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Assessment of jaguars *Panthera onca* (Mammalia: Carnivora: Felidae) and their prey in Manu National Park

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Resumen

Las áreas protegidas, como el Parque Nacional Manu en Perú (17.000 km²), son importantes para la protección de especies claves como el jaguar, siendo los estudios poblacionales una prioridad para conocer su estado de conservación. Realizamos un estudio usando 136 pares de trampas cámara instaladas en tres bloques en un área de 820 km² en el Parque Nacional del Manu, con el fin de estimar la densidad de jaguares. Así mismo, estimamos la disponibilidad de presas (ocho mamíferos y un ave) y el uso del espacio del jaguar y otros depredadores con modelos de ocupación, considerando variables ambientales, disponibilidad de presas y la presencia de competidores. La mayor parte de las especies de presas tuvieron una ocupación (psi) mayor a 0.70, sin presentar patrones en el uso del espacio. El uso del espacio fue intensivo por parte del ocelote (psi = 0.83, ES = 0.08) y el jaguar (psi = 0.67, ES = 0.33) y menos intensivo por parte del puma (psi = 0.25, SE = 0.07), sin detectarse patrones según las variables ambientales evaluadas, la disponibilidad de presas y la presencia de competidores. Estimamos una densidad poblacional de jaguares de 2 (ES=0.92; 95% CI =0.8-4.7) a 2.5 (ES=1.07, 95% CI = 1.1-5.6) ind/100 km², que corresponden a una población de 193-241 jaguares para las tierras bajas de Manu. Concluimos que los jaguares son aparentemente abundantes, tanto carnívoros mayores como sus presas pueden ser encontradas a lo largo de las tierras bajas del parque y su presencia no está afectada por variaciones espaciales del hábitat y presiones humanas.

Palabras clave: Bosque tropical, densidad, mamíferos, ocupación, Perú.

Abstract

Protected areas, such as the 17,000 km² Manu National Park in Peru, are important for vulnerable species such as the jaguar, and population studies are needed to understand their conservation status. We did a short-term study using 136 paired camera traps stations deployed in three blocks across an area of 820 km² in Manu National Park to estimate: the density and distribution of jaguars, evaluate the availability and distribution of key prey (eight mammals and a bird), and investigate the use of space by predators, using occupancy models that considered environmental variables, prey availability, and competitors. Most prey species had an occupancy (psi) greater than 0.70, without clear patterns in the use of space. The use of space was intensive for ocelot (psi = 0.83, ES = 0.08) and jaguar (psi = 0.67, ES = 0.33), and less intensive for puma (psi = 0.25, SE = 0.07), yet without clear patterns related to the environmental variables we evaluated, the availability of prey and the presence of competitors. We estimate a jaguar density of 2 (ES=0.92; 95% CI =0.8-4.7) to 2.5 (ES=1.07, 95% CI = 1.1-5.6) ind/100 km², corresponding to a population of 193-241 jaguars for the lowlands of Manu. We conclude that jaguars are apparently abundant, both large carnivores and their prey can be found throughout the lowlands of the park, and their presence is not affected by spatial variations in habitat and human pressures.

Keywords: Density, mammals, occupancy, Peru, tropical rainforest.

1. INTRODUCTION

Jaguars (*Panthera onca*) are apex predators in Neotropical forests that usually occur at low densities (Maffei et al. 2011, Noss et al. 2012) and have a relatively low reproduction rate, usually one or two cubs every three years (Seymour 1989). These characteristics, make them sensitive to threats such as habitat loss, reduction of wild prey, preventative and retaliatory killing as a result of conflict with livestock, and illegal killing for black-market trade (Weber & Rabinowitz 1996, Gittleman et al. 2001, Sunquist & Sunquist 2001, Reuter et al. 2018). The continuous increase in these threats has led to the decline and isolation of jaguar populations, considering them near threatened throughout their entire range (Quigley et al 2017). Due to its conservation status, ecological importance, cultural value and its usefulness as an umbrella species, the jaguar is considered a priority species in conservation and research programs (Cluff & Paquet 2003, Ray 2005, Steneck 2005).

Across their range and the variety of biomes they occupy, jaguars consume a wide number of prey species, mainly mammals, but also reptiles and birds (Emmons 1987, Seymour 1989). The distribution of the natural prey influences the boundaries of jaguar home ranges, making it an important factor in spatial use and the dynamics and distribution of their populations (Rabinowitz & Nottingham 1986, Gittleman et al. 2001, Polisar et al. 2003). In other cases, distribution and spatial use appears to be led by habitat features such as wetlands, plantations and pastures (Figel et al. 2019) or water availability (Soisalo & Cavalcanti 2006; Tobler et al. 2018). Assessing patterns of prey and habitat availability is key to understanding characteristics of jaguar populations that determine their conservation status.

Since jaguars have extensive home range requirements (Morato et al. 2016), large protected areas, such as the Manu National Park (hereafter Manu), are important to protect jaguar populations over the long term (Emmons 1987, Laurance 2005). Manu is the third largest protected area in Peru, covering more than 17,000 km², and encompassing a representative portion of numerous ecosystems ranging from highland grasslands to moist montane forest and tropical rain forest (SERNANP 2014a, b). The conservation goals of Manu are to protect terrestrial ecosystems, water-land interface ecosystems; and a set of priority species, among them large birds and mammals including the jaguar. The Manu Action Plan requires that research in the protected area addresses knowledge gaps and problems related to biodiversity and its conservation, especially jaguars (SERNANP 2014a).

In this paper we report on a large-scale survey with camera traps of jaguar and their prey across the lowland section of Manu to assess how jaguar use of space relates to prey occupancy and generate a density estimation of the jaguar population in the park.

2. MATERIALS AND METHODS

2.1 Survey Area

Our study area centered on the Manu River (the second largest river in the park) and the Cumerjali River (Figure 1). The elevation in this area ranges from 300 and 600 masl. The mean temperature is 22-26º C, and the annual precipitation between 1,500 and 2,100 mm (SERNANP 2014a, b). The vegetation is relatively homogeneous and is dominated by tropical humid broadleaf forest (CDC-UNALM 2006), with a canopy of ~40 m (SERNANP 2014a, b). Numerous streams and ravines create a slightly rugged micro-topography. The Amazonian part of the park (below 600 masl) harbors 169 mammalian species, 49 of which are considered medium-sized and large mammals (Solari et al. 2006). Three human settlements of indigenous people were either close to or within the survey area (Figure 1): Maizal (46 inhabitants), Yomibato (357 inhabitants) and Tayakome (338 inhabitants). Residents of these settlements practice a traditional livelihood based on slash and burn agriculture, extraction of timber and non-timber products, and subsistence hunting (with bow and arrow, not firearms)—these subsistence activities were permitted for indigenous residents, but not for other people within the park (SERNANP 2014a, b).

