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Cross-Continental Insights into Jaguar (Panthera onca) Ecology and Conservation

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CROSS-CONTINENTAL INSIGHTS INTO JAGUAR (*Panthera onca*) ECOLOGY AND CONSERVATION

by

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ABSTRACT

The jaguar *(Panthera onca)* is a widely distributed large carnivore and the focal species of a range-wide connectivity initiative known as the jaguar conservation network (JCN). Comprised of ~83 Jaguar Conservation Units (JCUs) and ~75 corridors from northern Mexico to Argentina, the JCN functions as a conduit for jaguar movement and gene flow. Key linkages in the network are imperiled by human population growth, large-scale agriculture, highway expansion, and other infrastructural development. Labeled "corridors of concern," these vulnerable linkages are imperative to the maintenance of connectivity and genetic diversity throughout jaguar distribution. I take a multi-faceted approach to analyze conservation issues and identify potential solutions in three of the most vulnerable connections of the JCN. I estimate densities and assess local residents' perceptions of jaguars in a fragmented JCU in western Mexico, analyze 3 years of data from 275 camera-trap sites to evaluate jaguar habitat use in a corridor of concern in Colombia, and quantify the umbrella value of jaguars for endemic herpetofauna in Nuclear Central America, a ~ 370,000 km^2 sub-region of the Mesoamerican biodiversity hotspot. My research produces the first jaguar density estimate in a JCU containing human population densities >50 people/km^2 and provides the strongest support for jaguar association with wetlands collected to date. In Nuclear Central America, one of the most important yet vulnerable areas of the JCN, I demonstrate the umbrella value of this wide-ranging felid. I conclude with a discussion on the need to reevaluate extirpation thresholds of jaguars in human-use landscapes, to direct more research on wetlands as keystone habitats for jaguars, and to further assess the utility of umbrella analyses using jaguars as focal species to support holistic conservation planning.

To *Panthera onca*, for teaching me the value of perseverance.

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LIST OF ACRONYMS

AOO	Area of Occupancy
EOO	Extent of Occurrence
FAO	Food and Agriculture Organization of the United Nations
IUCN	International Union for Conservation of Nature
JCN	Jaguar Conservation Network
JCU	Jaguar Conservation Unit
MBC	Mesoamerican Biological Corridor
NCA	Nuclear Central America
PA	Protected Area
SBM	San Blas Municipality
SECR	Spatially Explicit Capture–Recapture
SSL	Serranía San Lucas
SYNP	Serranía de los Yariguíes National Park
TDF	Tropical Dry Forest

CHAPTER ONE ~ INTRODUCTION[1]

Extending from the pine-oak woodlands in northern Mexico to the thorn forests ~8,500 km south in northern Argentina, the range-wide jaguar conservation network (JCN) encompasses ~75 corridors connecting jaguar populations in ~83 Jaguar Conservation Units (JCUs) (Figure 1) (Sanderson et al. 2002, Rabinowitz & Zeller 2010, Silveira et al. 2014, Olsoy et al. 2016). Functioning as a conduit for dispersal and movement, the JCN aims to increase landscape and genetic connectivity for jaguars which, unique among large carnivores, remain a single taxon (Eizirik et al. 2001).

Key corridor linkages throughout jaguar distribution are critically imperiled by rising human population densities, large-scale agriculture (including oil palm monoculture), and extensive infrastructural development (Rabinowitz & Zeller 2010, Figel 2011, De Angelo et al. 2013, Silveira et al. 2014, de la Torre et al. 2017). Corridors fragmented by such threats are more likely to contain lower genetic diversity and smaller effective population sizes (Luo et al. 2004, Wultsch et al. 2016). Consequently, these populations have poorer reproductive fitness and less resistance to disease, ultimately increasing probabilities of extirpation and extinction (Lacy 1997, Frankham 2005, Haag et al. 2010).

