

## RESEARCH ARTICLE

## Wetlands are keystone habitats for jaguars in an intercontinental biodiversity hotspot

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## Abstract

Agricultural development was the major contributor to South America's designation as the continent with the highest rates of forest loss from 2000–2012. As the apex predator in the Neotropics, jaguars (*Panthera onca*) are dependent on forest cover but the species' response to habitat fragmentation in heterogeneous agricultural landscapes has not been a subject of extensive research. We used occupancy as a measure of jaguar habitat use in Colombia's middle Magdalena River valley which, as part of the intercontinental Tumbes-Chocó-Magdalena biodiversity hotspot, is exceedingly fragmented by expanding cattle pastures and oil palm plantations. We used single-season occupancy models to analyze 9 months of data (2015–2016) from 70 camera trap sites. Given the middle Magdalena's status as a "jaguar corridor" and our possible violation of the occupancy models' demographic closure assumption, we interpreted our results as "probability of habitat use ( $\Psi$ )" by jaguars. We measured the associations between jaguar presence and coverage of forest, oil palm, and wetlands in radii buffers of 1, 3, and 5 km around each camera trap. Our camera traps recorded 77 jaguar detections at 25 of the camera trap sites (36%) during 15,305 trap nights. The probability of detecting jaguars, given their presence at a site, was 0.28 (0.03 SE). In the top-ranked model, jaguar habitat use was positively influenced by wetland coverage ( $\beta = 7.16, 3.20$  SE) and negatively influenced by cattle pastures ( $\beta = -1.40, 0.63$  SE), both in the 3 km buffers. We conclude that wetlands may serve as keystone habitats for jaguars in landscapes fragmented by cattle ranches and oil palm plantations. Greater focus on wetland preservation could facilitate jaguar persistence in one of the most important yet vulnerable areas of their distribution.

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## Introduction

South American rainforests experienced the highest rates of deforestation globally from 2000–2012 [1]. Large carnivores in the Neotropics are especially susceptible to the effects of forest loss and fragmentation due to their occurrence at low densities [2], propensity for conflict with humans [3–4], and dependence on landscape connectivity [5–7]. Yet, empirical data on large carnivore response to habitat loss and fragmentation in the Neotropics is scarce and, in the case of jaguars (*Panthera onca*), most studies have not been conducted in study areas of sufficient size to make robust inferences on the species' habitat requirements and population parameters [8].

Jaguars are the largest felid in the Americas and the largest terrestrial carnivore in the Neotropics. They favor tropical lowland habitats with sufficient natural cover and access to water and prey [9–11] but the species also inhabits numerous biomes ranging from tropical moist and tropical dry forests to coastal mangroves and herbaceous lowland grasslands [11–12]. Jaguar home ranges vary considerably in relation to prey abundance, habitat quality, and rates of human disturbance [13].

Prey availability is a key determinant of the distribution and abundance of large carnivores [14–15], including jaguars [16–17]. Among terrestrial mammalian species, jaguars tend to prefer capybara (*Hydrochoerus* spp.) and giant anteater (*Myrmecophaga tridactyla*) [18]. White-nosed coati (*Nasua narica*), nine-banded armadillo (*Dasyus novemcinctus*), white-lipped peccary (*Tayassu pecari*), and collared peccary (*Pecari tajacu*) are also frequently recorded in jaguar diet in lowland biomes of the Neotropics [19–22]. In seasonally flooded ecosystems, however, arboreal mammals (i.e. brown-throated sloths *Bradypus variegatus* and red howler monkeys *Alouatta juara*), can be principal prey [17]. In other wetland habitats, species in the reptilian orders of Crocodylia and Testudines dominate both available and consumed biomass [23–26].

Due primarily to habitat loss and poaching, jaguars have been extirpated from approximately 54% of their range, which now spans 18 countries from Mexico to Argentina [6]. The identification of corridors has been a focal strategy in efforts to facilitate connectivity and maintain genetic diversity among jaguar populations (jaguar conservation units, JCU) [6–7, 9–11]. JCU are defined as either: (1) areas with a stable prey base and adequate habitat capable of maintaining at least 50 adult jaguars or (2) areas with less than 50 jaguars but with adequate habitat and a stable, diverse prey base that could potentially support an increased jaguar population [11].

Jaguars are considered a vulnerable species in Colombia [27], a critical country within the species' distribution because it represents part of an intercontinental connection between Mesoamerican and South American JCU. Embedded in the northeastern portion of the 274,597 km<sup>2</sup> Tumbes-Chocó-Magdalena hotspot [28], the middle Magdalena River Valley (hereafter, middle Magdalena) is one of the most degraded and least protected biogeographic regions in Colombia [29–30]. It has also long been recognized as a key linkage between jaguar populations east and west of the Andes Mountains [31].