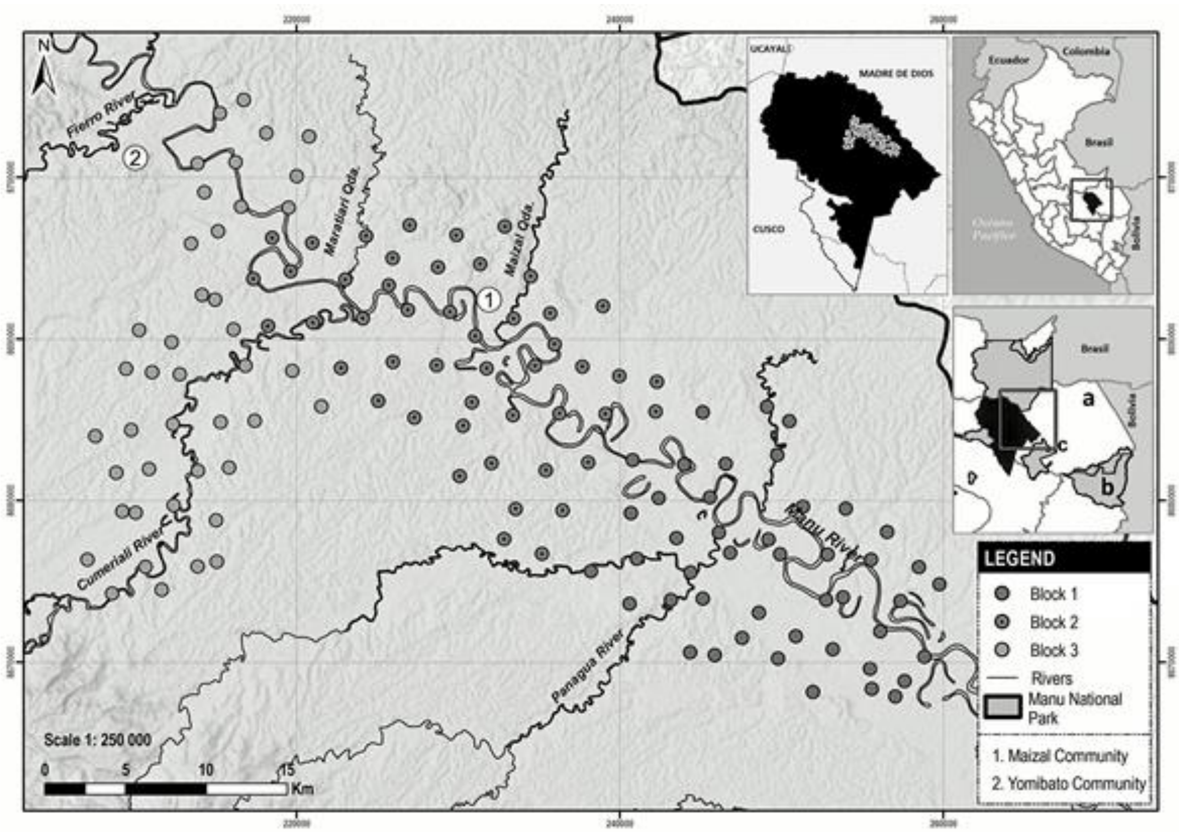

Figure 1. Camera trap stations at Manu National Park (MNP). Left inset map: lowlands (in black) of MNP with camera traps on grey dots. Right inset map: MNP in Peru. Lower inset map: location of nearby camera trap surveys (dark polygon): MNP, **a**: Espinoza Forestry Concession (Tobler et al. 2013 survey area), **b**: Bahuaja Sonene National Park (Tobler et al. 2013 and Kuroiwa 2009 surveys areas) and **c** Los Amigos Concession (Tobler et al. 2013).

2.2 Camera traps deployment

We did fieldwork from July to November 2014. We deployed camera-traps triggered by both heat and motion Camtrakker® MK 10 (Camtrack South Inc., Georgia, USA) and DeerCam® DC 300 (Park Falls Inc., Wisconsin, USA) in stations that consisted of two cameras placed one in front of the other at 4-10 meters apart. Cameras were programmed to take 3 pictures continuously when triggered (event) and one hour of delay after an event. Since there are no roads or trails in the selected study area, the stations were placed in areas frequented by animals, such as streams, open areas or animal paths, according to standard methods used for abundance and density estimations for jaguars. In some cases, it was necessary to clear the area with machetes to improve the visual area of the camera (Wallace 2003; Silver et al. 2004). Some cameras were set along streams and some in the middle of the forest. Camera-trap stations were spaced between 1 and 4 km apart from each other, with the distance between stations varying according to accessibility (limited by rugged topography and dense forests). The sampling was carried out in three consecutive blocks, of 30 days each, in order to assume closed population (Noss et al. 2013). After completing each block (30 days), cameras were cleaned, batteries were replaced, data was downloaded and the next block initiated. The first block was set in the vicinity of Pakitza Ranger Station (WGS48 -11.951 -71.262) from July 18 to August 23, 2014 with 46 stations. The second block was set around the Cocha Cashu Biological Station (WGS48 -11.885 -71.382), with 48 stations, from August 24 to September 27, 2014. The third block was located further upstream along the Cumerjali River (WGS48 -11.839 -71.600) with 42 stations between September 30 and November 5 (Figure 1). The entire grid encompassed 136 camera trap stations. We processed the data registering all the fauna photographed in Excel sheets considering different records of the same species in a station with at least one hour from the next (White & Garrott 1990, Long *et al*. 2003).

2.3 Jaguar prey availability

To evaluate the jaguar prey availability, we estimated the occupancy of the following seven species considered to be jaguar prey (Emmons 1987) classified as large home range species (>1 km^2): lowland tapir (*Tapirus terrestris*), collared peccary (*Pecari tajacu*) and brocket deer (*Mazama* spp.); and small home range species (<1 km^2): paca (*Cuniculus paca*), agouti (*Dasyprocta variegata*), armadillo (*Dasypus novemcintus*) and Razor-billed Curassow (*Mitu tuberosa*). Occupancy models indirectly assess the abundance of the species, given the strong positive correlation between abundance and occupancy when the sampling design is established according to the home range of each species (Royle & Dorazio 2008). Therefore, occupancy was estimated considering camera-trap stations and around each station sampling units of 1 km^2 and 0.04 km^2 for species with large and small home range, respectively (Isasi-Catalá et al. 2016). Detection history matrices were constructed for the 136 sampling units or sites (S = 136) and three occasions or visits (K = 3) defined each as a 10-day period (TC=10). Using *single season – single species* models, occupancy (*psi*) and detection (*p*) probability were estimated for each species using Presence 11.5 software (Hines 2006). We used seven environmental site covariates that we judged could potentially influence the occupancy patterns of prey species: 1) distance to navigable rivers (RP), 2) distance to all rivers (RQ), 3) distance to immigrant communities (CP), 4) distance to native communities (Cnat), 5) distance to park ranger camps (PVC), 6) distance to park boundaries (LPNM) and 7) distance to deforested areas (Def). The values of each covariate were calculated with the GIS Software ArcGis 10.6 (ESRI, Inc., Redlands, CA, USA). The null model (without covariates) was obtained for each species, as well as independent models for each site-defined covariate. We evaluated the adjustments and overdispersion of the data (bootstrap of 1000 iterations) to verify the reliability of the models. The models were selected based on an Akaike information criterion (AIC), considering only those within ΔAIC ≤ 3 as the models that most likely explain the spatial variability of the occupancy of each species (MacKenzie et al. 2006, Linkie 2008). Average occupancy and detection values were calculated from the selected models, using Presence 11.5 software (Hines 2006). Additionally, to determine the importance of the effect of each site covariates (SigB(CovS) on the occupancy of the species, we evaluated the beta coefficients (β) with a Wald test (Guillera-Arroita & Lahoz-Monfort 2012). The Wald test allows to evaluate whether the beta coefficients obtained for each covariate represent a significant effect on occupancy, i.e., beta coefficients other than zero. If the beta coefficients obtained for the selected models are significant, we can consider that the evaluated covariate not only better explains the spatial variability in the occupation of each species (according to the AIC criteria), but also that this variability represents a significant heterogeneous spatial pattern in occupation of each species. If the beta coefficients obtained for the selected models are not significantly different from zero, it is assumed a homogeneous occupation among all the sampling units evaluated (Guillera-Arroita & Lahoz-Monfort 2012).

2.4 Jaguar, Puma and Ocelot Spatial use

We used occupancy models to evaluate the spatial use by the jaguar and its potential competitors, puma (*Puma concolor*) and ocelot (*Leopardus pardalis*), at a scale of 1 km². Inferences based on occupancy models can serve for evaluation of spatial and habitat use (Tobler et al. 2008, 2015), if sampling units are small in relation to individual home range of the target species (MacKenzie et al. 2006). S*ingle season – single species* models were obtained (S = 136, K = 3) with camera-trap detection rates using Presence 11.5 software (Hines 2006). The five site covariates considered for prey were included, as well as the occupancy probability of seven prey species and other felids, resulting in a total of 14 site covariates evaluated for each carnivore. The null model (without covariates) was obtained for each species, as well as independent models for each site-defined covariate. Model selection was done following the same criteria described earlier for the prey species. Average occupancy and detection values were calculated from the selected models, using Presence 11.5 software (Hines 2006). We evaluated the significance of beta coefficients (β) with a Wald test (Guillera-Arroita & Lahoz-Monfort 2012).

2.5 Jaguar density estimation

Jaguars were individually identified by their natural body marks, and capture matrices were constructed based on the registers' date and time and on the location of the camera traps. Due to differences in each flank of the coat pattern, cameras were set in pairs in order to photograph simultaneously both sides of a jaguar (Silver et al. 2004). However, due to lack of records of both sides of individuals, photographs were analyzed separately by left and right side. We applied spatially explicit capture-recapture models (SECR) to estimate population density of jaguars. SECR models overcome edge effects that are problematic in conventional capture–recapture estimations of animal populations (Efford & Fewster 2013). SECR analyses were performed with a model fitted in a maximum-likelihood Framework (Borchers and Efford 2008), in the R package Secr (Efford 2011).