Vulnerable linkages of the JCN overlap my study sites in Nayarit, Mexico, Colombia's middle Magdalena River valley, and Nuclear Central America (NCA), a ~ 370,000 km² sub-region of the Mesoamerican biodiversity hotspot (Myers et al. 2000). Defined as the mainland area between the Isthmus of Tehuantepec in southern Mexico and the Nicaraguan Depression in

[1] Adapted from Figel JJ. 2014. Working Landscapes and the Western Hemisphere Jaguar Network. Pgs. 123-136 in J Levitt, ed. *Conservation Catalysts: The Academy as Nature's Agent.* Lincoln Institute of Land Policy. Cambridge, Massachusetts, USA.

northern Nicaragua (excluding Belize and the Yucatan Peninsula) (Schuchert 1935), NCA is a topographically and ecologically diverse region with high levels of endemism (Campbell 1999, Townsend 2014) and threat (Wultsch et al. 2016, de la Torre et al. 2017)

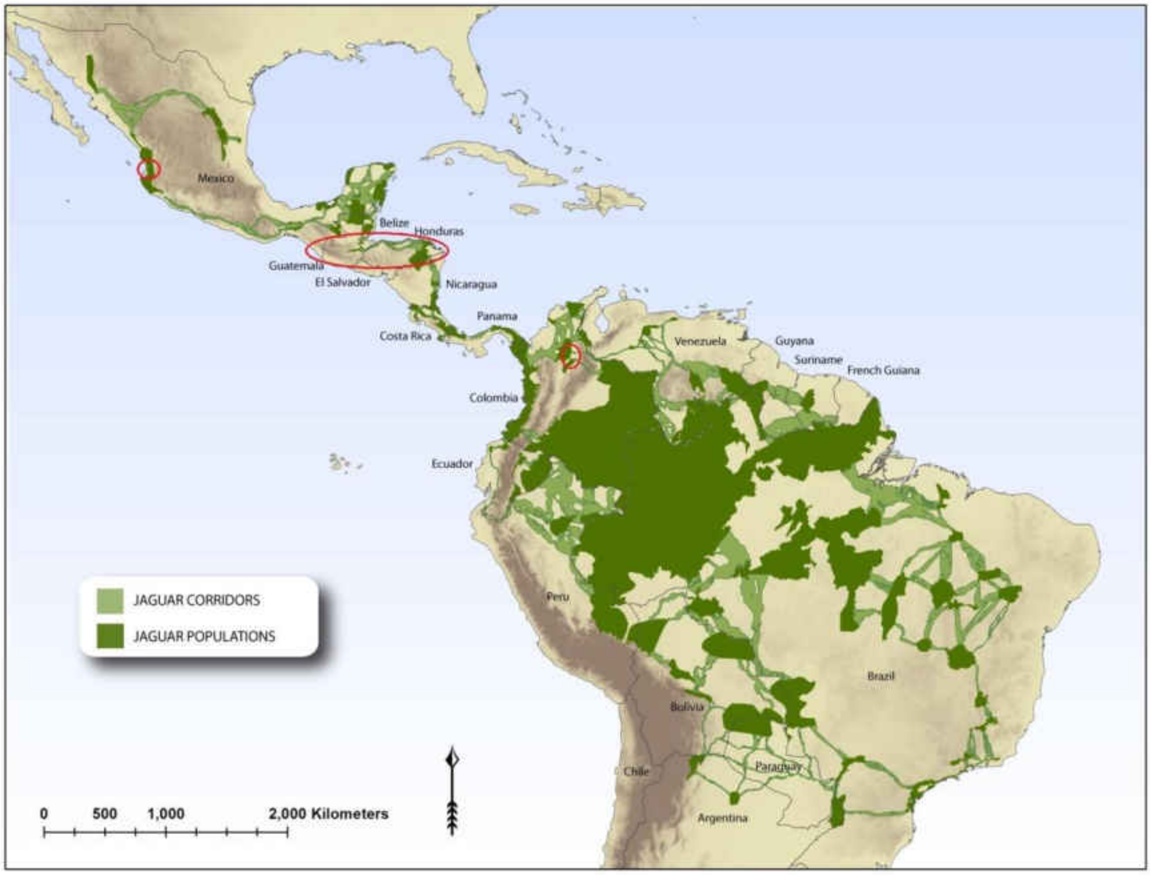

Figure 1. My three study areas (circled in red) within the range-wide jaguar conservation network. Map provided by Panthera.