Spanning ~1,291 km<sup>2</sup>, oil palm plantations are increasingly transforming jaguar habitat in the middle Magdalena (S1 Fig; see also [32]). Planted in mono-cropped rows, frequently in industrial-scale plantations that are characterized by high rates of human disturbance and habitat generalists, oil palm is one of the most incompatible land use types for the conservation of tropical biodiversity [33–35]. Colombia is the leading producer of palm oil in Latin America [36] and the middle Magdalena is one of the main areas of production. Information on jaguars in oil palm plantations is limited to studies that did not record jaguars or recorded too few

detections to draw conclusions about the species' response to these vast monocultures [34, 37–38].

Our study evaluated jaguar habitat use in a heterogeneous landscape of the middle Magdalena in an attempt to elucidate the habitat requirements associated with the species' presence at three spatial scales: 1, 3, and 5 km radii buffers surrounding each camera trap. Since the middle Magdalena is considered a jaguar corridor [39], not a JCU, we sought a better understanding of the probability of our study area being used by jaguars, rather than generating an estimate of their population size. Therefore, we used occupancy as a measure of jaguar habitat use, predicting that jaguar habitat use would increase as the proportion of forest cover and wetlands increased and oil palm and pasture decreased in each buffer size around the camera traps. We further predicted a positive correlation between jaguar detection probability and detections of their major mammalian prey species, defined here as species comprising >0.10 of consumed biomass in jaguar diet in tropical lowland forest and floodplain habitats. These predictions were made on the basis of better access to cover and greater prey availability for jaguars in natural habitats [7, 9, 10, 20–21, 34, 40].

## Materials and methods

### Study area

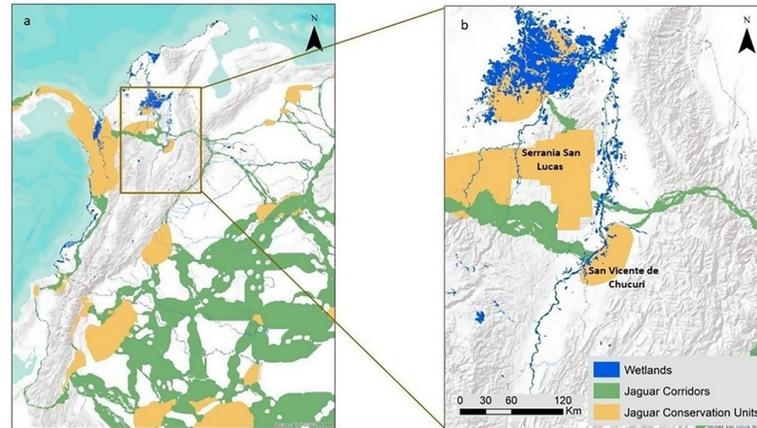
Located 400 km east of the intercontinental Colombia/Panama border, our study area spanned across ten municipalities within three provinces—Antioquia, Bolívar, and Santander—from 6° 36' to 7° 52' N, -74° 22' to -73° 29' W. The altitudinal range of sampled sites was 40–202 m asl. Mean annual temperature was 27°C and precipitation was 2,500–2,800 mm, and most rainfall occurred in a bimodal pattern from April–May and September–November. There was a distinct dry season from December–February when precipitation averaged less than 130 mm/month. January was the driest month and October was the wettest.

The wetlands in our study area consisted of seasonally flooded swamps, permanently flooded marshes, and open-water lakes and rivers [41]. One large forest block existed along the western border of our study area: 27,314 km<sup>2</sup> of forests encompassed by the Serranía San Lucas (Fig 1). A 3,770 km<sup>2</sup> portion of the Serranía San Lucas was under evaluation for a new national park in 2014 but extensive mining and occupation by guerilla groups has complicated the declaration process and the park has not yet been formally established.

### Data collection

We used data from camera trap surveys to estimate detection probabilities ( $p$ ) and jaguar occupancy as a measure of their habitat use ( $\psi$ ) from August 2015–April 2016. To minimize the possibility of recording false absences [42] (i.e. where no jaguars are detected despite their home range overlapping a camera trap site), we treated consecutive trap days as repeat surveys at each camera trap site. False absences are major sources of bias in occupancy surveys [43] but they can be differentiated from true absences (i.e. where no jaguars are detected because the camera trap is not placed within a jaguar's home range) by conducting multiple surveys [42, 44].

Most of our camera traps were placed on private lands where we required permission for access. A combination of security issues, seasonal flooding, and lack of permission from several large-scale oil palm plantations inhibited our ability to sample some sites southeast of the Serranía San Lucas and northwest of the Serranía de los Yariquíes (Fig 2). The average size of the sampled oil palm plantations was 4.27 km<sup>2</sup> (range 1.1–9.8 km<sup>2</sup>). The average distance between camera traps and the nearest wetland was 3.54 km (range 0.0–15.5 km). Pasture was the dominant land cover compared to forest, oil palm, and wetland (Table 1).



