 2014; di Fiore, 2002; Link & Di Fiore, 2013). Nevertheless, habitat type can influence predation on primates, since the density of vegetation can affect detectability and catch ability (Hayward et al., 2016). Therefore, as primate habitats become increasingly anthropogenic, their predation risk, potential predators, and susceptibility to predation are bound to change (McKinney, 2009). While forest fragmentation remains the most urgent driver of primate decline, the stochastic nature of predation, especially with increasing risk due to forest degradation, has a potential to rapidly eradicate groups, even when short-term surveys show stable or increasing populations (Irwin et al., 2009).

Information regarding the predation rates of primates by large cats is not readily abundant, since direct observations of predation events on primates are uncommon and gathering large cat scat samples to identify and quantify primate consumption is in itself a challenging procedure. Thus, the effects of these two predators on the

long-term survival of primate populations may be underestimated. Furthermore, we need to fully understand the effects concurrent land transformation and threats to primary prey species have on jaguar and puma already living in heavily degraded habitats in the Neotropics. Here, we present a study on primate predation in Veracruz, southern Mexico, a region which has been highly disturbed by human activities and is lacking in studies on the diet of top predators (Rodríguez-Soto et al., 2011). We collected and examined scat samples from jaguar and puma and classified the primate remains found within them. We combined traditional morphological techniques of diet determination with molecular information to corroborate predator species identity. We then assessed whether primate predation was influenced by habitat type and disturbance. We predicted primates would be occasional prey, and if predated, there would be a higher consumption of howler monkeys, given that they move more slowly and are less agile than spider monkeys (Cuarón, 1997; Peetz et al., 1992). We predicted habitat quality to be a main driver of primate consumption, with higher primate predation in more disturbed areas with less forest cover, where they would be more accessible as prey (Schwitzer et al., 2011). Our work aims to contribute toward a better understanding of jaguar and puma diet in an anthropogenically altered landscape, as well as to help assess the implications of large cat predation for primate conservation. In particular, information on large cat predation would provide necessary data to develop primate conservation strategies for our study site, since both spider (*Ateles geoffroyi*) and howler (*Alouatta palliata mexicana*) monkeys are classified as endangered (IUCN, 2023) and face increasing threat due to habitat transformation in the area (Galán-Acedo et al., 2018; Shedden et al., 2022).

2 | METHODS

2.1 | Study area

The Uxpanapa Valley in southeastern Mexico is one of the last main relicts of tall evergreen forest in the country and is classified as one of the most biodiverse areas in both Mexico and the world (World Wide Fund for Nature–Fundación Carlos Slim, 2018). It is currently unprotected and over 43% of the territory has undergone severe transformation since the 1970s (Hernández-Gómez et al., 2013). The current landscape is a mosaic dominated by pasture (26%) and secondary forest (38%), with smaller portions consisting of small corn (*Zea mays*) plantations and rubber tree (*Hevea brasiliensis*) cultivations (15%), remnant mature tall evergreen forest (16%), and village settlements (5%) (White, 2017) (Figure 1).

2.2 | Collection of predator scat samples

Surveys took place during the dry seasons (March to June) of 2010 and 2011, as seasonal floods during the rainy season make large parts of the region inaccessible during the rest of the year. Scat samples were found with the aid of a wildlife scat detection dog from the