Jaguars in each study area are threatened, to varying degrees, by high human population densities (up to 410 people/ km^2 on the north coast of Honduras), clandestine hunting, and expanding agriculture (Figure 2 and 3). Colombia and Honduras, in particular, are experiencing rapid development of oil palm plantations (Garcia-Ulloa et al. 2012, FAO 2014), which are characterized by low species diversity and decreased abundances of threatened taxa (Maddox et al. 2007, Cunha et al. 2015).

Indonesia and Malaysia currently account for 65% of the global oil palm cultivation area (FAO 2014). However, significant expansion is projected in the Neotropics (Butler & Laurance 2008, Garcia-Ulloa et al. 2012, Dinerstein et al. 2015) to meet the rising demand for palm oil, which is the most widely produced vegetable oil in the world (Corley & Tinker 2015). Plantation developers target well-drained coastal lowlands and inland alluvial floodplains (Trafton & Washburn 1968, Corley & Tinker 2015), which are productive habitats also favored by jaguars (Scognamillo et al. 2003, Tobler et al. 2013).

Depauperate monocultures already overlap critical linkages of the JCN from southeastern Mexico to the Amazon basin (Figel 2011, Aguilar-Gallegos et al. 2015, Cunha et al. 2015). Among jaguar range countries, oil palm plantation area is greatest in Ecuador (2,720 km^2), Colombia (2,665 km^2), Honduras (1,300 km^2), Brazil (1,266 km^2), and Guatemala (1,100 km^2) (FAO 2014). Plantation area is increasing in Costa Rica, Mexico, Venezuela, and Peru (FAO 2014).

Figure 2. Photographed by a remote camera, armed farmers accompanied by hunting dogs move through agricultural areas in Colombia (left) and Nayarit, Mexico (right). They are pursuing animals preyed upon by jaguars.

Figure 3. A depauperate expanse of oil palm monoculture in Honduras. Photo provided by HB Quigley.

Colombia is disproportionately important for the viability of the JCN because its northern border represents a critical intercontinental connection between jaguar populations in Central and South America (Figure 4). Nuclear Central America, a region under severe threat, comprises the linkage between two of the largest JCUs in Central America: the Maya Forest in the Yucatan Peninsula and Río Plátano-Bosawas Biosphere Reserves flanking the Honduras-Nicaragua border (Sanderson et al. 2002). In Nayarit, my study area is embedded in a vulnerable corridor connecting two of the most important protected areas for jaguars on Mexico's Pacific Coast: the *Marismas Nacionales* and the Sierra de Vallejo Biosphere Reserves (Figel et al. 2016).