**Fig 1. Jaguar corridors and jaguar conservation units in Colombia.** Displayed in relation to wetlands and the middle Magdalena River valley (a) and the Serranía San Lucas (b).

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Using ArcGIS 9.2 (ESRI, Inc.), we calculated proportions of forest cover, oil palm, pasture, and wetland in radii buffers of 1 km, 3km, and 5 km (3.14, 28.27, and 78.54 km<sup>2</sup>) around each camera trap site (S2 Fig; Table 2). Given the lack of GPS telemetry-based home range estimates from Colombia and the Tumbes-Chocó-Magdalena hotspot [45], we included the multiple buffer sizes to assess jaguar habitat use at varying scales. Species interact with the environment at different scales [46–48] and jaguars exhibit distinct responses to landscape variables at the home range versus foraging scale [49].

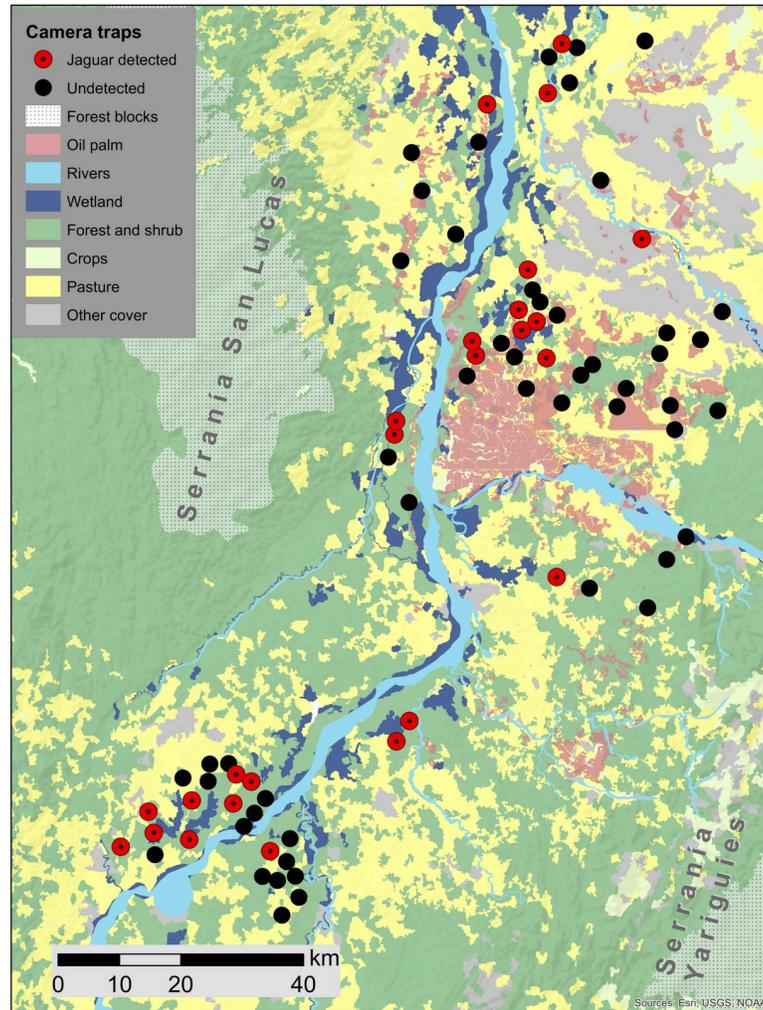
We also included detections of principal mammalian prey species as a sampling covariate. We specifically defined these prey species as armadillo, collared peccary, paca (*Cuniculus paca*), lesser capybara (*Hydrochoerus isthmius*), and giant anteater. Collectively, these species dominate the relative occurrence and mammalian biomass of jaguar diet in the lowland Neotropics [19, 20–22]. Our index of prey detections was the number of days on which a principal mammalian prey species was photographed, divided by the total number of trap nights at that site [*sensu* [50]].

Prior to running the analyses, we standardized the data using z scores  $(x - \bar{x}) / \sigma$ . Standardized z-scores can improve model convergence and facilitate the interpretation of the covariate coefficients [51]. Each covariate was selected *a priori* based on our knowledge of jaguar ecology.

## Camera trap surveys

We strategically placed remotely-triggered, passive infrared camera traps (Bushnell Trophy Cam®, Overland Park, KS, and Reconyx® HC500, Holmen, WI) and remotely-triggered, flash camera traps (Cuddeback® Attack, Green Bay, WI and Pantheracam® V4, New York, NY) in paired stations 30–40 cm above the ground. To offset slower trigger speeds of the Bushnell Trophy Cams (~0.6 seconds), we only paired these particular units with the other, faster-triggering, cameras (~0.18–0.30 sec) [52–53]. Average spacing between camera traps was 5.5 km (range 2.9–31.2 km) and camera traps were operational 24 h/day. The minimum convex polygon of our camera trap array covered an area of 7,337 km<sup>2</sup>.