3 RESULTS

Altogether, the three blocks of camera traps resulted in a sampling effort of 4,251 traps·nights. The polygon formed by the outer cameras of the entire survey was 820 km². In total, 4,165 photographic records were obtained of 27 mammal and 38 bird species (Annexes 1 & 2).

3.1 Occupancy patterns of prey species

The average occupancy probability obtained considering the most probable model and with the best fit was 0.76 for paca (SD = 0.03), 0.74 for agouti (SD = 0.04), 0.76 for collared peccary (SD = 0.05), 0.91 for brocket deer (SD = 0.08), and 0.85 for Razor-billed Curassow (SD = 0.02, Table 1; Annex 3). Tapir and armadillo occupancy probability was 0.69, SD = 0.01, and 0.57, SD = 0.07, respectively. For most species, the detectability (or detection probability) rate was between 0.55 and 0.71, with the exception of collared peccary (p = 0.37, SE = 0.05) and armadillo (p =0.26, SE = 0.05). In most cases, all the evaluated site covariates are within the models that best explain the heterogeneity of the occupancy of each of the species in the study area (Table 1, Annex 3). However, when evaluating the effect of each of these variables, we found no site-specific environmental covariate effects on the occupancy of the prey species between camera trap sites, (SigB(CovS) > 0.05, Table 1). Therefore, we conclude that the occupancy of prey species in Manu is homogeneous for these variables throughout the study area.

Table 1: Occupancy and detection probability, model parameters and site environmental covariates achieved for the jaguar, its prey and potential competitors in the Manu National Park, Peru, from July to November 2014.

	Analysis	X̄psi	SD	p	SE	Adjust.	CovS.eff	SigB(CovS)
Environmental covariates								
Cuniculus paca	S = 136	0.76	0.03	0.71	0.04	√	LPNM (-)	>0.05
	K = 2						RP (-)	>0.05
							Def (-)	>0.05
							Cnat (-)	>0.05
							PVC (-)	>0.05
							RQ (+)	>0.05
							CP (-)	>0.05
Dasyprocta punctata	S = 136	0.74	0.04	0.65	0.03	√	Def (-)	>0.05
	K = 3						LPNM (-)	>0.05
							Cnat (-)	>0.05
							PVC (-)	>0.05
							RP (-)	>0.05
							RQ (+)	>0.05
							CP (-)	>0.05
Myoprocta pratti	S = 136	0.42	0.04	0.58	0.05	√	LPNM (-)	>0.05
	K = 3						Def (-)	>0.05
							PVC (-)	>0.05
							RP (-)	>0.05
							Cnat (-)	>0.05
							CP (+)	>0.05
							RQ (+)	>0.05
Dasypus novemcintus	S = 136	0.57	0.07	0.26	0.05	√	RP (+)	>0.05
	K = 3						LPNM (+)	>0.05
							Def (+)	>0.05
							PVC (+)	>0.05
							CP (-)	>0.05

Tapirus terrestris	S = 136 K = 3	0.69	0.01	0.55	0.04	√	Cnat (-) LPNM (+) CP (+) RQ (-) PVC (-) RP (+) Def (+)	>0.05 >0.05 >0.05 >0.05 >0.05 >0.05 >0.05
Pecari tajacu	S = 136 K = 3	0.76	0.05	0.37	0.05	√	CP (-) Cnat (+) PVC (+) RQ (-) RP (-)	>0.05 >0.05 >0.05 >0.05 >0.05
***Mazama* spp.**	S = 136 K = 2	0.91	0.08	0.58	0.04	√	RQ (+)	>0.05
Mitu tuberosa	S = 136 K = 3	0.85	0.02	0.55	0.03	√	RQ (-) CP (-) Cnat (+) Def (+) PVC (+) LPNM (+) RP (-)	>0.05 >0.05 >0.05 >0.05 >0.05 >0.05 >0.05
Leopardus pardalis	S = 136 K = 3	0.82	0.17	0.37	0.04	√	**LPNM (-)** Def (-) **RP (-)** PVC (-)	0.011 >0.05 0.006 >0.05
Panthera onca	S = 136 K = 3	0.67	0.01	0.12	0.06	√	RP (-) PVC (+) Cnat (+) Def (+) LPNM (-) RQ (-) CP (-)	>0.05 >0.05 >0.05 >0.05 >0.05 >0.05 >0.05
Puma concolor	S = 136 K = 3	0.24	0.04	0.3	0.09	√	RP (-) CP (-) RQ (-) PVC (+) Cnat (+)	>0.05 >0.05 >0.05 >0.05 >0.05
Species covariates								
P. onca	S = 136 K = 3	0.67	0.02	0.12	0.06	√	*Mazama* spp. (-) *P. concolor* (+) *T. terrestris* (-) *D. novemcinc-* *tus* (-) *P. tajacu* (+) *L. pardalis* (+) *C. paca* (+) *D. puntata* (-)	>0.05 >0.05 >0.05 >0.05 >0.05 >0.05 >0.05 >0.05
P. concolor	S = 136 K = 3	0.25	0.15	0.3	0.09	√	***P. onca* (+)**	0.01

S: number of sampling units, K: number of sampling visits, x̄psi: average occupancy probability (Ψ), SD: standard deviation, p: detection probability, SE: standard error, Adjust: model adjustment (yes = √, not = X) according p_b > 0,05 and near 1, CovS.eff: covariates with effect positive (+) or negative (-) on occupancy models, SigB(CovS): p-value obtained from Wald test for site covariates (α = 0.05). RP: distance to navigable rivers, RQ: distance to all rivers, CP: distance to communities, Cnat: distance to native communities, PVC: distance to park ranger camps, LPNM: distance to park boundaries, Def: distance to deforested areas.

3.2 Spatial use by jaguars and other carnivores

Using occupancy as a proxy for spatial use, we found widespread intensive spatial use by ocelot (psi = 0.82, SD = 0.17), slightly less for jaguar (psi = 0.67, SD = 0.01) and less intensive spatial use by puma (psi = 0.24, SD = 0.04), according to the average of the most likely fitted models (Table 1, Annex 4). The detectability of these species was lower than 0.40 (Table 1), with the detectability of the jaguar the lowest of all species (p = 0.12, SE 0.06, Table 1). Similar to prey species, several site covariates are within the models that best explain the heterogeneity of the spatial use of each of the species in the study area (Table 1, Annex 4). However, when evaluating the effect of each of these variables, we found no site specific environmental covariate effects on the spatial use of these species between camera trap sites, (SigB(CovS) > 0.05, Table 1). Only for the ocelot, a significant negative effect was obtained from the distance to the limit of the protected area (LPNM) and to navigable rivers (RP). In this case, the use of space was greater near the limit of the area and the navigable rivers. For jaguar and puma site covariates did not generate a significant spatial pattern. There was no effect of prey availability and space use by competitors on spatial use by the jaguar and the ocelot (Table 1, Annex 5). However, a significant positive relationship was found between puma and jaguar spatial use (psi(P.onca),p(.), SigB(P.onca) = 0.01, Table 1); areas most used by the puma coincided with areas most used by the jaguar (B = 19.19, SE = 7.53).

3.3 Density of jaguars

We obtained 31 jaguar records but could only attribute 25 to individually-identified jaguars. In addition, most records were one-sided photos, so we calculated the abundance and density separately using either left or right-side photos. We identified 13 individuals using photographs of the right sides and 16 from the left sides. Recaptures were scarce; only five individuals were photographed in at least two different locations and the rest were recorded just once. From the right sides, most records could not be sexed, but from the left side set of identified individuals, seven were females, four were males and five were undetermined. Mean maximum distance moved (MMDM) for jaguars captured in at least two different stations was 3.9 km (SD±1.3) for the left-side records and 10.8 km (SD±6.7) for the right-side records. Density according to SECR models performed for each set of records was 2.5 ind/100km^2 (SE ± 1.07, 95% CI = 1.1 - 5.6) for the left side records and 2 ind/100 km^2 (SE ± 0.92, 95% CI = 0.8 - 4.7) for the right-side records and capture probability was low, from 0.0087 to 0.074.

