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Abstract

Background and Research Aims: Wildlife research in Panamá has focused primarily on protected areas along the Central Cordillera, where much of the remaining mature rainforest habitat is located. Information on large felid and prey habitat use in isolated habitats in Panamá is therefore limited. Here, we estimated occupancy and detection probabilities, as affected by habitat and anthropogenic influences, for 2 felid species (jaguars [*Panthera onca*] and pumas [*Puma concolor*]), and 2 prey species (white-lipped peccaries [*Tayassu pecari*] and collared peccaries [*Pecari tajacu*]).

Methods: Camera trap surveys were conducted during 2014–2015 at Cerro Hoya National Park (CHNP), an isolated remnant of tropical rainforest habitat, and Darién National Park (DNP), a large tract of continuous rainforest habitat. We used single-season, single-species occupancy modeling to estimate probabilities of detection and habitat use of our focal species.

Results: Three of the 4 focal species were detected at both sites, excluding white-lipped peccary at CHNP. Detection of jaguars and white-lipped peccaries at DNP was highest in February, while detection of collared peccaries at DNP and pumas at CHNP was highest in May and April, respectively. Peccary habitat use was uniform across sites and unaffected by habitat covariates. Both felids preferred habitat further away from anthropogenic disturbance, and jaguars preferred habitat at higher elevations than pumas.

Conclusion: We further confirm the presence of jaguars and likely local extirpation of white-lipped peccaries in CHNP. Temporal variations influenced detections of focal species. Habitat use of felids was negatively affected by anthropogenic disturbance and elevation.

Implications for Conservation Habitat fragmentation and human activities negatively influenced habitat use of felids at both study areas. Given that CHNP serves as one of the last remnants of forest habitat outside the Central Cordillera, we recommend that CHNP be considered a top priority area for wildlife conservation in Panamá.

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Keywords

Camera traps, fragmentation, jaguar, occupancy modeling, conservation corridor, peccary, puma

Introduction

The consequences of habitat loss and fragmentation are serious and far-reaching for long-term population persistence of mammals. In particular, populations of large-bodied mammals are unlikely to be sustained by small habitat fragments (Azevedo et al., 2020; Kinnaird et al., 2003; Peres, 2001). Large mammals are vulnerable to local extinction in fragmented habitats because they typically live at lower densities, need much larger areas to survive than smaller mammals, and are often exploited excessively by humans (Crooks, 2002; Urquiza-Haas et al., 2009). Considering that large mammals are often among the first to be impacted in disturbed areas, they can serve as indicator species to monitor biodiversity loss (Cardillo et al., 2005; Crooks et al., 2011; Poley et al., 2014). Given that jaguars (*Panthera onca*) and pumas (*Puma concolor*) are the largest carnivores in Central America, they are useful focal species to evaluate the effects of ecological disturbances (Crooks, 2002).

For Neotropical felids and their prey, Panamá is the only corridor for maintaining gene flow between North and South America. Further, Panamá is part of Mesoamerica, which is considered a “megadiversity hotspot” and is recognized as one of the world’s most biologically-diverse regions, supporting high levels of biodiversity and endemism (Asociación Nacional para la Conservación de la Naturaleza [ANCON], 2010; Chocó-Manabí Conservation Corridor: Colombia and Ecuador Critical Ecosystem Partnership Fund CEPF, 2005; Myers et al., 2000). However, regions of Panamá, and in particular the Azuero Peninsula, have been dramatically altered due to habitat loss and fragmentation and would likely be insufficient to provide connectivity for large mammals throughout their range (Meyer et al., 2019). Currently, jaguars are classified as Endangered in Panamá (Ministerio de Ambiente de Panamá (MINAM, 2016) with a critically endangered subpopulation in Central Panamá (De la Torre et al., 2017), while pumas are listed as Vulnerable in Panamá (MINAM, 2016). Further, the persistence of viable populations of large felids is dependent on prey availability, in particular ungulates, in tropical rainforests (Weckel et al., 2006). White-lipped peccaries (*Tayassu pecari*) and collared peccaries (*Pecari tajacu*) are important food sources for predators such as jaguars and pumas (Altrichter et al., 2012; Moreno, 2006) and also for rural people (Gottdenker & Bodmer, 1998). In Panamá, collared peccaries are listed as Vulnerable while white-lipped peccaries are listed as Endangered (MINAM, 2016) as their populations have been reduced significantly due to habitat destruction and poaching (International Union for Conservation of Nature IUCN, 2016; Reyna-Hurtado et al., 2017). However, white-lipped

peccaries experience a more substantial decline regionally and locally than collared-peccary due to loss of suitable habitats and anthropogenic disturbance (Thornton et al., 2020). Recent cases of local extirpations of white-lipped peccaries have been documented in Panamá, even in large, contiguous protected areas (Moreno & Meyer, 2014; Reyna-Hurtado et al., 2017).

Given that large mammal research in Panamá has occurred extensively along the main Central Cordillera (e.g., Donoso, 2009; Meyer et al., 2015, 2016; Moreno, 2006; Springer et al., 2012), knowledge on felids and their prey in the Azuero Peninsula, specifically at Cerro Hoya National Park (CHNP), was limited to only a few studies (Fort et al., 2014, 2018). Due to the presence of various wildlife species including the four felid species (jaguars, pumas, ocelots [*Leopardus pardalis*], and margays [*Leopardus wiedii*]) at CHNP (Fort et al., 2014), the protected area could serve as a valuable wildlife habitat (Nielsen & Fort, 2020). In this study, we aimed to estimate habitat use of large felid (i.e., jaguars and pumas) and two peccary species (i.e., white-lipped peccaries and collared peccaries) at two protected areas: CHNP, an isolated forest patch and Darién National Park (DNP), a large contiguous forest habitat, using occupancy modeling framework. Our goals were to 1) emphasize the importance of conserving a small, isolated habitat in the Azuero Peninsula and 2) assess habitat use of focal species in habitats with different surrounding land use and degree of isolation. Occupancy modeling has proven a useful approach to determine habitat use, which in turn aids in developing management plans and prioritizing areas of conservation concern (e.g., Anile et al., 2020; Long et al., 2010; Peterman et al., 2013). Identifying isolated populations of species of conservation concern can also justify support for existing protected areas. In addition, evaluating habitat use of felids and prey in isolated and continuous habitats may provide insight into the effects of habitat fragmentation and human disturbance.

Hypotheses and Predictions

We developed several hypotheses based on prior studies of focal species in Neotropical habitats. We expected

- (1) We expected higher levels of human disturbance would result in lower habitat use of large felids, particularly jaguars and white-lipped peccaries, as they are sensitive to anthropogenic disturbance (Cullen et al., 2000; Foster, 2008; Keuroghlian et al., 2004; Peres, 1996). However, habitat use of collared peccaries was expected to be higher near human settlement due to a high tolerance of anthropogenic

disturbance (Mandujano & Reyna-Hurtado, 2019; Thornton et al., 2020).

- (2) Jaguars are known to utilize habitats closer to water in many areas (e.g., De la Torre et al., 2017; Figel et al., 2019; Nowell and Jackson, 1996; Sollmann et al., 2012). Hence, we hypothesized jaguars to occupy habitat close to water and pumas would be more likely to occupy habitat farther from water than jaguars to potentially avoid competition.
- (3) We expected site occupancy of large felids to increase as elevation increased because the most prominent animal trails and travel corridors were located at higher-altitude ridgelines (Harmsen et al., 2009; Harmsen et al., 2010; Sollmann et al., 2012). In addition, habitats at lower elevation are often used for anthropogenic activities and livestock (Guerisoli et al., 2020).