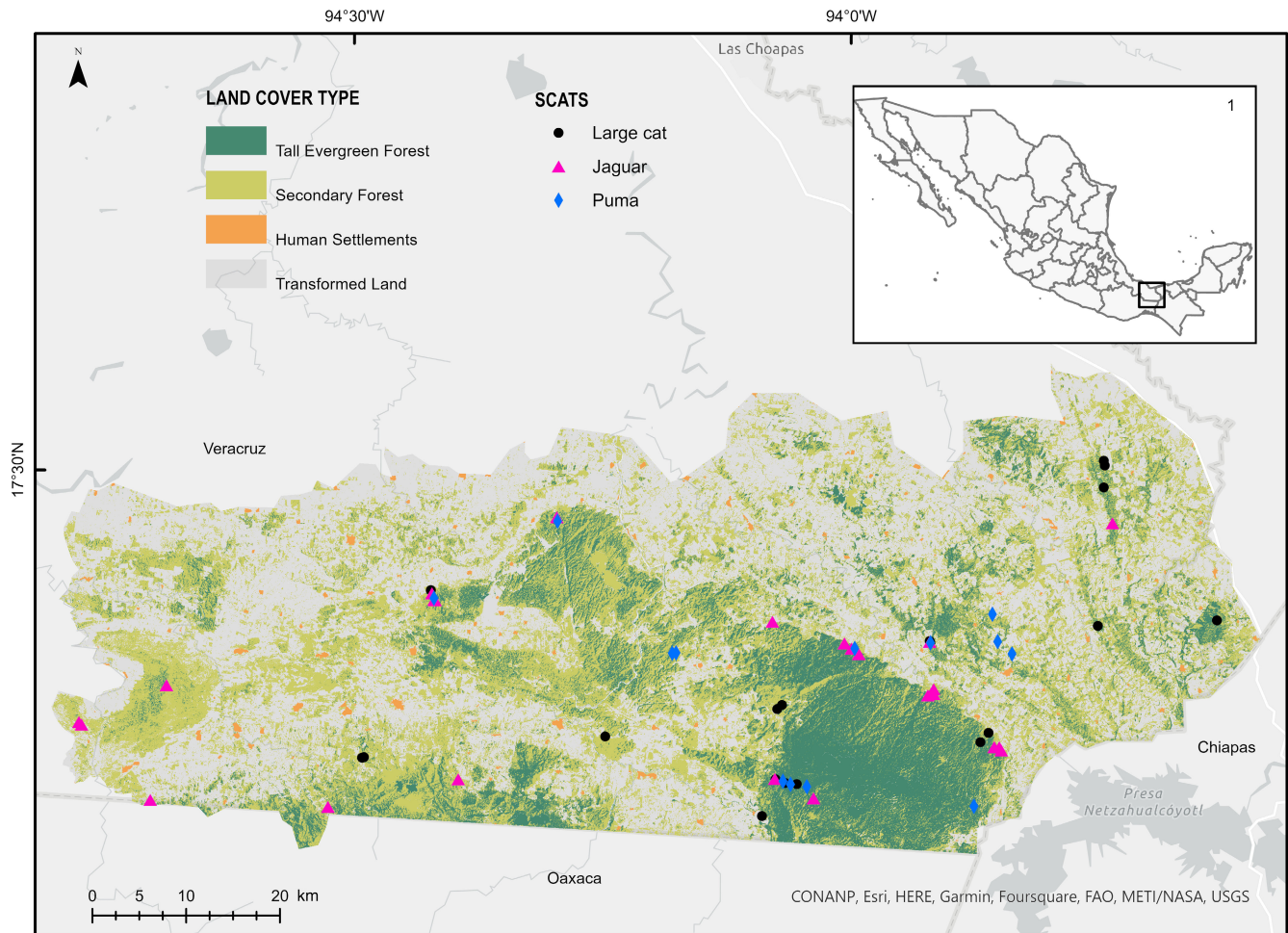


FIGURE 1 Study site in the state of Veracruz (box 1). Scat collection points across the Uxpanapa Valley (black circle representing Large Cat, pink triangle representing Jaguar and blue diamond representing Puma). Also showing a simplified vegetation classification (tall evergreen forest in dark green, secondary forest in light green, human settlements in orange, and transformed land in light gray).

Conservation Canines program at University of Washington (Wasser et al., 2004). The use of detection dogs allowed us to cover a large area effectively as olfactory search by dogs does not rely on visually conspicuous scat deposition on trails or roads. We surveyed a total of 608.5 km across 24 localities within the Uxpanapa Valley, collecting a total of 65 putative felid samples. Each scat sample was divided in two, one piece was preserved in plastic vials containing silica gel desiccants for diet analysis and kept at room temperature until further examination in the laboratory. The other piece was kept frozen for genetic identification of the felid species. Where the sample was of sufficient size, a portion was left in the field to minimize disruption of any territorial marking behavior. For each sample, we also registered geographic location (GPSMAP 60CSx, Garmin).