4 DISCUSSION

The prey species evaluated in this study appear to uniformly occupy the lowlands of Manu National Park according to the scale and covariates evaluated. This result seems to indicate that in the lower zone of Manu, at the scale of evaluation, these species are widespread, without being affected by any potential human activity or environmental factors. Even when no evidence of human disturbance was observed in the study area, the evaluated environmental covariates would have allowed us to detect possible effects of illegal hunting and logging and other human activities, when evaluating accessibility patterns (e.g. RP or CP), to surveillance centers of the areas protected (e.g. PVC) or to direct disturbances that currently exist (e.g. Def). Most species of prey recorded in this area had an occupancy rate greater than 0.70 psi, and detection probability greater than 0.50, which may indicate relatively negligible impact of indigenous subsistence hunting at Manu. In other protected areas of Peru, where subsistence hunting is allowed under management conditions, such as in Tamshiyacu Tahuayo Communal Regional Conservation Area and Pucacuro National Reserve, the occupancy probabilities estimated for some species were similar to those from this study (Table 2). In those areas the occupancy probabilities had been classified as high (psi > 0.70), medium (psi between 050 to 0.70) and low (psi < 050, Isasi-Catalá et al. 2017, Falcón-Ayapi et al. 2019). According to this classification, the occupancy of most species of jaguar prey at Manu would be considered high; spatial patterns are evident in the occupancy of some species like the collared peccary at Tamshiyacu and the Razor-billed Curassow at Pucacuro, suggesting a response to human presence. In those studies, occupancy rates decreased near populated centers or at the boundaries of the area. The absence of spatial variability in Manu according to the scale and covariates evaluated, where the same species' occupancy rate is also high, may indicate that wildlife populations have not been significantly affected by recent human activities.

Table 2. Comparison of the occupancy rate for common prey species between Manu National Park, Tamshiyacu Tahuayo Communal Regional Conservation Area (TTCR), and Pucacuro National Reserve (PUNR).

	Manu		TTCR (Isasi-Catalá et al, 2017)		PUNR (Falcón-Ayapi et al. 2019)	
	Psi (SE)	Model	Psi (SE)	Model	Psi (SE)	Model
Tapirus terrestris	0.69 (0.05)	psi(.)	0.52 (0.08)	psi(.)	0.67 (0.07)	psi(.)
Pecari tajacu	0.75 (0.08)	psi(.)	0.68 (0.26*)	psi(CP)+	0.74 (0.06)	psi(.)
Mazama spp.	0.93 (0.07)	psi(.)	0.51 (0.07)	psi(.)	-	-
Cuniculus paca	0.76 (0.05)	psi(.)	0.59 (0.26*)	psi(TO)+	0.94 (0.04)	psi(.)
Dasyprocta punctata	0.74 (0.04)	psi(.)	0.66 (0.10*)	psi(CP)+, psi(TO)+	0.98 (0.03)	psi(.)
Dasypus novemcintus	0.58 (0.11)	psi(.)	0.48 (0.17*)	psi(NR)-, psi(TC)-	0.69 (0.07)	psi(.)
Mitu tuberosa	0.84 (0.04)	psi(.)	-	-	0.36 (0.08)	psi(NR)+, psi(CP)+, psi(HA)-, psi(HI)+

Psi: occupancy probability, SE: standard error (* DE), psi(.): null model, psi(CP)+: model that indicates that the occupancy is greater far from the populated centers, psi(TO)+: model that indicates that the occupancy is higher in the highlands, psi(HA)-: model that indicates that occupancy is higher near hunting areas, psi(TC)-: model that indicates that the occupancy is greater near the hunting trails, psi(NR)+: model that indicates that the occupancy is greater far from the edge of the reserve, psi(HI)+: model that indicates that the occupancy is greater far from the main rivers.

Another factor that should be considered in Manu is habitat homogeneity. The entire area is covered with tropical humid forest, without notable variations in altitude (SERNANP, 2014a, b), despite local micro-site differences. However, in TTCRCA and RNPU some spatial patterns are evident in the occupancy of certain species. These spatial patterns are defined by environmental characteristics of the areas, such as topography in the case of agouti and armadillos at ACRCTT. Similarly, for other species, such as the collared peccary at ACRCTT and the Razor-billed Curassow at RNPU, the patterns show their vulnerability to human presence, indicating decreases in occupancy near populated centers or at the limit of the area, respectively. Finally, other spatial patterns show how hunting management is being effective, as it shows a greater occupancy of the species in areas close to the sites used by hunters, such as the case of armadillo at ACRCTT and razor-billed curassow at

RNPU. Although the occupancy of these species in the three areas is high, indicating low hunting pressure, the presence of certain spatial patterns, such as those observed in the ACRCTT, reflect a greater vulnerability of the species to human activities. The absence of spatial patterns in areas such as the MNP, where the occupancy of the species is also high, indicates the presence of populations with little impact from human activities.

In this study, the armadillo and the collared peccary had low detection probabilities, but this result could be "observer bias" in our sampling method related to these species' behavior. The low detection rate for armadillo might also be explained by the fact that this is a semi-fossorial species, with a small home range in prime habitat ~3.4 ha (Nowak 1991; Redford & Eisenberg 1992). Armadillos are also usually found in tangled vegetation (Emmons & Feer 1999), and they avoid human-made paths or disturbed areas in favor of small mammal trails (Weckel et al. 2006). Notwithstanding these qualifications, they may actually be less common in Manu as compared to other protected areas in Peru. Collared peccaries can be abundant, 3 to 11 individuals / 100 km² (Cullen 1997, Keuroghlian et al. 2004), but camera trap records may underestimate their detectability (few detections per site, even if they are detected in several sites), because peccaries may avoid human made trails or areas with some intervention like the ones we set the camera traps, where we cleaned the vegetation (Weckel et al. 2006). Isasi-Catalá et al. (2016) reported that detectability for collared peccary and armadillos was low ($p = 0.20$ and $p = 0.28$ respectively) in camera traps that were also set off road, in the forest, and found that other methods, such as observation of signs and tracks, provided better results to detect these species. Direct observations along line transects were effective in assessing collared peccaries in the Llanos of Venezuela (Polisar et al. 2008) and in the Petén of Guatemala (McNab et al. 2019). White-lipped peccaries (*Tayassu pecari*) were not included in our analysis because we obtained only three records, but in another survey in the same area with signals and tracks, 19 independent detections were recorded and the estimated spatial use based on an occupancy analysis was 0.46 (SD ± 0.15, $p = 0.16$, SE ± 0.05) without any significant spatial pattern (WCS 2015). White-lipped peccary herds have very large home ranges, up to 200 km², with migrations reported (Kiltie & Terborgh 1983); therefore, they may have been temporarily absent from our study area during the period our cameras were set in Manu. Fragoso et al. (2020) also reported that these peccaries can have periods of absence or low abundance of around 7 to 12 years.

We found no clear evidence that jaguar spatial use was correlated with clumped prey as other studies have found (Polisar et al. 2003, Polisar et al. 2008, Cavalcanti & Gese 2009), nor with any of the other covariates evaluated; we only found that the areas most used by pumas also had jaguar presence. The apparently homogenous availability of each of the prey species appears to have been reflected in a relatively homogenous spatial use of jaguar, puma and ocelot. Our results contrast sharply with observations in Costa Rica by Arroyo-Arce et al. (2014), where prey species were concentrated on the coast and jaguar occurrence was explained by green turtle (*Chelonia mydas*) nesting areas, or the observations of Mendes & Chivers (2007) that found that jaguar spatial use and movements could be partially driven by the distribution of prey such as peccaries (*Tayassu pecari* and *Pecari tajacu*). In Manu, we did find that jaguar and puma spatial use coincided extensively and may be a result of homogeneity in prey occupancy. Scognamillo et al. (2003) found a high degree of spatial overlap between jaguars and pumas in a radio-tracking survey in the Venezuelan Llanos, despite the two consuming distinct suites of prey species. In our study area Emmons (1987) studied the diets, using scat analysis, of three to five jaguars and two pumas in her survey area (7.5 km²) at Manu also, and found that pumas fed mainly on large rodents whereas jaguars fed on ungulates, large rodents and reptiles. Even though these results are not conclusive given the small size of the puma scat sample analyzed (7 versus 25 from jaguar), she found that large felids took prey in close proportion to their occurrence, using terrestrial prey with remarkable evenness and without sharp patterns of selection. Therefore, if, as we found, prey species are relatively evenly-distributed across Manu lowlands, the homogeneous distribution of both jaguar and puma suggests even prey selection by both felids.