Methods

Study Sites

Cerro Hoya National Park (325 km²) is an isolated remnant of tropical rainforest habitat, situated in the Azuero Peninsula between Veraguas and Los Santos provinces (Figure 1). It was designated a national park in 1984 but contains no roads or entrances and has remained largely undeveloped for tourism purposes. There were approximately 25 villages inside the park, and within those villages live approximately 2,000 inhabitants who are dependent upon cattle ranching and crop production (Autoridad Nacional del Ambiente ANAM, 2004).

Elevation ranges from sea level to 1,559 m with 80% of the park above 300 m. Vegetation ranges from lowland to montane rainforest dominated by *Euphorbiaceae*, *Annonaceae*, *Melastomataceae*, *Fabaceae* and *Theaceae*.

Bordering the Republic of Colombia, Darién National Park (Figure 1) is the largest national park (5,970 km²) in Central America and designated as a United Nations Educational, Scientific and Cultural Organization (UNESCO) world heritage site and biosphere reserve (UNESCO, 2015). It is characterized by a large tract of continuous rainforest habitat inhabited by indigenous communities and cattle farmers (Herlihy, 2003). Activities such as agricultural practices, cattle ranching, logging, and fishing occur in the park (ANCON, 2010; Hruska et al., 2016). We worked in the Serranía de Pirre (151 km²), an area within DNP covered by similar humid tropical lowland forest, cloud forest, and premontane rainforest as CHNP and with elevation ranging from 70–1,500 m.

Camera Trap Surveys

We used unbaited camera traps (Cuddeback remote cameras Model: Cuddeback Capture, Cuddeback Attack,

Cuddeback Attack IR, Cuddeback Black Flash E3, and Cuddeback Ambush Black Flash; Non-Typical, Inc., Park Falls, WI) in both CHNP and DNP during January–July 2014 and 2015. Due to homogeneity of forest cover of study areas, camera stations were located predominantly within areas of primary and mature secondary forest. Cameras were placed along animal trails due to a high density of forest vegetation off-trail and limited field of sight for camera traps, but also because our surveys were tailored to jaguar density estimation and wild cats tend to use trails (Harmsen et al., 2010). One or two cameras were placed 2–3 m apart at each station and strapped to trees or stakes 30–50 cm above ground. Cameras were active 24 hr/day with a 5-sec delay between photographs. All photos of the same species captured within a 24-hr period were counted as one detection and detection frequencies were calculated as the number of independent detections/100 camera nights. Camera station placement was originally designed as a systematic grid with randomized points within grid blocks. However, some areas within CHNP and DNP were inaccessible due to cliff edges and steep slopes, precluding access to several randomized camera station locations. Therefore, cameras were placed opportunistically but stratified among all elevation gradients. Due to limited camera availability and to thoroughly cover the study areas, we divided each sampling period (2014 and 2015) into two or three separate but adjacent sampling grids of ≤ 50 km² (Maffei et al., 2011). In CHNP, 21 camera stations were established in 2014 across three separate grids (seven, six, and eight camera stations) and 35 camera stations were established in 2015 across two grids (25 and 10 camera stations). In DNP, 40 camera stations were established in 2014 across two grids (35 and eight camera stations) and four camera stations were established in 2015 within one grid. At both study areas, camera stations that were established in 2015 were different from the camera stations in 2014. In total, 56 camera stations were set up in CHNP and 47 camera stations in DNP, for a total of 103 camera stations across both study areas (Table 1). Cameras were deployed on each grid for 30–75 days. We only used data up to a 50-day period in our analysis to meet the assumption of population closure (MacKenzie et al., 2006). Camera spacing for large mammal studies is usually large (> 1 km) to reduce the influence of spatial autocorrelation (e.g., Sollmann et al., 2012; Thornton et al., 2020); however, a wide range of camera spacings have been used (Meyer et al., 2015). Camera spacing might be small due to logistical constraints and site accessibility (Anile et al., 2020). In our study, placement of camera stations was largely constrained by accessibility and strenuous terrain, and therefore, the distances between camera stations were 0.2–3.5 km. However, because felids have a large home range size, we only used data from 94 camera stations which were at least 800 m apart to avoid spatial autocorrelation

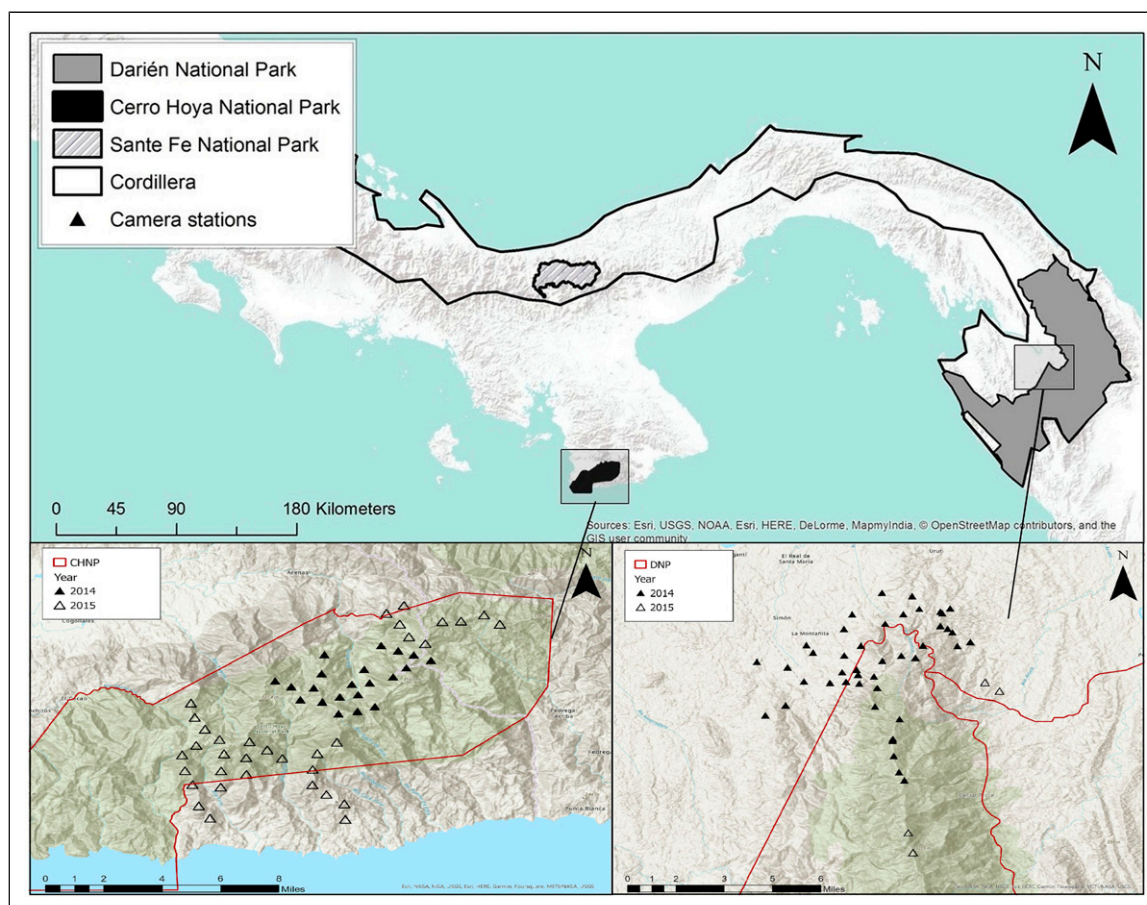


Figure 1. Camera Stations in Cerro Hoya National Park (below left) and Darién National Park (below right), Panamá, During February–May 2014–2015; the Cordillera, Darién National Park, and Santa Fé National Park (top) are included for reference.