To ensure proper functioning of the camera traps, we revisited our stations every 30–45 days. Camera trap placement was constrained by security issues and lack of permission from the management of several oil palm plantations. Our camera trap survey design was further



**Fig 2. Study area.** Land cover and camera trap locations, including sites of jaguar detections in the middle Magdalena River valley, Colombia.

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influenced by seasonal flooding in some inundated areas flanking the Magdalena River. We did not use scents or baits to attract animals. We placed all camera traps off-road because our reconnaissance surveys most commonly recorded jaguar sign on trails and footpaths, which are known travel routes for these cats [54–55]. Although jaguars also frequently use dirt roads for travel [56–57], oil palm workers constantly used dirt roads where risk of theft of our camera traps was a major concern.

**Table 1. Camera trap placement by habitat type.** Includes jaguar detections and mean values of habitat covariates at camera trap sites (n = 70) in the middle Magdalena River valley, Colombia.

Habitat	Number of camera traps	Number of camera traps with jaguar detections	Mean (SD) proportion of habitat in radii buffers around camera traps		
			1 km buffer	3 km buffer	5 km buffer
Forest	20	8	0.23 (0.21)	0.17 (0.13)	0.16 (0.10)
Wetlands	14	11	0.09 (0.24)	0.11 (0.21)	0.12 (0.18)
Pasture	20	4	0.45 (0.40)	0.46 (0.29)	0.45 (0.25)
Oil palm	16	2	0.09 (0.18)	0.10 (0.16)	0.10 (0.15)

<https://doi.org/10.1371/journal.pone.0221705.t001>

**Table 2. Definitions of covariates (size of radii buffers in km).** Summary of covariates used to evaluate jaguar habitat use in the middle Magdalena River valley, Colombia.

Abbreviations	Covariates
for (1, 3, 5)	Forest
wet (1, 3, 5)	Wetland
palm (1, 3, 5)	Oil palm
past (1, 3, 5)	Pasture
prey*	Detections of principal mammalian prey species

\*Detection covariate only

<https://doi.org/10.1371/journal.pone.0221705.t002>

## Data analysis

Treating each camera trap site as an individual sampling unit, we analyzed the data in an occupancy framework to estimate the probability of occurrence by incorporating an additional parameter of detection probability [58]. By accounting for detection probability, occupancy models remove the bias resulting from sites where a species was present, but not detected. We defined detection probability as the probability that jaguars were detected in a survey period, given the site was used by jaguars [*sensu* 59]. Single-season models have three key assumptions: (1) The system is demographically closed to changes in occupancy of sites during the sampling period (2) Species are not falsely detected and (3) Detection at a sampling unit (camera trap site) is independent of detection at other sampling units [59].

We constructed detection histories of jaguars for each camera trap site corresponding to a camera trap operational in a 4-week period. This resulted in 9 sampling occasions, which we imported into the program PRESENCE version 2.12.29 [51] to estimate jaguar occupancy (S1 Table). We first modeled detection probability keeping  $\Psi$  constant and then, under a maximum likelihood framework, applied the top-ranked detection model to the site occupancy models. Covariates were considered to have a significant influence on jaguar occupancy if their 90% CI did not overlap 0. We created individual (univariate) models for each covariate and used AIC to compare them with a null model that did not include covariates. If inclusion of a given covariate improved upon the null model by  $>2 \Delta AIC$  and the parameter estimate for that covariate did not include zero within a 90% CI, we considered the covariate informative and retained it for the next step of creating multivariate, additive models.

Two occupancy states were possible for each camera trap: occupied (corresponding probability is  $\Psi$ ) and unoccupied ( $1-\Psi$ ). Covariates were incorporated into the occupancy and detection components using the logit-link function, and estimated effect sizes can be interpreted in a similar manner to a logistic regression analysis.

We used Akaike's information criterion (AIC) corrected for small sample sizes (AICc,  $n = 70$  camera traps) and weighted the support of each model using AICc weights, with lower values indicating greater parsimony [60]. Jaguar detection probabilities were computed as a function of predictor variables using a logit link function. We performed a goodness-of-fit test for single season models to further assess the fit of the selected models [61].

Our data were unable to meet the assumption of population closure as camera traps operated continuously over a 9-month period, during which time the occupancy status of our study area could have varied (i.e. cubs becoming sub-adults and dispersing in or out of the middle Magdalena). Also, given the status of the middle Magdalena as a jaguar corridor [39] not a JCU, we were most interested in the probability of our study area being used by jaguars, rather than true occupancy. Thus, our results should be interpreted as jaguar "probability of habitat use ( $\Psi$ )" [48, 62].