Jaguar densities estimated from this survey were 2.5 ind/100km² (left profile; SE ±1.07, 95% CI = 1.1-5.6) and 2 ind/100 km² (right profile; SE±0.92, 95% CI =0.8-4.7), which is similar to 2.75 jaguars/100 km² reported by Kuroiwa (2009) at the nearby Tambopata National Reserve. The design in both surveys was similar, with camera traps set in the forest without any roads/trails. Our mean density estimation is lower than Tobler et al. (2013) –even though not statistically- that estimated 4.4 ±0.7 jaguars / 100 km² in three survey areas located 150 to 230 km from our survey area (Los Amigos Conservation Concession and Tambopata National Reserve), with similar habitat but setting the camera traps on a network of roads/trails. They found that trails, especially old ones, had a positive influence on detection probabilities for jaguars, being much higher on roads or trails than off. Tobler et al. (2015) also found in the Peruvian Amazon that jaguars, pumas, and ocelots had a higher detection probability on trails, but this was not the case for some other mammal species. In addition, Sollmann et al. (2011) in the Brazilian Cerrado reported that jaguar records were ten times higher in cameras set on roads than off roads. In our study and in Kuroiwa (2009), even though the habitat was undisturbed, it seems that jaguar detection probabilities were lower because the camera traps were set in the forest and no roads were available, a result echoed in the surveys of Perera-Romero (2012) in near-pristine areas in the Upper Caura in Venezuela.

Combining our density estimates of 2 and 2.5 jaguars / 100km² with our findings that their distribution is homogenous with no clear gradients of any type, we therefore assume that this density could be the same for the lowland areas of the Manu with suitable habitat for jaguars, namely all habitat below 1500 masl (14,374 km² of the total 17,162 km²) adjusted by our estimation of spatial use derived from the occupancy models: 0.67 (which means 67% of the area below 1500 masl = 9,630 km²), we consider a jaguar population for the park between 193 and 241 individuals (range: 115-805).

Our study shows the need for large secure protected areas to maintain the species in perpetuity. As there was no significant effect of the anthropic covariates in the occupancy models, we document that small populations of indigenous inhabitants practicing traditional lifestyles -with low population density, traditional hunting methods and absence of market hunting- may have a negligible impact on wildlife. The even spatial use by an estimated 193-241 individual jaguars across the vast lowlands landscape of Manu, together with the same even occupancy observed for prey species and even spatial use by other carnivores (puma and ocelot), suggest that all these species can be found throughout the lowlands of the park. We highlight the importance of the pristine Manu as a stronghold for its wildlife.

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Annex 1. Birds captured by camera traps in Manu Natural Park in 2014

ORDER	FAMILY	SPECIES	NAME	RECORDS	INDEX*
Accipitriformes	Accipitridae	*Buteogallus schistaceus*	Slate-colored Hawk	1	0.24
Accipitriformes	Accipitridae	*Buteogallus urubitinga*	Great Black Hawk	7	1.65
Accipitriformes	Accipitridae	*Elanoides forficatus*	Swallow-tailed Kite	1	0.24
Anseriformes	Anatidae	*Cairina moschata*	Muscovy Duck	3	0.71
Anseriformes	Anatidae	*Neochen jubata*	Orinoco Goose	5	1.18
Anseriformes	Anhimidae	*Anhima cornuta*	Horned Screamer	3	0.71
Cathartiformes	Cathartidae	*Cathartes melambrotus*	Yellow-headed Vulture	1	0.24
Columbiformes	Columbidae	*Geotrygon montana*	Ruddy Quail-dove	16	3.76
Columbiformes	Columbidae	*Geotrygon* sp.	Quail-dove	1	0.24
Columbiformes	Columbidae	*Leptotila rufaxila*	Gray-fronted Dove	35	8.23
Coraciiformes	Momotidae	*Momotus momota*	Amazonian Motmot	3	0.71
Cuculiformes	Cuculidae	*Neomorphus geoffroyii*	Rufous-vented cuckoo	1	0.24
Eurypygiformes	Eurypygidae	*Eurypyga helias*	Sunbittern	4	0.94
Galliformes	Cracidae	*Mitu tuberosa*	Razor-billed Curassow	324	76.22
Galliformes	Cracidae	*Penelope jacquacu*	Spix's Guan	21	4.94
Galliformes	Cracidae	*Pipile cumanensis*	Blue-throated Piping-guan	3	0.71
Galliformes	Odontophoridae	*Odontophorus* sp.	Wood-quail	10	2.35
Galliformes	Odontophoridae	*Odontophorus stellatus*	Starred Wood-Quail	4	0.94
Gruiformes	Psophidae	*Psophia leucoptera*	White-winged Trumpeter	395	92.92
Gruiformes	Raliidae	*Aramides cajanea*	Grey-necked Wood-rail	3	0.71
Gruiformes	Raliidae	*Pardirallus nigricans*	Blackish Rail	12	2.82
Passeriformes	Formicariidae	*Formicarius analis*	Muscovy Duck	3	0.71
Passeriformes	Formicariidae	*Formicarius colma*	Rufous-capped Antthrush	1	0.24
Passeriformes	Formicariidae	*Formicarius* sp.	Antthrush	10	2.35
Passeriformes	Formicidae	*Chamaeza nobilis*	Striated Antthrush	9	2.12
Passeriformes	Furnariidae	*Furnarius leucopus*	Pale-legged Hornero	1	0.24
Passeriformes	Icteridae	*Molothrus oryzivorus*	Giant Cowbird	1	0.24
Passeriformes	Tyrannidae	*Conopias trivirgatus*	Three-striped Flycatcher	1	0.24
Passeriformes	Tyrannidae	*Ochthornis littoralis*	Drab Water-tyrant	1	0.24
Pelecaniformes	Ardeidae	*Ardea cocoi*	Cocoi Heron	1	0.24
Pelecaniformes	Ardeidae	*Tigrisoma fasciatum*	Fasciated Tiger Heron	2	0.47
Piciformes	Ramphastidae	*Pteroglossus azara*	Ivory-billed Araçari	1	0.24
Piciformes	Ramphastidae	*Ramphastos tucanus*	White-throated Toucan	1	0.24
Struthioniformes	Tinamidae	*Crypturellus bartletti*	Bartlett's Tinamou	7	1.65
Struthioniformes	Tinamidae	*Crypturellus soui*	Little Tinamou	10	2.35
Struthioniformes	Tinamidae	*Crypturellus* sp.	Tinamou	5	1.18
Struthioniformes	Tinamidae	*Crypturellus undulatus*	Undulated Tinamou	22	5.18
Struthioniformes	Tinamidae	*Crypturellus variegatus*	Variegated Tinamou	5	1.18
Struthioniformes	Tinamidae	*Tinamus guttatus*	White-throated Tinamou	1	0.24
Struthioniformes	Tinamidae	*Tinamus major*	Great Tinamou	95	22.35
Struthioniformes	Tinamidae	*Tinamus* sp.	Tinamou	37	8.70
Struthioniformes	Tinamidae	*Tinamus tao*	Grey Tinamou	73	17.17

*Index: captures per 1000 trap/days, based on the 4251 trap/day effort.

Annex 2. Mammals captured by camera traps in Manu Natural Park in 2014.