Table 1. Camera Stations, Naïve Habitat Use (% of Camera Stations with Detections of a Certain Species), and Detection Rate (% of Number of Photos Taken with the Presence of a Certain Species) of Focal Species During January–July 2014–2015 in Cerro Hoya National Park (CHNP) and Darién National Park (DNP), Panamá.

Species	Common name	CHNP			DNP		
		No. of camera stations	Naïve occupancy	Detection rate (total sampling occasions)	No. of camera stations	Naïve occupancy	Detection rate (total sampling occasions)
Felids							
<i>Panthera onca</i>	Jaguar	56	14.3%	3.5% (280)	38	34.2%	10.5% (190)
<i>Puma concolor</i>	Puma	56	23.2%	5.7% (280)	38	50%	13.7% (190)
Prey							
<i>Pecari tajacu</i>	Collared peccary	56	80.4%	35% (280)	47	36.2%	11.5% (235)
<i>Tayassu pecari</i>	White-lipped peccary	56	0%	0% (280)	47	23.4%	7.7% (235)

(Table 1). Although we recognized a relatively large home range of white-lipped peccaries, we decided to include data from all camera stations due to sparse detection of the species. The effect of spatial autocorrelation was assumed to be minimal in our study because camera traps were not

baited, which would reduce the possibility of the same individuals being attracted to nearby camera stations within the same area. Since we identified no individual in consecutive camera stations during the same day, we assumed this was appropriate for our analysis.

Habitat Use Modeling

Opportunistic placement of camera stations may have confounded our interpretations of occupancy within the study areas. The non-consistent camera spacing could allow movement of individuals to exceed a camera station boundary and change the occupancy state at the station, hence, leading to violation of closed population assumption (Efford & Dawson, 2012; Mackenzie & Bailey, 2004). Therefore, we suggest our results of occupancy be interpreted as “habitat use” at camera stations rather than occupancy within the given study areas (MacKenzie & Royle, 2005; MacKenzie et al., 2006). In addition, when interpreting our results, the relative habitat use probabilities among focal species should not be compared because of differences in their movements and home range sizes.

We used the single-season, single-species modeling framework with package ‘unmarked’ (v1.0.1, Fiske & Chandler 2011) in Program R (v3.0.2; R Core Team, 2013) to estimate probabilities of detection (p) and habitat use (ψ) for our four focal species at all camera stations on both study areas (MacKenzie et al., 2002). Collared peccary and white-lipped peccary were chosen as focal prey species based on their importance in felid diets and conservation status (Altrichter et al., 2012; MINAM, 2016; Moreno, 2006). Models were run separately for each study area using the data from both 2014 and 2015. For white-lipped peccaries, we used data collected from 47 stations because the species was only detected in DNP (Table 1). We divided the 50-day sampling period into five 10-day sampling occasions (O’Connell et al., 2002; Sarmiento et al., 2010) to build a series of detection histories, with the exception of 13 camera stations having only four 10-day sampling occasions due to camera failure. We used the logit-link function to estimate ψ and p as functions of sampling period- and/or camera station-specific covariates. We used the secondary candidate set approach to conduct model selection to improve estimation of importance of covariates, recover total Akaike model weights, and identify top models as suggested by Morin et al. (2020). Specifically, we fit all possible combinations of detection covariates while holding habitat use constant [ψ (.)] and fit all possible combinations of habitat use covariates while holding detection constant [p (.)]. Due to relatively small sample sizes in our study, lack of convergence would occur in models that were overparameterized; to avoid this, we constructed models with two or less parameters for within-stage models. Models that did not converge or produced inestimable parameters (i.e., an extremely large or negative standard error) were removed from model sets prior to selection (e.g., Burns et al., 2019). Models that were $\Delta AICc \leq 5$ from the top model and did not contain uninformative parameters advanced to the final model selection step (Arnold, 2010; Morin et al., 2020).

For the final model selection step, we constructed all possible combinations models using the sub-model sets

selected during within-stage model selection step. We used the Mackenzie-Bailey goodness-of-fit test on the most parameterized model or model with the highest weight when multiple models contained the same number of parameters to assess the possibility of overdispersion and model fit (MacKenzie & Bailey, 2004). If the model failed the goodness-of-fit test ($P < 0.05$), we removed the model from consideration and selected the next parameterized model. When $\hat{c} > 1$, we accounted for overdispersion and performed model selection based on the quasi-likelihood version of the $AICc$ value ($QAICc$). Otherwise, the best fit model was selected based on $AICc$ values (MacKenzie et al., 2006). If there were more than one plausible model ($\Delta AICc < 2$), we performed model averaging among competing models to derive predicted habitat use estimates.

Environmental Variables

Detection. We tested the effect of five variables (temporal, environmental, and survey design factors) on detection (Table A1). We used (1) Julian date (Julian), considering 1 January as day 1 and 31 December as day 365, to represent seasonal changes based on day of the year during the study period. We included (2) whether the species of interest had been detected at the camera station in the previous sampling period (Response; 0/1) to account for temporal autocorrelation of detection (e.g., Naidoo and Burton, 2020), and (3) camera type (CamModel; i.e., black flash/flash/combination). Due to the lack of variation in camera types at DNP, this variable was not included in any models at this study site. Camera failure due to technical issues (i.e., battery life), climate (i.e., heavy rains and humidity) and blockages to sensors (i.e., fallen trees) can negatively bias estimates (Foster, 2008; Swann et al., 2011). Therefore, we recorded (4) the total number of functioning camera-days per sampling period (CamDays; 0–20, depending on whether one or two cameras were used at each station). Changes in photographic rates over time could also result from factors unrelated to those mentioned above. Therefore, we incorporated (5) year of survey (Year) as a covariate potentially affecting detection. Prior to modeling, we standardized all continuous variables to z-scores and predicted the direction of effects of the covariates on detection (Table A1).

Habitat Use

We used digitized land cover maps of both CHNP and DNP study areas provided by the Smithsonian Tropical Research Institute GIS Database (<http://www.stri.si.edu/>) and ArcGIS 10.3 (ESRI, Redlands, California, USA) to calculate seven habitat covariates to model habitat use (Table A1). We measured (1) distance from each camera station to the nearest river (DTRV) and (2) distance to the nearest tributary (DTTB). We included these as separate covariates because of the differences in canopy cover (river systems being more open)

and the potential for river systems to act as travel corridors in addition to other water sources. We also calculated (3) distance to forest edge (DFE; i.e., forest edge created by the clearing of mature forest for logging, cattle pasture, or agriculture), (4) distance to the nearest human settlement (active communities with more than three houses; DTHS), and (5) elevation (EVA). The number of houses that were considered as human settlement was chosen because we noticed that when there were more than three houses, it indicated an active community. However, when there were less than three houses, it was usually a homestead or a cabin that was infrequently visited. To assess potential competition and predator-prey relationships, we additionally included (6) observed detection frequencies of predator species (jaguars and pumas) as one of the parameters in prey (collared and white-lipped peccaries) habitat use models. We further included (7) the detection frequency of collared peccaries in the white-lipped peccary models, and vice versa, to assess a potential effect of interspecific competition on habitat use between the two species. Due to the placement of camera traps, areas surrounding each camera station were generally within the primary forest; therefore, we did not include proportional land cover variables in our analysis. We used a Pearson correlation matrix to identify correlated variables, and any variables with $r = |0.6|$ were not included in the same model. At DNP, we found EVA, DFE, and DTHS to be correlated ($r > 0.6$); therefore, these parameters were not modeled together. Prior to modeling, we standardized all continuous variables to z-scores and predicted the direction of effects of the covariates on habitat use based on the literature (Table A1).