2.3 | Predator ID through molecular methods

Predator species ID was confirmed using mitochondrial DNA sequencing of sloughed intestinal cells (Chaves et al., 2011). The ATP6 region (approximately 175 bp) was used to distinguish all sympatric carnivore species (White, 2017). Additionally, predator hair found in

the scats (ingested during auto-grooming) was used to support the species ID. We confirmed 32 jaguar and 15 puma scats, with 18 large cat scats for which DNA quantity and quality was not sufficient to discriminate between jaguar and puma, nor was there enough hair from self-grooming to establish this.

2.4 | Predator diet analysis

Prey identification was based on macroscopic and microscopic patterns of the guard hairs found in these scats following a modification of the standard procedure suggested by Arita and Aranda (1987). Each sample was placed in water and allowed to sit for 24–48 h. The hair was then placed in a petri dish and rinsed with soap-water to eliminate dirt and other biological materials. A macroscopic examination of the shape and coloration patterns of the hairs was made under a dissection microscope. Microstructural patterns of the cuticle were determined by making an impression of the cuticle in a glass slide with nail polish and observing it under the light microscope. To describe the medulla, hairs were cleared by soaking them for 24 h in Xilol, then the widest distal region of the hair observed under a light microscope.

Hair guides were employed to determine the prey species of each hair (Baca-Ibarra & Sánchez-Cordero, 2004; Juárez et al., 2010; Pech-Canché et al., 2009). The primate guard hairs found in the scats were identified and differentiated by their morphology, specifically by their patterns in the medulla and scales, which allows howler and spider monkeys to be distinguished (Figure S1). We considered all primate items of the same species found in a scat as representing one individual prey item. Hairs of mammals that did not appear in any of the guides we consulted were classified as “unknown mammal.”

Prey data were analyzed for three categories according to predator species: jaguar, puma, and large cats, which encompasses all of the samples (jaguar + puma + non-identified large cat). We calculated the frequency of occurrence of each prey found as $FO = Fs/N \times 100$, where F_s is the number of scats in which a prey species was detected, and N is the total number of scats analyzed. We also estimated the percentage of occurrence (PO) of primate remains by dividing the total frequency of a primate item by the sum of the frequencies of all prey species. To determine the energetic contribution of each prey, we estimated the total and relative consumed biomass applying the Ackerman et al. (1984) correction factor for prey larger than 2 kg ($Y = 1.98 + 0.035 X$, where $Y =$ consumed biomass/scat and $X =$ average prey weight, both in kilograms—kg). We used Aranda (2000) as a source of mean prey body weight.

2.5 | Primate detection in the field

Primate surveys were performed in parallel and within the same areas as large cat scat collection, as part of a larger project studying biodiversity in the region (Shedden et al., 2022). Two species of primates were found in our study site: the Mexican mantled howler monkey (*Alouatta palliata mexicana*) and the spider monkey (*Ateles geoffroyi*), both classified as Endangered in the IUCN Red List (Cuarón et al., 2020; Rosales-Meda et al., 2020). The data on primate occurrences and number of groups used for our analysis were derived from these surveys (Shedden et al., 2022).

2.6 | Vegetation mapping

Vegetation data were based on a supervised classification of five SPOT 5 satellite images captured in the dry season of March and April 2011 (88.25% classification accuracy, Kappa coefficient = 0.85) (C.A. Muñoz-Robles, unpublished data). We used ArcMap v. 10.6.1 to create 5 km buffers around each scat, an approximate size of a jaguar home range (White, 2017). Within each buffer, we determined the number of primate groups, number of villages, and percentage of the area covered by different land use.

2.7 | Data analysis

To assess primate predation by large cats in relation to habitat type and quality, we analyzed the presence/absence of primate remains in each

scat as a dependent variable with the number of spider monkey groups, howler monkey groups, number of villages, and percentage of each land use type within 5 km buffers, using generalized linear models (GLMs) with a logit link function and binomial error structure (Crawley, 2007).