GROUP	FAMILY	SPECIES	NAME	REC-ORDS	INDEX*
Marsupials	Didelphidae	*Didelphis marsupialis*	Opossum	304	71.5
Xenarthrans	Dasypodidae	*Dasypus novemcinctus*	Nine-banded armadillo	73	17.2
Xenarthrans	Chlamyphoridae	*Priodontes maximus*	Giant armadillo	8	1.9
Xenarthrans	Myrmecophagidae	*Myrmecophaga tridactyla*	Giant anteater	16	3.8
Xenarthrans	Myrmecophagidae	*Tamandua tetradactyla*	Southern anteater	2	0.5
Primates	Cebidae	*Cebus albifrons*	White-fronted capuchin	6	1.4
Primates	Cebidae	*Cebus apella*	Tufted capuchin	2	0.5
Primates	Cebidae	*Saimiri boliviensis*	Squirrel monkey	1	0.2
Carnivores	Mustelidae	*Eira barbara*	Tayra	33	7.8
Carnivores	Procyonidae	*Nasua nasua*	Coati	7	1.6
Carnivores	Procyonidae	*Procyon cancrivorous*	Racoon	3	0.7
Carnivores	Canidae	*Atelocynus microtis*	Short-eared dog	12	2.8
Carnivores	Felidae	*Puma yagouaroundi*	Jaguarundi	8	1.9
Carnivores	Felidae	*Leopardus wiedii*	Margay	5	1.2
Carnivores	Felidae	*Leopardus pardalis*	Ocelot	172	40.5
Carnivores	Felidae	*Leopardus* sp.[1]	-	19	4.5
Carnivores	Felidae	*Puma concolor*	Puma	34	8.0
Carnivores	Felidae	*Panthera onca*	Jaguar	31	7.3
Lagomorpha	Leporidae	*Sylvilagus brasiliensis*	Tapeti	31	7.3
Rodents	Cuniculidae	*Cuniculus paca*	Paca	389	91.5
Rodents	Dasyproctidae	*Dasyprocta punctata*	Agouti	436	102.6
Rodents	Dasyproctidae	*Myoprocta pratti*	Green acouchi	209	49.2
Rodents	Sciuridae	*Sciurus* sp.	Squirrel	61	14.3
Rodents	Caviidae	*Hydrochaeris hydrochaeris*	Capybara	3	0.7
Rodents	Erethizontidae	*Coendou bicolor*	Bicolor porcupine	1	0.2
Rodents	Cricetidae/Echimyidae	-	Unidentified rodent	424	99.7
Ungulates	Tayassuidae	*Pecari tajacu*	Collared peccary	185	43.5
Ungulates	Tayassuidae	*Tayassu pecari*	White-lipped peccary	3	0.7
Ungulates	Cervidae	*Mazama* spp.[2]	Brocket deer	249	58.6
Ungulates	Tapiridae	*Tapirus terrestris*	Lowland tapir	276	64.9

*Index: captures per 1000 trap/days, based on the 4251 trap/day effort.
[1]Could be *L. pardalis* or *L. wiedii*
[2]*M. americana* and *M. nemorivaga*

Annex 3. Occupancy and detection probability, model parameters and effect of site environmental covariates achieved for the jaguar preys in the Manu National Park, Perú

		Model			**Occupancy**			**Detection**		**Adjustment**		**Betas**						
Analysis	**Model**	**AIC**	**ΔAIC**	***wi***	Naive	**psi**	**SE**	**p**	**SE**	**pb**	**c**	**B(psi)**	**SE**	**B(CovS)**	**SE**	**B(p)**	**SE**	**Sig B(CovS)**
C. paca	psi(.),p(.)	342.1	0.0	0.20	0.68	**0.76**	**0.05**	0.71	0.04	1.00	0.00	1.15	0.27			0.88	0.22	
	psi(LPNM),p(.)	342.5	0.4	0.2				0.71	0.04	1.00	0.00	1.17	0.29	-0.30	0.24	0.88	0.22	0.212
S = 136	psi(RP),p(.)	342.7	0.6	0.1				0.71	0.04	1.00	0.01	1.17	0.28	-0.27	0.22	0.88	0.22	0.223
K = 2	psi(Def),p(.)	342.8	0.7	0.1				0.71	0.04	1.00	0.00	1.16	0.28	-0.28	0.25	0.89	0.22	0.270
CovS = 7	psi(Cnat),p(.)	343.4	1.3	0.1				0.71	0.04	1.00	0.00	1.15	0.28	-0.20	0.24	0.89	0.22	0.420
	psi(PVC),p(.)	343.6	1.5	0.1				0.71	0.04	1.00	0.00	1.15	0.28	-0.18	0.25	0.88	0.22	0.486
	psi(RQ),p(.)	343.9	1.8	0.1				0.71	0.04	1.00	0.00	1.15	0.27	0.10	0.24	0.88	0.22	0.684
	psi(CP),p(.)	344.1	2.0	0.1				0.71	0.04	1.00	0.00	1.15	0.27	-0.02	0.25	0.88	0.22	0.948
					x̄	**0.76**		**0.71**	**0.04**									
					SD	**0.03**												
D. puntata	psi(Def),p(.)	501.2	0.0	0.19	0.70			0.65	0.03	0.06	1.84	1.09	0.23	-0.34	0.23	0.62	0.14	0.131
	psi(.),p(.)	501.6	0.4	0.15		**0.74**	**0.04**	0.65	0.03	0.05	1.94	1.07	0.23			0.62	0.14	
S = 136	psi(LPNM),p(.)	501.7	0.5	0.1				0.65	0.03	0.05	1.88	1.08	0.23	-0.30	0.22	0.62	0.14	0.168
K = 3	psi(Cnat),p(.)	502.0	0.8	0.1				0.65	0.03	0.07	1.82	1.08	0.23	-0.27	0.23	0.62	0.14	0.223
CovS = 7	psi(PVC),p(.)	502.1	0.9	0.1				0.65	0.03	0.06	1.84	1.08	0.23	-0.27	0.23	0.62	0.14	0.231
	psi(RP),p(.)	502.4	1.1	0.1				0.65	0.03	0.05	1.90	1.08	0.23	-0.23	0.21	0.62	0.14	0.254
	psi(RQ),p(.)	502.7	1.5	0.1				0.65	0.03	0.05	1.95	1.09	0.23	0.23	0.26	0.62	0.14	0.388
	psi(CP),p(.)	502.9	1.7	0.1				0.65	0.03	0.06	1.89	1.07	0.23	0.18	0.22	0.62	0.14	0.417
					x̄	**0.74**		**0.65**	**0.03**									
					SD	**0.04**												
M. pratti	psi(LPNM),p(.)	369.3	0.0	0.2	0.38			0.58	0.05	0.48	0.95	-0.32	0.20	-0.29	0.20	0.30	0.20	0.146
	psi(.),p(.)	369.5	0.2	0.2		**0.42**	**0.05**	0.57	0.05	0.45	0.96	-0.31	0.20			0.30	0.20	
S = 136	psi(Def),p(.)	369.8	0.5	0.2				0.58	0.05	0.47	0.96	-0.32	0.20	-0.25	0.19	0.31	0.20	0.192
K = 3	psi(PVC),p(.)	370.3	0.9	0.1				0.58	0.05	0.53	0.89	-0.32	0.20	-0.21	0.19	0.31	0.20	0.266
CovS = 7	psi(RP),p(.)	370.4	1.1	0.1				0.57	0.05	0.47	0.96	-0.31	0.20	-0.20	0.20	0.30	0.20	0.311
	psi(Cnat),p(.)	370.5	1.2	0.1				0.58	0.05	0.47	0.94	-0.31	0.20	-0.19	0.19	0.31	0.20	0.317
	psi(CP),p(.)	371.3	2.0	0.1				0.58	0.05	0.48	0.94	-0.31	0.20	0.08	0.19	0.30	0.20	0.688
	psi(RQ),p(.)	371.5	2.2	0.1				0.57	0.05	0.47	0.95	-0.31	0.20	0.02	0.19	0.30	0.20	0.902
					x̄	**0.42**		**0.58**	**0.05**									
					SD	**0.04**												
D. novemcintus	psi(RP),p(.)	337.5	0.0	0.3				0.26	0.05	0.76	0.59	0.35	0.50	0.64	0.48	-1.07	0.27	0.185
	psi(LPMN),p(.)	338.6	1.1	0.2				0.26	0.05	0.76	0.60	0.29	0.46	0.43	0.31	-1.05	0.28	0.170
S = 136	psi(.),p(.)	338.9	1.4	0.1	0.34	**0.58**	**0.11**	**0.26**	**0.05**	0.55	0.81	0.31	0.46			-1.07	0.28	
K = 3	psi(Def),p(.)	339.3	1.8	0.1				0.26	0.05	0.58	0.78	0.30	0.46	0.34	0.29	-1.06	0.28	0.236
CovS = 7	psi(PVC),p(.)	339.4	2.0	0.1				0.26	0.05	0.59	0.78	0.32	0.48	0.34	0.31	-1.07	0.28	0.261
	psi(CP),p(.)	340.4	2.9	0.1				0.26	0.05	0.57	0.78	0.32	0.48	-0.21	0.32	-1.08	0.29	0.501
					x̄	**0.57**		**0.26**	**0.05**									
					SD	**0.07**												
	psi(Cnat),p(.)	340.5	3.0	0.1				0.26	0.05	0.54	0.81	0.31	0.46	0.17	0.29	-1.07	0.28	0.567
	psi(RQ),p(.)	340.9	3.4	0.1				0.26	0.05	0.58	0.78	0.31	0.46	-0.01	0.29	-1.07	0.28	0.982
T. terrestris	psi(.),p(.)	493.6	0.0	0.3	0.61	**0.69**	**0.05**	**0.55**	**0.04**	0.43	1.01	0.80	0.24			0.20	0.16	
	psi(Cnat),p(.)	494.8	1.2	0.1				0.55	0.04	0.52	0.89	0.80	0.24	-0.20	0.22	0.20	0.16	0.375
S = 136	psi(LPNM),p(.)	495.1	1.5	0.1				0.55	0.04	0.44	0.99	0.80	0.24	0.15	0.23	0.20	0.16	0.507
K = 3	psi(CP),p(.)	495.3	1.8	0.1				0.55	0.04	0.45	0.97	0.80	0.24	0.11	0.23	0.20	0.16	0.620
CovS = 7	psi(RQ),p(.)	495.4	1.8	0.1				0.55	0.04	0.41	1.03	0.80	0.24	-0.09	0.21	0.20	0.16	0.656
	psi(PVC),p(.)	495.5	1.9	0.1				0.55	0.04	0.43	0.99	0.80	0.24	-0.05	0.22	0.20	0.16	0.818
	psi(RP),p(.)	495.5	2.0	0.1				0.55	0.04	0.47	0.97	0.80	0.24	0.04	0.22	0.20	0.16	0.852
	psi(Def),p(.)	495.6	2.0	0.1				0.55	0.04	0.46	0.98	0.80	0.24	0.00	0.22	0.20	0.16	0.988
					x̄	**0.69**		**0.55**	**0.04**									
					SD	**0.01**												
P. tajacu	psi(CP),p(.)	453.4	0.0	0.3	0.54			0.36	0.05	0.06	1.87	1.34	0.78	-0.67	0.65	-0.58	0.22	0.300
	psi(.),p(.)	453.9	0.6	0.2		**0.75**	**0.08**	**0.37**	**0.05**	0.05	1.95	1.08	0.42			-0.53	0.19	
S = 136	psi(Cnat),p(.)	454.1	0.8	0.2				0.37	0.05	0.05	1.92	1.18	0.51	0.45	0.38	-0.54	0.20	0.239
K = 3	psi(PVC),p(.)	455.0	1.6	0.1				0.37	0.05	0.05	1.92	1.16	0.51	0.35	0.42	-0.54	0.20	0.401
CovS = 7	psi(RQ),p(.)	455.7	2.3	0.1				0.37	0.05	0.05	1.96	1.09	0.43	-0.14	0.30	-0.53	0.19	0.639
	psi(RP),p(.)	455.8	2.4	0.1				0.37	0.05	0.05	1.93	1.08	0.42	-0.12	0.27	-0.53	0.19	0.658
					x̄	**0.76**		**0.37**	**0.05**									