## Results

Across the 70 sites, the total sampling effort was 15,305 trap nights. We photographed (detected) 12 unique adult jaguars 77 times (6 males, 4 females, and 2 individuals of unknown sex). Jaguars were detected at 25 (36%) of the 70 camera trap stations. We never photographed jaguars at sites without wetlands inside 5 km buffers ( $n = 16$ ). Three unique females with cubs were photographed at 3 separate camera trap sites during September 2015 and March and April 2016. At sites where we photographed cubs ( $n = 3$ ), the mean (SD) proportion of habitat in the 1 km radii buffer ( $3.14 \text{ km}^2$ ) around the camera trap stations was 0.79 (0.32) forest, 0.12 (0.21) pasture, and 0.09 (0.12) wetland. Oil palm plantations were absent from the 1 km radii at sites of cub detections.

Jaguar habitat use was most strongly associated with the proportion of wetlands, especially in 3 km buffers ( $\Sigma w = 0.85$ ) (Tables 3 and 4, Fig 3). The most parsimonious best-fit model for jaguar habitat use— $\text{psi}(\text{wet3}, \text{past3})\text{p}(\text{wet3}, \text{palm3})$  (Table 3)—was consistent with our *a priori* expectations of positive associations of jaguar habitat use in buffers with greater spatial extent of wetlands and negative associations with pasture. Jaguar habitat use was also positively associated with the proportion of forest cover, but that association was not significant at any scale.

Jaguar habitat use was negatively correlated with the proportion of pasture ( $\beta = -1.40, 0.63 \text{ SE}$ ) and oil palm ( $\beta = -1.21, 0.65 \text{ SE}$ ). Once extent of plantation coverage reached ~50% of the area inside 3 km buffers around camera traps, jaguar habitat use declined significantly (Fig 4). Our goodness-of-fit test for the most parameterized multivariate model revealed no evidence of overdispersion (lack of independence), suggesting the models provided an adequate description of the data (Model 2:  $\chi^2 = 255.10, P = 0.97, \hat{c} = 0.40$ ).

The probability of detecting jaguars, given their presence at a site, was 28% (0.03 SE). There was very strong evidence that detection probabilities were positively influenced by wetland coverage in 3 km buffers ( $\beta = 0.36, 0.14 \text{ SE}$ ) and negatively influenced by oil palm plantations in 3 km buffers ( $\beta = -0.75, 0.33 \text{ SE}$ ). Contrary to expectation, there was a negative association between detections of jaguars and their principal mammalian prey ( $\beta = -0.71, 0.40 \text{ SE}$ ).

**Table 3. Top single-season covariate\* models.** Ranking of the 14 models evaluated for habitat use of jaguars in the middle Magdalena River valley, Colombia.

Model	AICc	deltaAICc	AICc wgt	Model Likelihood	No. of parameters	Log. likelihood	Cumwt
1. $\text{psi}(\text{wet3}, \text{past3}), \text{p}(\text{wet3}, \text{palm3})$	248.05	0.00	0.42	1.00	6	236.05	0.42
2. $\text{psi}(\text{wet3}, \text{palm3}, \text{past3}), \text{p}(\text{wet3}, \text{palm3})$	248.25	0.20	0.38	0.90	7	234.25	0.80
3. $\text{psi}(\text{wet5}), \text{p}(\text{wet5}, \text{palm5})$	250.36	2.31	0.13	0.32	5	240.36	0.93
4. $\text{psi}(\text{wet3}, \text{palm3}), \text{p}(\text{wet3}, \text{palm3})$	253.26	5.21	0.03	0.07	6	241.26	0.96
5. $\text{psi}(\text{wet3}), \text{p}(\text{wet3}, \text{palm3})$	253.73	5.68	0.02	0.06	5	243.73	0.98
6. $\text{psi}(\text{palm3}, \text{past3}), \text{p}(\text{wet3}, \text{palm3})$	258.87	10.82	0.01	0.00	6	246.87	0.98
7. $\text{psi}(\text{past3}), \text{p}(\text{wet3}, \text{palm3})$	261.90	13.85	0.00	0.00	5	251.90	0.98
8. $\text{psi}(\text{wet1}), \text{p}(\text{wet1})$	264.05	16.00	0.00	0.00	4	256.05	0.99
9. $\text{psi}(\text{palm3}), \text{p}(\text{wet3}, \text{palm3})$	264.14	16.09	0.00	0.00	5	254.14	0.99
10. $\text{psi}(\text{for5}), \text{p}(\text{wet5}, \text{palm5})$	264.77	16.72	0.00	0.00	5	254.77	0.99
11. $\text{psi}(\cdot), \text{p}(\text{wet3}, \text{palm3})$	267.26	19.21	0.00	0.00	4	259.26	1.00
12. $\text{psi}(\cdot), \text{p}(\text{wet5}, \text{palm5})$	268.44	20.39	0.00	0.00	4	260.44	1.00
13. $\text{psi}(\cdot), \text{p}(\text{wet1})$	273.21	25.16	0.00	0.00	3	267.21	1.00
14. $\text{psi}(\cdot), \text{p}(\cdot)$	274.57	26.52	0.00	0.00	2	270.57	1.00

\*Site and sampling covariates: wet1 = percentage of wetland coverage in 1 km buffers around each camera trap, wet3 = percentage of wetland coverage in 3 km buffers around each camera trap, palm3 = percentages of oil palm coverage in 3 km buffers around each camera trap, for5 = percentage of forest cover in 5 km buffers around each camera trap.