We conducted three separate analyses to predict the presence/absence of primate remains in feline scats: (1) both primates together, (2) spider monkey only, and (3) howler monkey only. The land cover predictor variables were the percentage of secondary forest (SF), secondary mature forest (SMF), young secondary forest (YSF), and tall evergreen forest (TEF) estimated for each sampled plot. These variables were included since both large cats and primates need forest to survive. We also included as predictors the percentage of water bodies (WB), clearings (CL), rubber plantations (RP), farmland (FL), grassland (GL), and area occupied by human settlements (HS), as well as the number of primate groups and villages per buffer. These variables were selected since water bodies are known to be important for jaguar, while plantations and cleared land represent the disturbances that could be affecting our focal species. Finally, human settlements and number of villages are considered as proxies for poaching pressure. We carried out all statistical analyses in R software 4.0.3 (R Core Team, 2020). To assess collinearity among explanatory variables, Pearson's correlation estimates were produced using the *PerformanceAnalytics* package (Peterson & Carl, 2020), and correlated variables ($r > .7$) were not included in the same models (Dormann et al., 2013). We ran the GLMs with a logit link function and binomial error structure using the *MASS* package (Venables & Ripley, 2002) and the function “dredge” from the *MuMIn* package (Barton, 2022) to select the best model based on the Akaike's information criterion (AIC) using a two-variable cutoff due to our small sample size.

3 | RESULTS

3.1 | Predator diet composition

We identified a total of 21 mammal species as prey of large cats in the Uxpanapa Valley, 11 and eight mammal species present in the diet of jaguar and puma respectively (Table 1). The average number of different prey species per scat was 1.2, with most of the scats containing only one mammal species (87.5% for jaguar, 77.7% for puma, and 84% for large cats). Primates represented the most frequent prey, with nearly 35% of all found items belonging to a primate species (Table 2). Spider monkeys showed higher frequency of occurrence than any other prey species for both puma and jaguar, while howler monkeys showed a higher frequency of occurrence in puma than in jaguar scats (Tables 1 and 2). Likewise, primates constituted approximately half of the biomass consumed by these felines in this area (Table 2).

3.2 | Predictors of primate predation

When analyzing the data on overall primate predation, the percentage of tall evergreen forest (TEF) had a negative association

TABLE 1 Frequency of occurrence (FO) in predator scats and relative biomass (RBC) of prey consumed by jaguars, pumas, and large cats in the Uxpanapa Valley, Mexico.

Prey	Jaguar (<i>Panthera onca</i>)			Puma (<i>Puma concolor</i>)			Large cats		
	N = 32			N = 15			N = 65		
	n	FO	RBC (%)	n	FO	RBC (%)	n	FO	RBC (%)
<i>Alouatta palliata</i>	2	6.3	7.87	2	13.3	15.69	8	12.3	12.66
<i>Ateles geoffroyi</i>	7	21.9	26.90	5	33.3	38.30	19	29.2	29.36
<i>Bassariscus sumichrasti</i>				1	6.7	3.15	2	3.1	1.27
<i>Chironectes minimus</i>	1	3.1	0.97				1	1.5	0.39
<i>Coendou mexicanus</i>	1	3.1	3.65	2	13.3	14.53	5	7.7	7.33
<i>Conepatus</i> sp.	4	12.5	14.63				4	6.2	5.88
<i>Cuniculus paca</i>	1	3.1	4.03				3	4.6	4.86
<i>Cyclopes didactylus</i>				1	6.7	1.75	1	1.5	0.35
<i>Galictis vittata</i>	1	3.1	3.63				1	1.5	1.46
<i>Lontra longicaudis</i>							1	1.5	1.64
<i>Marmosa mexicana</i>				1	6.7	0.24	1	1.5	0.05
<i>Mazama temama</i>	1	3.1	4.76	2	13.3	18.99	4	6.2	7.66
<i>Mustela frenata</i>							1	1.5	0.21
<i>Nasua narica</i>							1	1.5	1.51
<i>Pecari tajacu</i>	2	6.3	9.59				2	3.1	3.86
<i>Potos flavus</i>				1	6.7	7.35	2	3.1	2.97
<i>Procyon lotor</i>							1	1.5	1.53
<i>Sciurus</i> sp.							1	1.5	0.42
<i>Tamandua mexicana</i>	2	6.3	7.56				2	3.1	3.04
<i>Tapirus bairdii</i>							1	1.5	6.95
<i>Tayassu pecari</i>	3	9.4	16.41				3	4.6	6.60
Unknown mammals	11	34.4		3	20.0		14	21.5	