Results

Survey effort for CHNP (152 km²) was 1519 (57 km²) and 2538 (95 km²) camera-days in 2014 and 2015, respectively. Survey effort for DNP (151 km²) was 3361 (138 km²) and 400 (13 km²) camera-days in 2014 and 2015, respectively. Three of the four focal species were detected (all but white-lipped peccaries at CHNP) in both study areas. Naïve habitat use (% of camera stations with detections of a certain species) and detection (% of number of photos taken with the presence of a certain species) were higher for all species, except for collared peccaries, at DNP than at CHNP (Table 1). At CHNP, collared peccaries were detected most frequently, followed by pumas and jaguars, respectively (Table 1). At DNP, collared peccaries were detected most frequently, followed by white-lipped peccaries, pumas, and jaguars, respectively (Table 1).

Detection

Factors affecting detection probabilities of each species apparently differed between the two study sites (Table 2). At CHNP, detection probability of collared peccaries was higher in 2015 (0.53; 95% CI = 0.41–0.64) than 2014 (0.37; 95% CI

= 0.13–0.68). Among camera types, detection probability of collared peccaries was the higher for the black flash camera model (0.53; 95% CI = 0.41–0.68) than flash (0.49; 95% CI = 0.38–0.60) and combination (0.41; 95% CI = 0.18–0.68). Detection of pumas at CHNP was higher in 2015 (0.07; 95% CI = 0.02–0.18) than 2014 (0.03; 95% CI = 0.004–0.13) and the detection of pumas was the highest in April (Figure 2; Table 3). The number of functioning camera-days positively affected detection of jaguars at CHNP (Figure 3).

At DNP, detection of collared peccaries was the highest in May (Table 3; Figure 4), and we also found evidence of a temporal correlation effect on their detection. Among the top models, the detection probability was negatively correlated with Julian date for white-lipped peccaries (Table 2), by which the highest detection probability was in February, and the number of functioning camera-days positively affected detection of white-lipped peccaries (Figure 5; Table 3). We also found evidence of a temporal correlation effect on the detection of white-lipped peccaries (Table 2). For jaguars, detection was the highest in February (Figure 6; Table 3). However, detection of pumas at DNP was constant across the study area and unaffected by any covariates measured (Tables 2 and 3).

Habitat Use

At CHNP, habitat use of collared peccaries was constant across the study area and unaffected by any covariates measured (Table 2). Jaguars used habitat at relatively higher elevations (Figure 7; Tables 2 and 3). Estimations of habitat characteristics that influenced puma habitat use at CHNP resulted in large confidence intervals (0–1) due to small sample size (Table 3); therefore, we regarded the habitat use model of the species to be inconclusive.

At DNP, habitat use of collared peccaries and white-lipped peccaries was constant across the study area and unaffected by any covariates measured (Table 2). Pumas used habitat closer to rivers (Figure 8; Tables 2 and 3), while jaguars used habitat at a higher elevation and farther from human settlement (Figure 9; Tables 2 and 3).

Discussion

Anthropogenic disturbance and habitat fragmentation lead to a decrease in suitable habitats and an increase in human-wildlife conflict, negatively affecting the persistence of many mammal species (e.g., Crooks et al., 2017; Guerisoli et al., 2020). Our study represents the first study to assess factors that influenced habitat use and detection of felids and peccaries at CHNP, an isolated remnant of rainforest habitat, in comparison with habitat use of the focal species at DNP, a continuous rainforest habitat. Factors affecting habitat use differed between CHNP and DNP and among species. Although human settlements and anthropogenic activities influenced habitat use, species responded differently to these

Table 2. Top-ranked Model Results ($\Delta AIC_c \leq 2$) for Focal Species During February–May 2014–2015 in Cerro Hoya National Park (CHNP) and Darién National Park (DNP), Panamá. Variable acronyms are defined in Table A1.

Site	Species		K ^a	QAIC _c /AIC _c ^b	$\Delta QAIC_c/\Delta AIC_c$ ^c	w ^d	Log(L) ^e
	Model name						
CHNP	Jaguar						
	$p(\text{CamDays}) \psi(.)$		3	86.99	0	0.3	−40.26
	$p(.) \psi(\text{EVA})$		3	87.37	0.39	0.24	−40.46
	$p(.) \psi(.)$		2	87.46	0.47	0.23	−41.62
	$p(\text{CamDays}) \psi(\text{EVA})$		4	87.5	0.51	0.23	−39.36
	Puma						
	$p(\text{Year}+\text{Julian}) \psi(\text{DTHS})$		5	111.77	0	0.28	−50.28
	$p(\text{Year}+\text{Julian}) \psi(\text{DFE})$		5	112.34	0.57	0.21	−50.57
	$p(\text{Year}+\text{Julian}) \psi(.)$		4	112.63	0.87	0.18	−51.92
	$p(\text{Julian}) \psi(\text{EVA})$		4	113.17	1.41	0.14	−52.19
	$p(\text{Julian}) \psi(.)$		3	113.65	1.88	0.11	−53.59
	$p(\text{Julian}) \psi(\text{DTHS})$		4	115.29	3.52	0.05	−53.25
	$p(\text{Julian}) \psi(\text{DFE})$		4	115.78	4.02	0.04	−53.5
	Collared peccary (QAIC)						
$p(\text{Year}) \psi(.)$		4	328.02	0	0.64	−159.62	
$p(\text{CamModel}) \psi(.)$		5	329.15	1.14	0.36	−158.98	
DNP	Jaguar						
	$p(\text{Julian}) \psi(\text{DTHS})$		4	114.02	0	0.41	−52.4
	$p(\text{Julian}) \psi(\text{EVA})$		4	115.57	1.55	0.19	−53.18
	$p(\text{Julian}) \psi(\text{DFE})$		4	116.18	2.16	0.14	−53.48
	$p(.) \psi(\text{EVA})$		3	117.61	3.59	0.07	−55.45
	Puma						
	$p(.) \psi(\text{DTRV})$		3	154.15	0	0.69	−73.72
	$p(.) \psi(.)$		2	155.79	1.65	0.31	−75.72
	Collared peccary (QAIC) (c-hat=1.07)						
	$p(\text{Julian}+\text{Response}) \psi(.)$		5	146.05	0	0.52	−67.29
	$p(\text{Julian}) \psi(.)$		4	146.2	0.15	0.48	−68.62
	White-lipped peccary (QAIC) (c-hat=1.81)						
	$p(.) \psi(.)$		3	70.7	0	0.27	−31.97
	$p(\text{CamDays}) \psi(.)$		4	71.09	0.59	0.2	−31.07
	$p(\text{Response}) \psi(.)$		4	71.12	0.62	0.2	−31.08
	$p(\text{Julian}) \psi(.)$		4	71.36	0.86	0.18	−31.21
	$p(.) \psi(\text{DTTB}+\text{JaguarDetFreq})$		5	72.8	2.3	0.09	−30.67
$p(\text{Julian}) \psi(\text{DTTB}+\text{JaguarDetFreq})$		6	75.02	4.52	0.03	−30.46	
$p(\text{CamDays}) \psi(\text{DTTB}+\text{JaguarDetFreq})$		6	75.12	4.62	0.03	−30.51	

^aNumber of model parameters.^bAIC_c = Akaike Information Criterion adjusted for small samples.^c ΔAIC_c = difference in current model from the top model.^dModel weight, interpreted as the relative model likelihood.^eLog(Likelihood), interpreted as a measure of model fit.

factors, depending on resource partitioning and tolerance to anthropogenic activities (e.g., Figel et al., 2021; Thompson et al., 2020).