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**Table 4. Results of the top models.** Parameter estimates and 90% credible intervals (CI) influencing jaguar habitat use in the middle Magdalena River valley, Colombia. Covariates were considered to have a significant influence on jaguar habitat use when their 90% CI did not overlap zero (marked in bold).

Models	$\beta$ int (90% CI)	$\beta$ wet5 (90% CI)	$\beta$ wet3 (90% CI)	$\beta$ palm3 (90% CI)	$\beta$ past3 (90% CI)
Model1	2.02 (-0.23,4.27)	-	<b>7.16 (1.89,12.43)</b>	-	<b>-1.40 (-0.37,-2.43)</b>
Model2	0.70 (-0.91,2.05)	-	<b>4.94 (1.33,8.55)</b>	<b>-1.32 (-0.09,-2.55)</b>	<b>-1.36 (-0.33,-2.39)</b>
Model3	7.14 (-1.99, 16.27)	15.38 (-0.97, 31.73)	-	-	-
Model4	-0.13 (-1.23, 1.07)	-	<b>2.76 (0.47, 5.05)</b>	<b>-1.21 (-2.27,-0.15)</b>	-

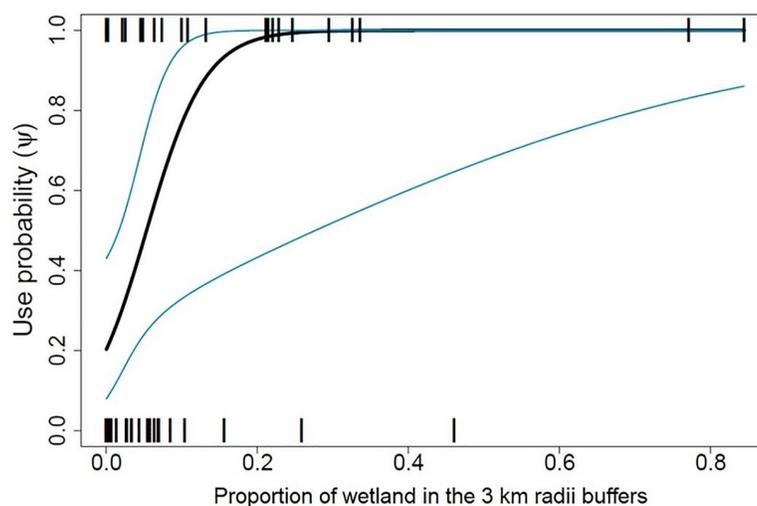
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Peccary and paca were the most frequently detected prey species and were also recorded at the greatest number of camera traps (Table 5). Giant anteaters and paca were most frequently detected in wetland habitats. Armadillo, capybara, and giant anteater were not detected in oil palm plantations. However, insufficient giant anteater and capybara detections prevented detailed analyses for these two species.

### Discussion

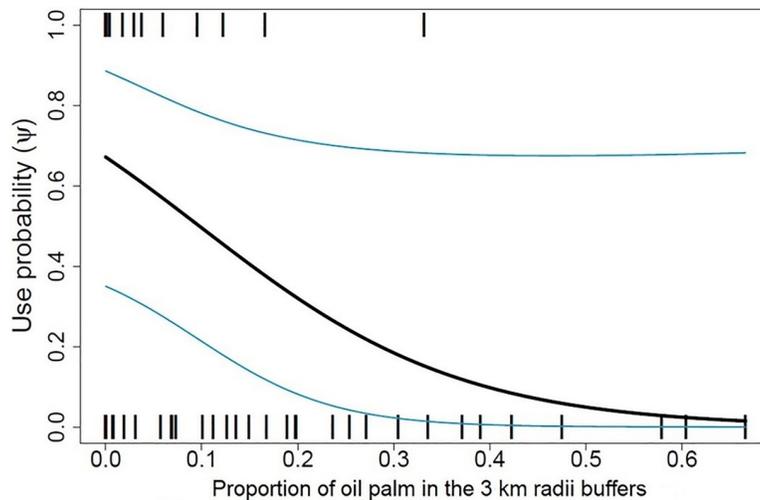
Despite their well-documented affinity for habitats near permanent surface water [9, 19, 40, 57, 63–65] this is one of the first studies to quantify associations between wetlands and jaguar habitat use. Wetlands in the Brazilian Pantanal and in the Venezuelan llanos are known strongholds for jaguars [9, 20, 63, 66] but previous studies in these areas were not specifically designed to identify associations between habitat features and jaguar presence in landscapes heavily modified by agriculture.