with presence of primate remains in scat ($\beta = -0.030$, $SE = 0.01$, $z\text{-value} = -2.05$, $p = .041$). Primate remains were more likely to be found in scats surrounded by the lowest percentage of TEF. The percentage of other land cover types, number of primate groups, and number of villages, although part of the delta AIC threshold, did not have significant effects on the probability of presence of primate remains in large cat scats (Table 3; Table S1).

For spider monkey predation, the number of villages ($\beta = 0.28$, $SE = 0.14$, $z\text{-value} = 1.98$, $p = .047$) and the percentage of secondary mature (SMF) ($\beta = 0.09$, $SE = 0.05$, $z\text{-value} = 1.73$, $p = .083$) were the strongest predictors. Spider monkey remains were more likely to be found in scats surrounded by more villages and a higher amount of SMF. The percentage of other land cover types and number of primate groups did not have significant effects on the probability of presence of spider monkey remains in large cat scats (Table 3; Table S2).

For howler monkey predation, the number of howler groups ($\beta = 1.74$, $SE = 0.57$, $z\text{-value} = 3.05$, $p = .002$) and the percentage of tall

evergreen forest (TEF) ($\beta = -0.17$, $SE = 0.09$, $z\text{-value} = -1.93$, $p = .053$) were the strongest predictors for finding howler monkey remains in scat. Howler monkey remains were more likely to be found where there were more howler monkey groups and in scats surrounded by the lowest percentage of TEF. None of the remaining variables had a significant effect on the likelihood of howler monkey remains being present in scats (Table 3; Table S3).

4 | DISCUSSION

Our results show that primate predation by jaguar and puma in our study site was surprisingly high compared to that of other wild mammals found in the area and compared to previous studies of large cats' diet in Mexico (Aranda & Sánchez-Cordero, 1996; Galindo-Aguilar et al., 2022; Piña-Covarrubias et al., 2023; Rubio-Rocha et al., 2023). This is a marked difference from the general understanding that Neotropical primates are not usually targeted as prey

TABLE 2 Consumption of primates by large cats in the Uxpanapa Valley, Mexico.

	Jaguar	Puma	Large cats
	(<i>Panthera onca</i>)	(<i>Puma concolor</i>)	
<i>Alouatta palliata</i>			
<i>n</i>	2	2	8
kg	7.5	7.5	7.5
PO	5.5	11.1	10.3
TCB	4.5	4.5	17.9
RCB	7.9	15.7	12.7
<i>Ateles geoffroyi</i>			
<i>n</i>	7	5	19
PO	19.4	27.8	24.4
kg	6	6	6
TCB	15.3	11	41.6
RCB	26.9	38.3	29.4
Primates			
<i>n</i>	9	7	27
PO	25	38.9	34.6
TCB	19.8	15.4	59.6
RCB	34.8	54	42

Abbreviations: kg, mean prey weight; *n*, number of scats with primate remains; PO, Percentage of occurrence; RCB, percentage of relative biomass consumed; TCB, total corrected biomass consumed (kg).

by large cats (Bidner, 2014; di Fiore, 2002; Hart, 2007; Hayward et al., 2016; Santos et al., 2014).