					SD	**0.05**												
Mazama spp.	psi(RQ),p(.)	351.6	0.0	0.6				0.57	0.05	0.77	0.35	4.17	2.73	3.48	3.34	0.35	0.17	0.297
	psi(.),p(.)	354.3	2.7	0.2	0.74	**0.93**	**0.07**	**0.57**	**0.05**	0.77	0.28	2.62	1.12			0.28	0.21	
					x̄	**0.91**		**0.58**	**0.04**									
					SD	**0.08**		0.57	0.05									
S = 136	psi(PVC),p(.)	355.6	4.0	0.1				0.57	0.05	0.88	0.17	3.02	1.85	0.85	1.44	0.27	0.20	0.556
K = 2	psi(LPN),p(.)	356.2	4.6	0.1				0.57	0.05	0.81	0.24	2.59	1.07	0.18	0.55	0.29	0.21	0.750
CovS = 7	psi(Def),p(.)	356.3	4.6	0.1				0.57	0.05	0.81	0.24	2.62	1.11	0.15	0.61	0.29	0.21	0.808
	psi(Cnat),p(.)	356.3	4.7	0.1				0.57	0.05	0.82	0.25	2.63	1.13	0.08	0.74	0.28	0.21	0.915
M. tuberosa	psi(.),p(.)	535.8	0.0	0.2	0.76	**0.84**	**0.05**	**0.55**	**0.03**	0.31	1.16	1.69	0.35			0.21	0.14	
	psi(RQ),p(.)	536.4	0.6	0.2				0.55	0.04	0.34	1.13	1.76	0.39	-0.35	0.29	0.20	0.14	0.226
S = 136	psi(CP),p(.)	536.7	0.9	0.1				0.55	0.03	0.30	1.18	1.74	0.38	-0.33	0.34	0.20	0.14	0.327
K = 3	psi(Nat),p(.)	536.9	1.1	0.1				0.55	0.03	0.31	1.15	1.74	0.37	0.30	0.33	0.20	0.14	0.360
CovS = 7	psi(Def),p(.)	537.3	1.5	0.1				0.55	0.04	0.34	1.12	1.74	0.39	0.26	0.40	0.20	0.14	0.514
	psi(PVC),p(.)	537.5	1.7	0.1				0.55	0.03	0.32	1.18	1.71	0.36	0.18	0.34	0.20	0.14	0.595
	psi(LPNM),p(.)	537.8	2.0	0.1				0.55	0.03	0.34	1.15	1.69	0.35	0.04	0.36	0.21	0.14	0.906
	psi(RP),p(.)	537.8	2.0	0.1				0.55	0.03	0.33	1.15	1.69	0.35	-0.02	0.32	0.21	0.14	0.947
					x̄	**0.85**		**0.55**	**0.03**									
					SD	**0.02**												

S: number of sampling units, K: number of sampling visits, AIC: Akaike Information Coefficient, ΔAIC: delta of AIC (only models with ΔAIC ≤ 3), Wi: Model Weight, naive: naive occupancy, psi: occupancy probability (Ψ), SE: standard error, **x̄**: average occupancy, SD: standard deviation, p: detection probability, pb: model adjustment (pb > 0,05), c: overdispersion of the data (near 1), B(psi): beta coefficient value without site covariate, B(CovS): SigB beta coefficient value with site covariate (CovS), B(p): beta coefficient value without detection covariate, Sig B(CovS): p-value obtained from Wald test for covariates (α = 0.05). RP: distance to navigable rivers, RQ: distance to all rivers, CP: distance to communities, Cnat: distance to native communities, PVC: distance to park ranger camps, LPNM: distance to park boundaries, Def: distance to deforested areas.

Annex 4: Occupancy and detection probability, model parameters and effect of site environmental covariates achieved for the jaguar and other predators in the Manu National Park, Perú.