Notably, jaguar habitat use in the middle Magdalena was most strongly associated with the intermediate spatial scale (3-km buffer). This scale (28.27 km<sup>2</sup>) most closely corresponds to the size of a female jaguar home range size in seasonally flooded habitats [13]. Considering the lack of home range estimates from both Colombia and the Tumbes-Chocó-Magdalena hotspot



**Fig 3. Jaguar habitat use ( $\pm$  90% CI) as a function of wetland coverage.** Displayed at camera trap sites surrounded by 3 km buffers in the middle Magdalena River valley, Colombia.

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**Fig 4. Jaguar habitat use ( $\pm$  90% CI) as a function of oil palm coverage.** Displayed at camera trap sites surrounded by 3 km buffers in the middle Magdalena River valley, Colombia.

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[45], the 3-km scale could be the most accurate representation of the utilization of habitats present within the home range of a female jaguar in the middle Magdalena. Selection for preferred habitats (i.e. forests for hiding and raising cubs and wetlands for foraging) will influence how jaguars move in relation to these landscape components and the scale at which they affect habitat use [49]. For example, compared to the mean proportion of habitats across our study area, the proportions at sites of cub detections ( $n = 3$ ) included similar wetland coverage but significantly greater forest cover and less disturbed habitats (oil palm and pasture).

Nonetheless, the clear lack of support for forest cover in our models suggests that jaguars may be less dependent on forests in areas dominated by wetlands or they may preferentially select wetlands in areas lacking forest cover. Across eight study areas in Brazil and Argentina, jaguars showed increasingly strong selection for forests in landscapes with  $>58\%$  forest cover but they showed less avoidance of non-forest areas at sites with greater proportions of open and deforested areas [49].

Excluding the Serranía San Lucas JCU, which is the largest contiguous block of forest in our study area (27,314 km<sup>2</sup>), 93% of natural habitats in the middle Magdalena had been

**Table 5. Summary of prey detections.** Prey detections by habitat type and mean values of habitat covariates in 1 km radii buffers at camera trap sites ( $n = 70$ ) in the middle Magdalena River valley, Colombia.

Species	Number of camera traps with detections	Naïve occupancy	Total detections	Mean (SD) proportion of habitat in 1 km radii buffers around camera traps			
				Forest	Wetland	Oil palm	Pasture
Collared peccary	21	0.30	76	0.33 (0.22)	0.03 (0.07)	0.08 (0.25)	0.25 (0.23)
Paca	19	0.27	76	0.29 (0.24)	0.08 (0.23)	0.02 (0.06)	0.29 (0.27)
Armadillo	15	0.21	44	0.30 (0.23)	0.01 (0.05)	0.00 (0.00)	0.37 (0.31)
Capybara	4	0.06	16	0.10 (0.11)	0.00 (0.00)	0.00 (0.00)	0.56 (0.37)
Giant anteater	4	0.06	10	0.17 (0.13)	0.19 (0.26)	0.00 (0.00)	0.62 (0.43)

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converted to agriculture by 2006 [29]. Wetlands could provide increasingly important habitat for jaguars in degraded landscapes of the middle Magdalena, because the Serranía San Lucas experienced the fourth-greatest extent of habitat loss among JCUs range-wide, losing 1,590 km<sup>2</sup> (5.82%) of its forest cover from 2000–2012 [39].

Given the oil palm industry's demanding water footprint of 5,000 m<sup>3</sup> ton<sup>-1</sup> [67], wetlands are now at greater risk to draining in the middle Magdalena, which was recently identified as one of 14 hotspots of wetland loss in Colombia [68]. Beyond the middle Magdalena, one of the primary zones targeted for oil palm expansion is the tropical savannah of the Orinoco region [69–70], an ecoregion that contains both 55% of Colombia's wetlands [71] and the Orinoco-Amazon JCU [11]. Wetlands in this region, as elsewhere in Colombia, lack protection.

The Ramsar Convention, which requires a national policy for the management and protection of wetlands and their biodiversity, has resulted in the establishment of only five Ramsar sites in Colombia. A Ramsar site is defined as 'a wetland of international importance that contains representative, rare or unique wetland types important for maintaining biodiversity, supporting threatened species or communities and providing refuge during adverse conditions in a particular biogeographic region' [72]. The Estrella Fluvial Inírida is the only Ramsar site in Colombia's Orinoco ecoregion, where jaguars are present [37]. Ramsar sites are entirely absent from the middle Magdalena.

Around the world, Ramsar sites provide important habitat for large carnivores besides jaguars. These protected wetlands overlap several key tiger (*Panthera tigris*) conservation units such as the Sunderbans in Bangladesh and the Beeshazar region of the Terai landscape in Nepal [73]. In the Terai, tiger occupancy is positively correlated with wetlands, particularly the highly productive alluvial floodplains and riverine forests, both of which harbor high densities of ungulate prey [74–75]. Similarly, the Osceola National Forest-Okefenokee Swamp ecosystem provides important foraging habitat for one of the largest remaining black bear (*Ursus americanus*) populations in the southeastern USA [76].