Due to the elusiveness of the species studied, detection rates were low. We recognize small sample sizes may have resulted in large confidence intervals and lack of significance for some variables (i.e., habitat covariates did not affect peccary habitat use). This could pose a bias in habitat use estimations and interpretation of the results. However, our

results have important implications for mammal conservation in Panamá. Moreover, our study could serve as a baseline study for future camera trap studies at CHNP and DNP.

Detection

All focal species were detected at both sites, except for white-lipped peccaries which were detected only at DNP. In addition, more detections were observed for felid species and

white-lipped peccaries at DNP than CHNP. Given local density of a given species affects its detection probability (Bailey et al., 2004; Lopez & Pfister, 2001; Royle & Nichols, 2003), higher detection of felids and white-lipped peccaries in DNP are likely partly explained by more abundant populations there than in CHNP. Higher abundances of wildlife are possible in DNP because it supports a large contiguous habitat (Kinnaird et al., 2003; Meyer et al., 2019). In contrast, little forest remains between the fragmented forests north of CHNP and the Cordillera, which are separated by approximately 125 km, the Pan-American Highway, and numerous developed areas.

Factors affecting detection probabilities differed between the two study sites for each species, although time of surveys (Julian date and year) appeared to influence detection of most focal species. At DNP, jaguar detection was lower at the start of the rainy season in May, likely due to seasonal changes in movements (Crawshaw & Quigley, 1991; Foster, 2008; Núñez et al., 2002; Scognamillo et al., 2003). Although some studies indicate jaguars reduce home range size and travel less in the wet season due to flooding (Cavalcanti & Gese, 2009; Crawshaw & Quigley, 1991), montane rainforest in Panamá does not flood and thus seasonal differences in movement patterns of jaguars in DNP may be influenced by another variable, such as prey availability (Weckel et al., 2006).

As for pumas at CHNP, given Craighead (2019) found pumas utilized habitat dominated by agricultural land and livestock during the wet season, our observation in puma detection at CHNP closer to the wet season may have been a pursuit of prey. However, pumas are flexible in exploiting available resources in both wet and dry seasons; therefore, an increase in puma detection at CHNP near the wet season could coincide with habitat preferences and toleration of anthropogenic disturbance, rather than changes in temporal use of a habitat (Craighead et al., 2022). In contrast to pumas, jaguar detection at CHNP was not influenced by time of surveys. We speculated that detection of jaguars at CHNP could be due to the presence of preferred habitat features and resources, such as the presence of wetlands and prey species (e.g., Figel et al., 2021; Weckel et al., 2006) rather than changes in seasonality. In addition, felids have a large home range size and disperse long distances (Gonzalez-Borrajó et al., 2016; Thompson et al., 2020), which could affect our ability to detect the species. However, jaguar detection was higher when survey effort (CamDays) increased, providing support for the need for intensive surveys due to the rarity of jaguars at CHNP.

Collared peccary detection was influenced by camera model (i.e., flash type) and year at CHNP and Julian date at DNP. We also found the black flash camera model to obtain more detections of collared peccary at CHNP than the flash model. Flash types (i.e., traditional white flash, infrared, and black flash) could affect detection and influence fleeing response of species (Cove & Jackson, 2011; Henrich et al.,

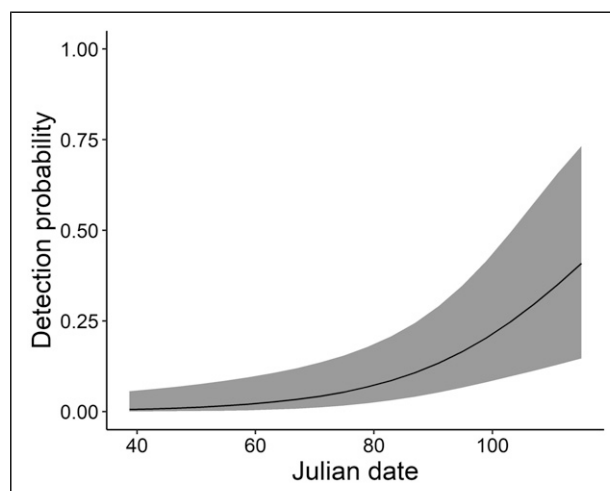


Figure 2. Effect of Julian Date with 95% Confidence Intervals (shaded areas) on Puma Detection in Cerro Hoya National Park, Panamá, During February–May, 2014–2015. Julian date reflected the survey period given that 1 January was day 1; the survey period occurred between February and May, which represented the seasonal change from the dry season (December–May) to the beginning of rainy season (June–November).

2020; Taggart et al., 2019). Camera models such as infrared and black flash may yield a higher detection rate in some species such as bobcats (*Lynx rufus*; Cove & Jackson, 2011; Herrera et al., 2021). An increase in detection between years could be due to spatial differences in collared peccary movements where camera grids were located. With the decline of white-lipped peccary populations in most regions of Panamá (Moreno & Meyer, 2014; Reyna-Hurtado et al., 2017), collared peccaries may be experiencing the positive effects of the localized extirpation of a competitor. For example, some documentation exists of collared peccaries avoiding the larger-bodied white-lipped peccaries (Keuroghlian et al., 2004). In addition, collared peccary detection increased from February to May and was highest at the onset of the rainy season at DNP. In tropical environments, collared peccary home range sizes and movements are positively correlated with fruit productivity, with wider distributions during the wet season (Judas & Henry, 1999; Mendes Pontes & Chivers, 2007).

White-lipped peccaries were not detected in CHNP during this study or in our pilot study (Fort et al., 2014). However, at DNP, white-lipped peccary detection was influenced by Julian date and the number of functioning camera-days. We found the detection of white-lipped peccaries was higher in the dry season (December–May) and slightly decreased toward the wet season. Although seasonal home ranges of white-lipped peccaries were not significantly different at DNP, animals may move more during the dry season to search for fruit during low-productivity periods (Meyer, Moreno, Martínez-Morales, and Reyna-Hurtado, 2019). In addition, due to a large home range size of white-lipped peccaries

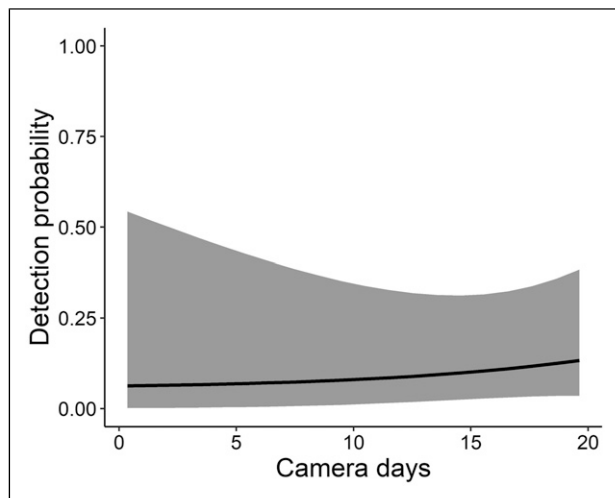
Table 3. Model-averaged Estimates, SEs, and 95% Confidence Interval for All Predictors on Habitat Use Probability (ψ) and Detection Probability (p) for Focal Species During February–May 2014–2015 in Cerro Hoya National Park (CHNP) and Darién National Park (DNP), Panamá. All values are shown based on logit scale and variable acronyms are defined in Table A1. The dash symbol indicates covariates not included among the top-ranked models in the final selection step; NA indicates parameters that were not included in the within-stage modeling steps.