		Model			**Occupancy**			**Detection**		**Adjustment**		**Betas**						
Analysis	**Model**	**AIC**	**ΔAIC**	***wi***	Naive	**psi**	**SE**	**p**	**SE**	**pb**	**c**	**B(psi)**	**SE**	**B(CovS)**	**SE**	**B(p)**	**SE**	**Sig B(CovS)**
L. pardalis	psi(LPNM),p(.)	459.5	0.0	0.4	0.60			0.37	0.04	0.56	0.85	1.97	0.76	-1.28	0.50	-0.54	0.16	0.011
	psi(Def),p(.)	459.7	0.3	0.3				0.36	0.04	0.59	0.83	2.52	1.43	-1.80	1.13	-0.57	0.15	0.109
S = 136	psi(RP),p(.)	461.2	1.7	0.2				0.38	0.04	0.57	0.86	1.58	0.58	-0.87	0.32	-0.51	0.17	0.006
K = 3	psi(PVC),p(.)	461.8	2.3	0.1				0.36	0.04	0.57	0.85	2.36	1.50	-1.58	1.20	-0.57	0.16	0.188
					x̄	**0.82**		**0.37**	**0.04**									
					SD	**0.17**												
CovS = 7	psi(Cnat),p(.)	465.1	5.6	0.0				0.38	0.04	0.54	0.89	1.60	0.61	-0.79	0.46	-0.51	0.17	0.082
	psi(CP),p(.)	466.6	7.2	0.0				0.37	0.04	0.57	0.84	1.62	0.63	0.64	0.42	-0.53	0.18	0.130
	psi(.),p(.)	467.7	8.2	0.0		**0.83**	**0.08**	**0.36**	**0.04**	0.62	0.79	1.59	0.60			-0.56	0.19	
	psi(RQ),p(.)	469.5	10.0	0.0				0.37	0.04	0.59	0.82	1.58	0.59	0.16	0.35	-0.55	0.19	0.653
P. onca	psi(.),p(.)	213.0	0.0	0.3	0.20	**0.67**	**0.33**	**0.12**	**0.06**	0.07	1.87	0.70	1.47			-2.00	0.59	
	psi(RP),p(.)	214.6	1.6	0.1				0.12	0.06	0.07	1.83	0.68	1.47	-0.29	0.48	-1.99	0.58	0.545
S = 136	psi(PVC),p(.)	214.9	1.9	0.1				0.12	0.06	0.07	1.83	0.73	1.55	0.20	0.60	-2.01	0.60	0.739
K = 3	psi(Cnat),p(.)	214.9	1.9	0.1				0.12	0.06	0.07	1.85	0.70	1.47	0.15	0.50	-2.00	0.58	0.761
CovS = 7	psi(Def),p(.)	215.0	1.9	0.1				0.12	0.06	0.06	1.82	0.71	1.52	0.13	0.57	-2.00	0.59	0.815
	psi(LPNM),p(.)	215.0	1.9	0.1				0.12	0.06	0.07	1.85	0.71	1.52	-0.14	0.58	-2.00	0.60	0.811
	psi(RQ),p(.)	215.0	1.9	0.1				0.12	0.06	0.06	1.87	0.68	1.44	-0.09	0.42	-1.99	0.58	0.823
	psi(CP),p(.)	215.0	1.9	0.1				0.12	0.06	0.05	1.87	0.69	1.45	-0.10	0.46	-2.00	0.58	0.826
					x̄	**0.67**		**0.12**	**0.06**									
					SD	**0.01**												
P. concolor	psi(RP),p(.)	189.3	0.0	0.3	0.15			**0.31**	**0.09**	0.56	0.86	-1.25	0.39	-0.66	0.40	-0.82	0.40	0.097
	psi(CP),p(.)	189.7	0.4	0.2				0.30	0.09	0.61	0.79	-1.18	0.38	-0.49	0.28	-0.84	0.41	0.078
S = 136	psi(.),p(.)	191.0	1.7	0.1		**0.24**	**0.07**	0.30	0.09	0.58	0.83	-1.13	0.37			-0.83	0.41	
K = 3	psi(RQ),p(.)	191.1	1.8	0.1				0.30	0.09	0.62	0.80	-1.17	0.38	-0.40	0.31	-0.83	0.40	0.198
CovS = 7	psi(PVC),p(.)	191.7	2.4	0.1				0.30	0.09	0.57	0.82	-1.14	0.38	0.30	0.27	-0.84	0.41	0.262
	psi(Cnat),p(.)	191.9	2.6	0.1				0.30	0.09	0.61	0.80	-1.15	0.37	0.28	0.26	-0.83	0.41	0.296
					x̄	**0.24**		**0.30**	**0.09**									
					SD	**0.04**												
	psi(Def),p(.)	192.8	3.4	0.1				0.30	0.09	0.59	0.82	-1.13	0.37	0.14	0.27	-0.84	0.41	0.597
	psi(LPNM),p(.)	192.9	3.5	0.0				0.30	0.09	0.56	0.85	-1.14	0.37	-0.12	0.28	-0.83	0.41	0.672

S: number of sampling units, K: number of sampling visits, AIC: Akaike Information Coefficient, ΔAIC: delta of AIC (only models with ΔAIC ≤ 3), Wi: Model Weight, naive: naive occupancy, psi: occupancy probability (Ψ), SE: standard error, x̄: average occupancy, SD: standard deviation, p: detection probability, pb: model adjustment (pb > 0,05), c: overdispersion of the data (near 1), B(psi): beta coefficient value without site covariate, B(CovS): SigB beta coefficient value with site covariate (CovS), B(p): beta coefficient value without detection covariate, Sig B(CovS): p-value obtained from Wald test for covariates (α = 0.05). RP: distance to navigable rivers, RQ: distance to all rivers, CP: distance to communities, Cnat: distance to native communities, PVC: distance to park ranger camps, LPNM: distance to park boundaries, Def: distance to deforested areas.

Annex 5: Occupancy and detection probability, model parameters and effect of site preys and competitor covariates achieved for the jaguar and puma in the Manu National Park, Perú.

		MV			Occupancy			Detection		Adjustment		Betas						
Analysis	**Model**	**AIC**	**ΔAIC**	***wi***	Naive	**psi**	**SE**	**p**	**SE**	**pb**	**c**	**B(psi)**	**SE**	**B(CovS)**	**SE**	**B(p)**	**SE**	**Sig B(CovS)**
P. onca	psi(.),p(.)	213.0	0.0	0.2	0.20	0.67	0.33	0.12	0.06	0.06	1.89	0.70	1.47			-2.00	0.59	
	psi(Mazamas*),p(.)	214.3	1.3	0.1				0.12	0.06	0.07	1.79	5.37	7.64	-5.23	7.53	-1.96	0.54	0.488
S = 136	psi(Pconcolor),p(.)	214.5	1.4	0.1				0.12	0.06	0.08	1.76	-1.69	3.02	9.55	14.02	-1.96	0.53	0.496
K = 3	psi(Tterrestris),p(.)	214.5	1.5	0.1				0.12	0.06	0.06	1.86	63.38	ER	-90.10	ER	-2.13	0.34	
CovS = 8	psi(Dasypus),p(.)	215.0	1.9	0.1				0.12	0.06	0.07	1.81	1.41	3.93	-1.27	5.99	-2.00	0.59	0.833
	psi(Ptajacu),p(.)	215.0	2.0	0.1				0.12	0.06	0.07	1.82	-0.43	6.14	1.48	8.11	-2.00	0.58	0.855
	psi(Lpardalis),p(.)	215.0	2.0	0.1				0.12	0.06	0.07	1.88	0.23	2.62	0.57	3.01	-2.00	0.59	0.850
	psi(Cpaca),p(.)	215.0	2.0	0.1				0.12	0.06	0.05	1.92	-1.13	16.24	2.41	21.58	-2.00	0.59	0.911
	psi(Dpuntata),p(.)	215.0	2.0	0.1				0.12	0.06	0.06	1.87	1.75	11.23	-1.41	14.72	-2.00	0.59	0.924
					x̄	**0.67**												
					SD	**0.02**		**0.12**	**0.06**									
P. concolor	psi(Ponca),p(.)	189.8	0.0	0.8	0.15			0.28	0.08	0.52	0.84	-5.92	1.88	19.19	7.53	-0.96	0.40	**0.011**
					x̄	**0.25**		**0.28**	**0.08**									
S = 136					SD	**0.15**												
K = 3	psi(Tterrestris),p(.)	195.1	5.3	0.1				0.28	0.08	0.52	0.87	38.45	1.18	-57.42	1.72	-0.96	0.41	0.000
CovS = 7	psi(Mazamas*),p(.)	195.4	5.6	0.0				0.28	0.08	0.55	0.83	3.74	3.15	-5.36	3.43	-0.98	0.41	0.118
	psi(.),p(.)	195.7	5.9	0.0		**0.25**	**0.07**	0.28	0.08	0.49	0.90	-1.10	0.38			-0.97	0.41	
	psi(Ptajacu),p(.)	195.7	5.9	0.0				0.28	0.08	0.52	0.88	-6.45	3.35	7.01	4.37	-0.96	0.40	0.108
	psi(Dasypus),p(.)	197.3	7.5	0.0				0.28	0.08	0.51	0.86	0.04	1.92	-2.05	3.36	-0.97	0.41	0.541
	psi(Dpuntata),p(.)	197.5	7.7	0.0				0.28	0.08	0.51	0.89	1.21	5.16	-3.11	6.92	-0.97	0.41	0.653
	psi(Lpardalis),p(.)	197.5	7.7	0.0				0.28	0.08	0.53	0.88	-1.62	1.39	0.63	1.61	-0.97	0.41	0.699
	psi(Cpaca),p(.)	197.6	7.8	0.0				0.28	0.08	0.53	0.86	-2.84	6.68	2.29	8.79	-0.97	0.41	0.794

S: number of sampling units, K: number of sampling visits, AIC: Akaike Information Coefficient, ΔAIC: delta of AIC (only models with ΔAIC ≤ 3), Wi: Model Weight, naive: naive occupancy, psi: occupancy probability (Ψ), SE: standard error, x̄: average occupancy, SD: standard deviation, p: detection probability, pb: model adjustment (pb > 0,05), c: overdispersion of the data (near 1), B(psi): beta coefficient value without site covariate, B(CovS): SigB beta coefficient value with site covariate (CovS), B(p): beta coefficient value without detection covariate, Sig B(CovS): p-value obtained from Wald test for covariates (α = 0.05). *Mazamas includes *M. americana and M. nemorivaga*.

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