The lack of a positive correlation between detections of jaguars and their terrestrial mammalian prey raises hypotheses about wetlands as important foraging areas for jaguars. Across our study area, the ratio of detections of jaguars and principal mammalian prey was 1:1 for peccary and paca, 1:0.57 for armadillo, 1:0.21 for capybara, and 1:0.13 for giant anteater. These ratios are suggestive of a depleted mammalian prey base because camera trap surveys—even those targeting jaguars—generally record more detections of prey than jaguars [16, 34, 55].

In wetlands, significant proportions of jaguar diet may be comprised of aquatic and semi-aquatic species [23, 25–26, 77]. In the middle Magdalena, potential reptilian prey include spectacled caiman (*Caiman crocodilus*), American crocodiles (*Crocodylus acutus*), Magdalena River turtles (*Podocnemis lewyana*) and Colombian slider turtles (*Trachemys callirostris*). In flooded forests of the Amazon basin, spectacled caimans were recorded in 41% of jaguar scat samples [78] and reptiles comprised 36% of jaguar diet in the floodplains of the San Jorge and Cauca rivers [24], which are located 150 km northwest of our study area. We observed evidence of jaguar depredation on Colombian sliders in the middle Magdalena where this species is widely distributed [79].

We recommend future studies in wetland areas examine the importance of reptilian prey, which were undetected by our terrestrial, heat-sensitive camera traps. Also, we suggest finer-scale analyses that differentiate jaguar habitat use of specific wetland habitat types (i.e. marshes, swamps, and floodplain forests). Globally, there are significant data gaps for the spatial extent of wetland classes—particularly for lower order streams, ponds, and marshes [80]—but recent advancements have contributed to improved inventories at regional scales [81].

Finally, we stress the importance of long-term monitoring to evaluate trends in jaguar habitat use and occupancy in the middle Magdalena. As the proportion of oil palm and pasture

increases relative to forests and wetlands, the habitat is likely to become less suitable for jaguars. For example, recent camera trap surveys did not detect tigers in oil palm landscapes of lowland Peninsular Malaysia [82–84], which is one of their historical strongholds [85–86]. Globally, most palm oil is produced in Malaysia and Indonesia where its destructive impacts on threatened species have been well documented [87–90].

With oil palm cultivation projected to increase in Latin America—including Colombia [69–70]—there is greater urgency to collect data on jaguars in oil palm landscapes to guide the identification and implementation of appropriate land use planning and zoning measures. Our results suggest that jaguars may tolerate oil palm smallholdings but avoid large-scale plantations because habitat use declined significantly once extent of plantation coverage reached ~50% of the area inside 3 km buffers around camera traps. Jaguar avoidance of oil palm plantations is likely a response to the depauperate prey bases and greater rates of human disturbance in these monocultures [33–35, 87].

## Conclusion

Evaluation of occupancy and habitat use at large spatial scales is necessary for identifying the ecological needs of wide-ranging species [8, 91]. To our knowledge this study is one of the largest, in terms of spatial coverage and sampling effort, to survey jaguars with camera traps using an occupancy approach. On the basis of our results, we propose that wetlands receive greater consideration as keystone habitats for jaguars. Keystone habitats have disproportionately large effects relative to their availability and contain resources (i.e. reptilian prey for jaguars) not provided by other available habitats [92]. Wetlands comprise ~30% of the Amazon basin [93] where 16 Ramsar sites span some 342,084 km<sup>2</sup>, 4.9% of the entire basin. Beyond the Amazon basin—which is the jaguar’s range-wide stronghold [10–11, 39]—favorable policies for wetland conservation are grossly lacking [93–95]. For example, there are only 11 Ramsar sites spanning some 1,330 km<sup>2</sup> in the Tumbes-Chocó-Magdalena hotspot [S2 Table]. Greater protection of wetlands and riparian buffers—which is already required under Colombian law (Resolution No. 200.41.11–1130, 2011) [96]—could facilitate jaguar persistence in fragmented landscapes and areas undergoing oil palm and pasture development.

## Supporting information

**S1 Fig. Overlap between oil palm plantations and modeled jaguar corridors in Colombia.** (TIF)

**S2 Fig. Example showing the radii buffers of 1 km, 3km, and 5 km (3.14, 28.27, and 78.54 km<sup>2</sup>) around camera trap site.**

(TIF)

**S1 Table. Jaguar detection matrix uploaded to PRESENCE version 12.17.**

(XLSX)

**S2 Table. Ramsar sites in the Tumbes-Chocó-Magdalena biodiversity hotspot.**

(XLSX)

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