Species	Parameter	CHNP				DNP				
		Estimate	SE	95% confidence interval		Estimate	SE	95% confidence interval		
				Lower	Upper			Lower	Upper	
Jaguar	ψ	Intercept	-0.73	0.89	-2.48	1.00	-0.14	0.63	-1.38	1.10
		EVA	0.37	0.56	-0.40	1.94	0.55	0.92	0.16	3.31
		DTRV	–	–	–	–	–	–	–	–
		DTTB	–	–	–	–	–	–	–	–
		DFE	–	–	–	–	–	–	–	–
	p	DTHS	–	–	–	–	1.36	1.16	0.31	3.65
		Intercept	-2.18	0.71	-3.58	-0.78	-1.24	0.35	-1.92	-0.55
		Year (2015)	–	–	–	–	–	–	–	–
		Julian	–	–	–	–	-0.7948	0.3471	-1.4750223	0.1145574
		CamDays	0.37	0.50	-0.25	1.66	–	–	–	–
Puma	ψ	CamModel	–	–	–	–	NA	NA	NA	NA
		Response	–	–	–	–	–	–	–	–
		Intercept	2.97	3.66	-4.20	10.14	1.94	1.80	-1.59	5.48
		EVA	-0.74	2.46	-13.59	3.81	–	–	–	–
		DTRV	–	–	–	–	-1.11	1.12	-3.57	0.39
	p	DTTB	–	–	–	–	–	–	–	–
		DFE	1.25	3.10	-3.05	14.01	–	–	–	–
		DTHS	1.21	2.36	-1.30	9.24	–	–	–	–
		Intercept	-3.73	0.91	-5.52	-1.95	-1.61	0.32	-2.23	-0.99
		Year (2015)	1.09	0.09	0.07	2.92	–	–	–	–
Collared-peccary	ψ	Julian	1.26	0.41	0.45	2.07	–	–	–	–
		CamDays	–	–	–	–	–	–	–	–
		CamModel	–	–	–	–	NA	NA	NA	NA
		Response	–	–	–	–	–	–	–	–
		Intercept	2.05	0.55	0.98	3.12	1.18	1.93	-2.61	4.97
	p	EVA	–	–	–	–	–	–	–	–
		DTRV	–	–	–	–	–	–	–	–
		DTTB	–	–	–	–	–	–	–	–
		DFE	–	–	–	–	–	–	–	–
		DTHS	–	–	–	–	–	–	–	–
White-lipped peccary	ψ	JaguarDetFreq	–	–	–	–	–	–	–	–
		PumaDetFreq	–	–	–	–	–	–	–	–
		White-lipped peccaryDetFreq	NA	NA	NA	NA	–	–	–	–
		Intercept	-0.58	0.69	-1.93	0.77	-2.00	0.55	-3.07	-0.93
		Year (2015)	0.68	0.59	0.49	1.71	–	–	–	–
	p	Julian	–	–	–	–	0.73	0.24	0.28	1.20
		CamDays	–	–	–	–	–	–	–	–
		CamModel (Flash)	-0.16	0.30	-1.12	0.29	–	–	–	–
		CamModel (Combination)	-0.50	0.68	-2.04	-0.60	NA	NA	NA	NA
		Response	–	–	–	–	0.70	0.86	-0.29	2.80
White-lipped peccary	ψ	Intercept	NA	NA	NA	NA	-0.59	0.94	-2.43	1.26
		EVA	NA	NA	NA	NA	–	–	–	–
		DTRV	NA	NA	NA	NA	–	–	–	–
		DTTB	NA	NA	NA	NA	–	–	–	–

(continued)

Table 3. (continued)

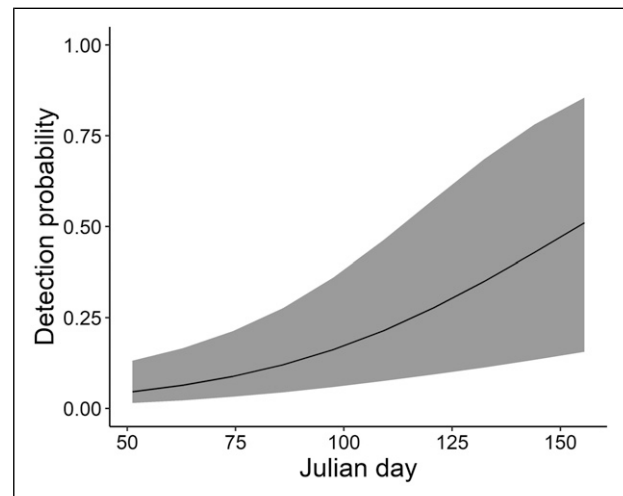
Species	Parameter	CHNP				DNP			
		Estimate	SE	95% confidence interval		Estimate	SE	95% confidence interval	
				Lower	Upper			Lower	Upper
	DFE	NA	NA	NA	NA	–	–	–	–
	DTHS	NA	NA	NA	NA	–	–	–	–
	JaguarDetFreq	NA	NA	NA	NA	–	–	–	–
	PumaDetFreq	NA	NA	NA	NA	–	–	–	–
	Collared-peccaryDetFreq	NA	NA	NA	NA	–	–	–	–
p	Intercept	NA	NA	NA	NA	–1.31	0.77	–2.83	0.20
	Year (2015)	NA	NA	NA	NA	–	–	–	–
	Julian	NA	NA	NA	NA	–0.13	0.29	–1.26	0.12
	CamDays	NA	NA	NA	NA	0.18	0.33	–0.05	1.25
	CamModel	NA	NA	NA	NA	NA	NA	NA	NA
	Response	NA	NA	NA	NA	0.48	0.94	–0.45	3.73

**Figure 3.** Effect of Functioning Camera-days with 95% Confidence Intervals (shaded areas) on Jaguar Detection in Cerro Hoya National Park, Panamá, During February–May, 2014–2015.

(Meyer, Moreno, Martínez-Morales, and Reyna-Hurtado, 2019), an increase in survey effort (CamDays) increased the chance of detecting the species.

Habitat Use

Our prediction that anthropogenic disturbance would negatively affect jaguars more than pumas was supported at DNP, with jaguar habitat use lower near human settlement. Our results follow previous studies that showed a tendency for jaguars to use extensive forest cover and avoid open pasture and human settlement (Craighead et al., 2022; Cullen et al., 2005; Schaller & Crawshaw, 1980; Figel et al., 2021). Even though we did not observe the effect of anthropogenic

**Figure 4.** Effect of Julian Date with 95% Confidence Intervals (shaded areas) on Collared Peccary Detection in Darién National Park, Panamá, During February–May, 2014–2015. Julian date reflected the survey period given that 1 January was day 1; the survey period occurred between February and May, which represented the seasonal change from the dry season (December–May) to the beginning of rainy season (June–November).

disturbance on puma habitat use in our study, pumas tend to use open habitats to a greater extent than jaguars, including croplands and pastures, and are more tolerant to human activities (Craighead et al., 2022; Figel et al., 2021; Foster, 2008; Scognamiglio et al., 2003).