In our study area, spider monkeys represent the most preyed species for both jaguar and puma. This high predation rate contrasts with previous findings within the spider monkey distribution range (di Fiore, 2002; Hart, 2007; Urbani, 2005). Scats containing spider monkey remains were more likely to be found in sites where more villages were present. A higher number of villages can signify increased human activity and presence, with associated possible greater habitat perturbation and greater extraction of the preferred prey of large cats. On a global scale, prey depletion is a threat to large carnivores (Wolf & Ripple, 2016), and human accessibility to forest areas is generally associated with heightened poaching pressure on large cat's prey base (Paviolo et al., 2018). Specifically, studies have shown that depletion of primary prey species by humans in unprotected forests can lead to dietary changes in jaguars (Foster et al., 2010), while deforestation can lead to changes in puma diet (Magioli & Paschoaletto, 2021). In Central America, consumption of primates by jaguar and puma has been reported to be greater in areas with intense hunting activities compared to non-hunting areas (Novack et al., 2005), while abundance of alternative non-primate prey, particularly ungulates, has been shown to affect the intensity of predation on primates at four sites in Africa and Asia (Hart, 2007). One of the few studies on bushmeat in an area of the Selva Zoque adjacent to our study site shows that the most

sought-after bushmeat prey are red brocket deer (*Mazama temama*), collared and white-lipped peccary (*Pecari tajacu* and *Tayassu pecari*), lowland paca (*Cuniculus paca*), and armadillos (*Dasypus novemcinctus*) (Lira-Torres et al., 2014). These bushmeat preferences were confirmed in our study area through numerous conversations with local residents during our field surveys (Shedden-Gonzalez, 2016). Furthermore, all of these species, except armadillos, were found in our jaguar and puma scat samples (Table 1). This points toward human-feline competition for prey, as hunting is a common activity throughout our study site.

Presence of howler monkey remains in scats was lower than that of spider monkeys and was associated with a lower percentage of TEF and higher number of howler monkey groups in the area. There are several possible reasons for lower predation on howler monkeys than spider monkeys. First, the overall prevalence of howler monkeys appears to be lower than that of spider monkeys in the region (Shedden et al., 2022), and large cats tend to use prey in accordance with their abundance (Hayward et al., 2016). This abundance-based difference is supported by our finding that howler monkey consumption was higher in sites with more howler monkey groups.

Additionally, there may be behavioral differences between the primate species that make spider monkeys more susceptible to predation. During our surveys, we observed mobbing behaviors from spider monkeys toward the scat detection dog, which was never observed with howler monkeys. Mobbing by spider monkeys has been recorded in other studies (Matsuda & Izawa, 2008; Mourthe & Barnett, 2014; Ramos-Fernández, 2008) and can involve primates coming close to the ground (Tórrez et al., 2012) which we directly observed when the spider monkeys reacted to the detection dog. Such behavior may contribute to higher exposure of spider monkeys to felid predation than howler monkeys. Moreover, recent reports on primate predation by jaguar and puma in Mexico, while showing low occurrence and low contribution to the consumed biomass, also show higher consumption of spider monkeys over howler monkeys (Piña-Covarrubias et al., 2023). This study was carried out in private ecological reserves of continuous forest with a few interspersed rural communities, which would explain the lower primate predation compared to our study site which is mainly composed of remnants of forest within an anthropic vegetation matrix.

When considering both primate species together, our results indicate that felid predation on primates is increased with the reduction of tall evergreen forest. This agrees with reports that forest transformation may intensify predation on canopy dwelling primates by facilitating access to prey (Irwin et al., 2009), due to a lack of large trees and especially in areas close to the forest edge, where the presence of other mammals can be lower (Slater et al., 2023). Additionally, changes in the environment and habitat structure (e.g., microclimate and large tree availability) may also force both spider and howler monkeys to seek resources such as water on the ground (Delgado-Martínez et al., 2021; Youlatos & Guillot, 2015), or to cross through open areas to reach disconnected forest fragments

TABLE 3 Best models that predict primate consumption by large cats in Uxpanapa Valley, southeast Mexico.