Our prediction that both felid species would respond positively to elevation was only partially supported; elevation influenced habitat use of jaguars at both CHNP and DNP, where jaguars preferred habitat at higher elevation. Our findings corroborate those of Monroy-Vilchis et al. (2008) in that jaguars preferred higher elevations and areas farther

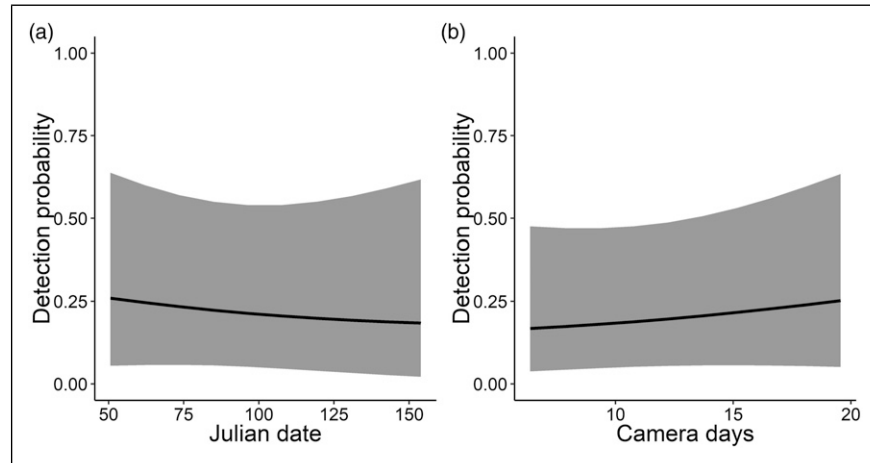


Figure 5. Effect of (a) Julian Date and (b) Functioning Camera-days with 95% Confidence Intervals (shaded areas) on White-lipped Peccary Detection in Darién National Park, Panamá, During February–May, 2014–2015. Julian date reflected the survey period given that 1 January was day 1; the survey period occurred between February and May, which represented the seasonal change from the dry season (December–May) to the beginning of rainy season (June–November).

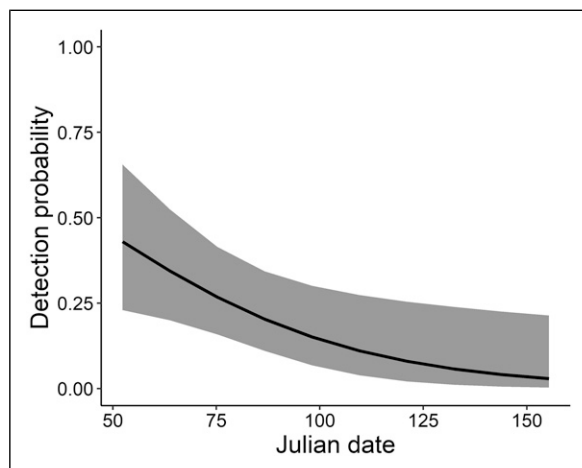


Figure 6. Effect of Julian Date with 95% Confidence Intervals (shaded areas) on Jaguar Detection in Darién National Park, Panamá, During February–May, 2014–2015. Julian date reflected the survey period given that 1 January was day 1; the survey period occurred between February and May, which represented the seasonal change from the dry season (December–May) to the beginning of rainy season (June–November).

away from cattle ranches and crop agriculture to avoid human activity and potential retaliation killing (Moreno et al., 2015). However, it is possible for jaguars to utilize areas at lower elevations when human activities are limited (Morato et al., 2014). Differences in jaguar and puma habitat use were most likely due to niche partitioning between species to avoid interspecific competition (Figel et al., 2021; Harmsen et al., 2009; Pierce et al., 1999; Scognamillo et al., 2003; Sollmann et al., 2012).

Our prediction that jaguars would use habitat closer to water than pumas could not be tested. Due to numerous

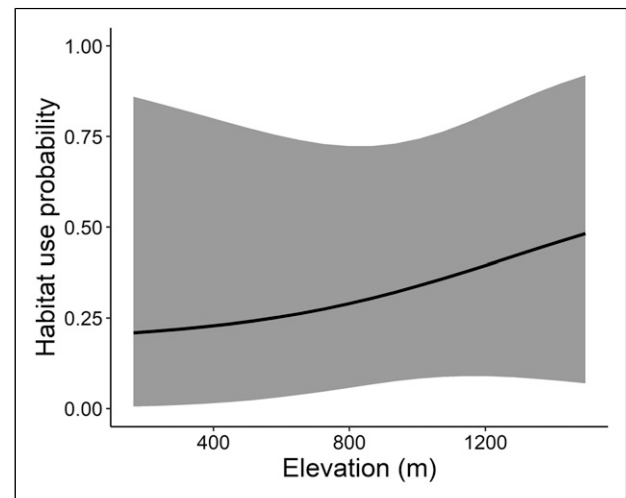


Figure 7. Effect of Elevation with 95% Confidence Intervals (shaded areas) on Jaguar Habitat Use in Cerro Hoya National Park, Panamá, During February–May, 2014–2015.

small riverways throughout the forests, it is possible that all small river channels were not included in the GIS layer, and therefore, our results may have been influenced by the inaccuracy of tributaries data obtained from the GIS database. However, we found pumas used habitat closer to rivers (i.e., the main channels) at DNP. Although jaguar habitat use has been associated with water in South America (Mondolfi & Hoogesteijn, 1986; Núñez et al., 2002; Sollmann et al., 2012), likely due to higher presence of prey such as capybaras (*Hydrochoerus* spp.) and caimans (*Caiman* spp.) (Crawshaw & Quigley, 1991; Emmons, 1987), Monroy-Vilchis et al. (2008) suggested human activity may displace large cats away from watercourses and towards higher elevations with steeper slopes. Given the likely more-dominant

jaguar (Harmsen et al., 2009; Sollmann et al., 2012; Sunquist & Sunquist, 2002) used these high-use and high-elevation ridgelines, pumas may have used lower-elevation water systems such as rivers to avoid interactions with jaguars. Furthermore, Boron et al. (2020) found differential use of water sources between species, as jaguar habitat use was associated with wetland habitat, while puma habitat use was higher near streams and ponds. In addition, our study was conducted during the dry season; as such, jaguars may have preyed on species not dependent on larger water sources (e.g., rivers and streams), given that brown-throated sloth (*Bradypus variegatus*) was among the most commonly found prey items in feces of jaguars in DNP (Moreno, 2006).

We found no habitat characteristics measured influenced habitat use of either peccary species at both study

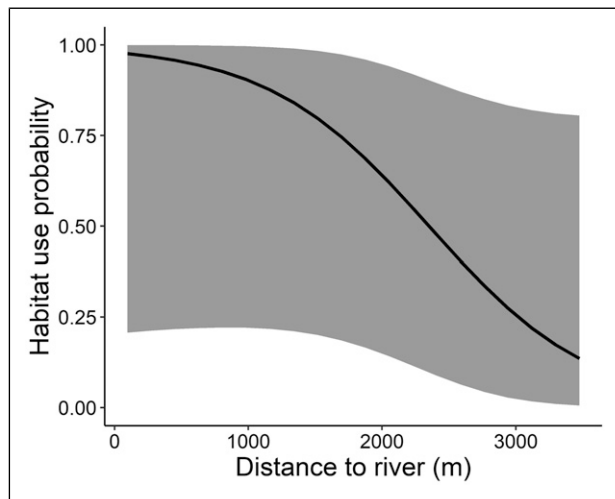


Figure 8. Effect of Distance to Nearest River System (m) with 95% Confidence Intervals (shaded areas) on Puma Habitat Use in Darién National Park, Panamá, During February–May, 2014–2015.