Predictors												
	TEF	CL	GL	PG	HS	VI	SMF	SF	YSF	HG	Δ AIC	Weight
Primates	-0.03*										0.00	0.08
	-0.04	-0.23									1.04	0.05
	-0.04	-0.59	0.14								1.09	0.04
	-0.04			0.09							1.28	0.04
	-0.03				-0.85	0.09					1.72	0.03
	-0.03						0.03				1.81	0.03
	-0.04							-0.02			1.83	0.03
										1.98	0.03	
Spider monkeys						0.28*	0.09				0.00	0.10
									0.84		1.89	0.04
						0.22					1.92	0.04
							0.07				1.96	0.04
						0.20			0.64		2.00	0.04
Howler monkeys										1.74*	0.58	

Abbreviations: CL, clearings; GL, grassland; HG, howler groups; HS, human settlements; PG, primate groups; SF, secondary forest; SMF, secondary mature forest; TEF, tall evergreen forest; VI, villages; YSF, young secondary forest.

*Significant associations with primate predation ($p \leq .05$) are in bold font.

(Campbell et al., 2005; Martínez-Mota et al., 2007), which potentially explains the high levels of primate consumption at our study site.

Global carnivore declines are driven mainly by the loss or degradation of habitat and prey base (di Minin et al., 2016), and in the Uxpanapa Valley, human pressures seem to be pushing jaguar and puma to rely on alternative prey compared to more intact ecosystems. Lack of tree cover and potential prey depletion due to unregulated bushmeat hunting and habitat loss could potentially be the drivers behind the high primate predation in our study area, though long-term monitoring and larger sample sizes are needed to fully understand any dietary shifts occurring in this region. Nevertheless, this has important implications for both primates and felines, especially since the region is unprotected and has rapid and ongoing deforestation (Carvajal-Hernández et al., 2018). One major concern for primate conservation is the potential for habitat loss and increased predation acting multiplicatively. Even if populations survive landscape transformation, the subsequent increased predation may have a greater-than-additive effect on population extinction rates. There are already signs of disruption in gene flow and genetic loss in howler monkeys within this region (Dunn et al., 2013; Solórzano-García et al., 2021) signaling the need for rapid conservation actions for both primate species. At the same time, large cats could face local extinction if prey continue to diminish and forest tracts are further reduced. The abundance of some prey species may be a better proxy for the threat to jaguars than landscape transformation, and unregulated hunting pressure could result in substantial prey/predator population declines (De Thoisy et al., 2016). Two of the five species of ungulates found in the region are classified as endangered, and although ungulate populations are still prevalent in areas surrounding Uxpanapa Valley, recent studies highlight reduction in connectivity and overhunting as conservation concerns for these species (Lira-Torres et al., 2014; Pérez-Irinea & Santos-Moreno, 2016). Consequently, the high proportion of primates found in scats within our study site could be an early indication that populations of ungulates and other “typical” prey are beginning to collapse, and urgent conservation interventions are needed.

The predation patterns observed here show an increase in primate consumption by large cats in altered habitats, making primate populations living in perturbed habitats highly vulnerable to predation. Moreover, the flexible and opportunistic hunting nature of jaguar and puma enables them to feed on prey that are either more vulnerable or more available. Thus, shifts in diet patterns of top predators reflect changes in ecosystem structure due to environmental or anthropogenic pressures. The landscape heterogeneity, limited sample size, and fixed temporality of the present study provide a partial notion of primate-predator dynamics. Further studies that incorporate larger samples sizes across climatic seasons in intact and fragmented forest will aid to confirm the patterns presented here for a better understanding of the variations on ecological processes and dynamics in human dominated landscapes. Our results highlight the importance of maintaining tall forest cover and ecosystem biodiversity and for management strategies that mitigate overhunting

the primary prey of large cats to avoid disruption of prey predator interactions, before the negative effects on both primate and large cat populations become irreversible.

AUTHOR CONTRIBUTIONS

ASG, PKG, and AHK conceptualized and designed the research. ASG, BSG, and JMW performed the fieldwork and conducted data analyses. BSG and JMW performed laboratory work. ASG wrote the original draft, and all co-authors reviewed/edited the manuscript and agreed on the submission.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

Model outputs are available in supporting information. The data that support the findings of this study are available on request from the corresponding author. The editor in chief has waived the required archiving due to privacy or ethical restrictions.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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