areas. However, anthropogenic activities are known to negatively affect habitat use of both peccary species, although collared peccaries can tolerate a higher degree of disturbance than white-lipped peccaries (Mandujano & Reyna-Hurtado, 2019; Tejada-Cruz et al., 2009). In addition, as a generalist species, habitat use of collared peccaries could be influenced by microhabitat characteristics (Mandujano & Reyna-Hurtado, 2019), which we did not measure. We did not detect white-lipped peccaries at CHNP, although the IUCN lists the species as “Probably Extant” in the Azuero Peninsula (IUCN, 2016). A report by Garcés (1999) is the only published confirmation of white-lipped peccaries in CHNP. Due to larger herd sizes and area requirements (Altrichter et al., 2012; Meyer, Moreno, Martínez-Morales, and Reyna-Hurtado, 2019; Reyna-Hurtado et al., 2017), white-lipped peccary populations are particularly susceptible to effects of human activity and land use (Peres, 1996), and consequently their range has declined drastically in the last few decades (Thornton et al., 2020). Recent studies confirm the extirpation of white-lipped peccaries in central Panamá surrounding the Panamá Canal (Meyer et al., 2015, 2016; Springer et al., 2012), and some populations remain only along the Atlantic coast (Moreno & Meyer, 2014). Moreover, interviews with local inhabitants during 2014–2015 (Fort et al., 2018) suggest the presence of a small herd and potentially the last remaining individuals in the park (J. Fort, unpublished data). Movements and home range of white-lipped peccary varied by season and available resources (Jorge et al., 2019). However, these changes were not significantly different in areas with available year-round water sources (Meyer, Moreno, Martínez-Morales, and Reyna-Hurtado, 2019). Although the absence of white-lipped peccary at CHNP may be due to temporal extirpation during the dry season when our study was conducted, this was unlikely given the absence of white-lipped peccaries observed in other local studies

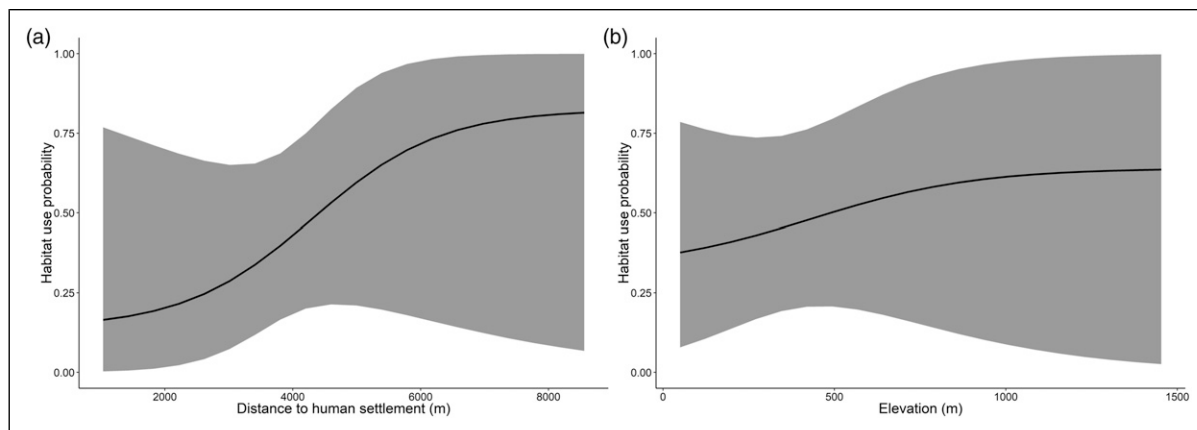


Figure 9. Effect of (a) Elevation and (b) Distance to Nearest Human Settlement (m) with 95% Confidence Intervals (shaded areas) on Jaguar Habitat Use in Darién National Park, Panamá, Panamá, During February–May, 2014–2015.

(Moreno & Meyer, 2014). However, future research with increased survey effort is needed to clarify the status of white-lipped peccaries at CHNP and the surrounding areas.

Implications for Conservation

Our study emphasized the influence of anthropogenic variables on habitat use of felids and peccaries, with the focus on CHNP and DNP. Given that Panamá represents the only land bridge allowing movement of animals between North and South Americas, conserving large tracts of forest, such as DNP, to provide connectivity and support for large-bodied mammals such as felids and peccaries is crucial for the persistence of mammal populations. Sanderson et al. (2002) characterized the tropical moist montane forests of the Choco-Darién, where DNP is located, to be of high habitat quality with high connectivity of Jaguar Conservation Units and frequent dispersal between stable jaguar populations.

We further confirmed jaguar presence in CHNP (Fort et al., 2014; Sanderson et al., 2002) and provide further evidence of the potential local extirpation of white-lipped peccaries in the southwest Azuero Peninsula, making CHNP an area of further conservation concern. The Azuero Peninsula was characterized as having low probability of long-term survival for jaguars given no habitat corridors remain between the fragmented forests north of CHNP and the Central Cordillera (Sanderson et al. 2002). An increase in fragmentation of CHNP could induce genetic and geographic isolation of its wildlife which could lead to reduced reproductive success (Frankham et al., 2002), smaller effective population sizes (Frankham, 1996; Soulé, 1976), and an increase in levels of genetic drift and inbreeding (Soulé & Mills, 1998), all of which can increase risk of local extinction (Frankham, 2005). However, in areas with high human disturbance, relatively small patches of habitat could provide a refuge for game species and species likely to be killed from human-wildlife conflict (Meyer et al., 2015). Given CHNP represents one of the last forest remnants outside the Central Cordillera, we recommend that Panamá's Ministry of the Environment (Ministerio de Ambiente) and collaborating organizations target CHNP as a top priority area for wildlife and habitat conservation in Panamá. Future research efforts could include extending distribution and habitat assessments of jaguars to the fragmented forests surrounding CHNP and identifying potential travel corridors within these fragments (LaRue & Nielsen, 2008; Rabinowitz & Zeller, 2010). Furthermore, a long-term monitoring at CHNP should be conducted to assess the seasonal effect on habitat use by our focal species.

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Declaration of Conflicting Interests

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Appendix A

Table A1. Environmental Covariates and Expected Influence on Beta-coefficients [β ; indicated as + ($\beta > 0$), - ($\beta < 0$), 0 (no expected effect), n/a (not applicable)] on Detectability (p) and Habitat Use (ψ) of Focal Wildlife Species During February–May 2014–2015 in Cerro Hoya National Park (CHNP) and Darién National Park (DNP), Panamá.

Covariate	Description	Expected result			
		Jaguar	Puma	White-lipped peccary	Collared peccary
Detection					
Year	Survey year (2014, 2015)	+	+	+	+
Julian	Julian date	+	+	+	+
Response	If the species was detected during a previous visit (1 = yes, 0 = no)	-	-	+	+
CamDays	Number of functioning camera-days per camera	+	+	+	+
CamModel	Black flash, flash, or combination cameras	n/a	n/a	n/a	n/a
Occupancy					
EVA	Elevation (m)	+	+	-	-
DTRV	Distance (m) to nearest river system	-	-	0	0
DTTB	Distance (m) to nearest tributary system	-	-	0	0
DTHS	Distance (m) to nearest human settlement (>3 houses)	+	+	0	0
DFE	Distance (m) to forest edge	+	+	+	0
DetFreq	Detection frequencies for each species per camera station	n/a	n/a	n/a	n/a