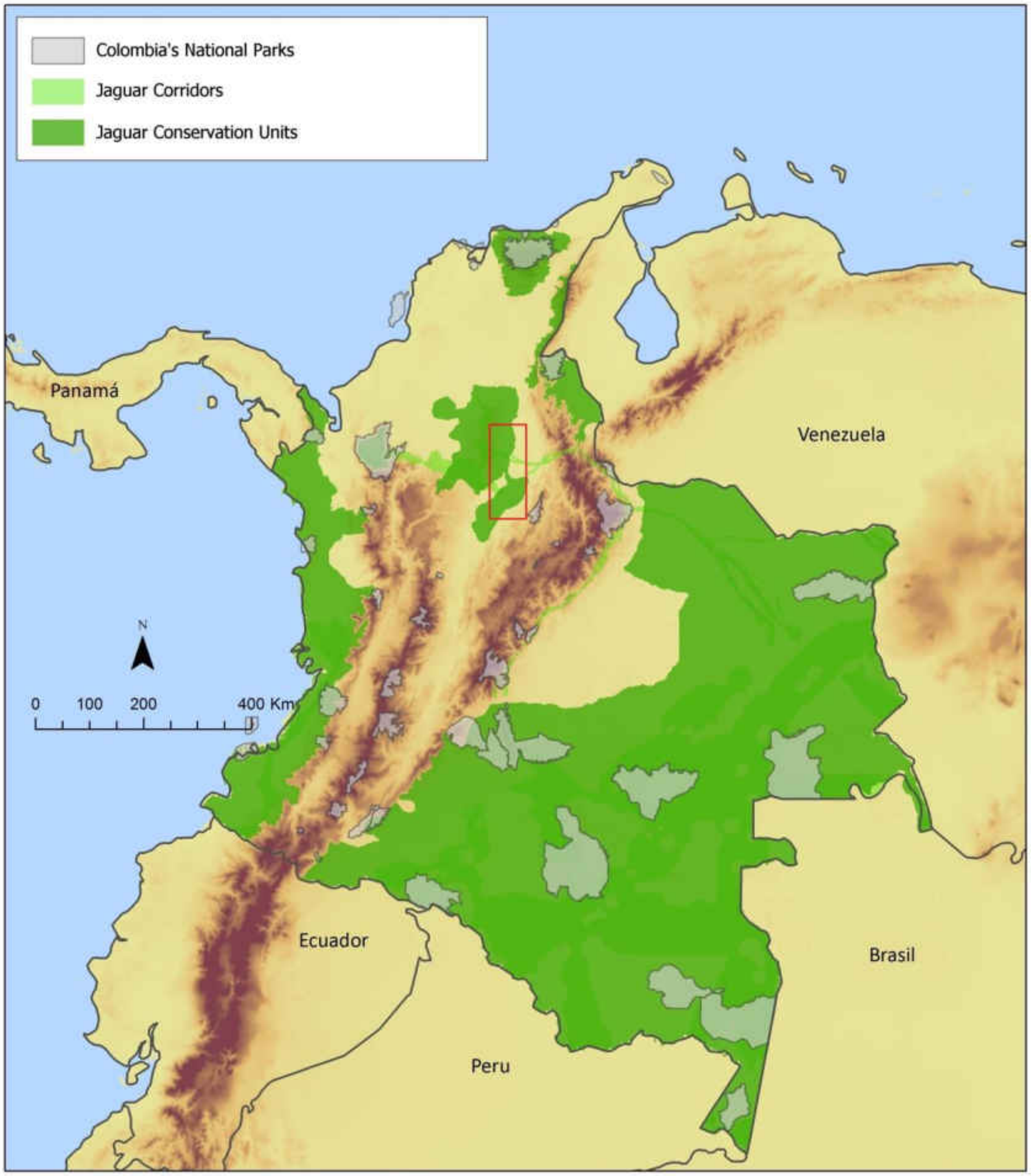

Figure 4. Colombia's northwestern border is a crucial linkage for the Jaguar Conservation Network. My study area in the middle Magdalena River valley is framed in red. Map provided by Panthera.

My study sites in Mexico, Honduras, and Colombia have disparate histories of anthropogenic disturbance, an important consideration for large landscape conservation planning

(Noss & Daly 2006). Jaguars will likely be more dependent on active restoration in Nuclear Central America, where the spatial and temporal extent of habitat conversion is much greater than Nayarit and Colombia's middle Magdalena River valley (Standley 1931, Yuncker 1940, Trafton & Washburn 1968). During field surveys in the early 20th century, American botanist Paul Standley believed the fauna of the Lancetilla Valley in northern Honduras included "probably an occasional jaguar" (Standley 1931). By 2014, the extent of palm cultivated in Honduras comprised ~1,300 km^2 (FAO 2014) which, collectively, is nearly equal the area of the largest JCU (Texiguat-Pico Bonito) on the country's north coast. Conversely, late 19th century explorers in the Magdalena floodplains of Colombia reported the forests to "abound" with "plentiful" jaguars (Millican 1891).

In western Mexico, the historical jaguar literature is prodigious. For decades after the turn of the 20th century, the *Marismas Nacionales* (hereafter, *Marismas*) in coastal Nayarit was a fertile collecting and hunting destination. In 1904, on behalf of the American Museum of Natural History, professional collector James H. Batty collected mammals out of the town of Escuinapa, Sinaloa, which is the northern gateway to the *Marismas* (Allen 1906). In the ensuing decades, the *Marismas* was targeted by North American outfitting and collecting expeditions, most of which specifically sought jaguars as trophies (Carmony & Brown 1991). Dale Lee and his brothers were pioneer houndsmen who specialized in guiding jaguar hunts to the *Marismas* where they took the majority of the 124 jaguars they killed during their 1935-1965 hunting career (McCurdy 1979). Of the 45 North American jaguar records maintained by the Boone & Crockett Club from 1955 to 1983, 24 (53%) originated from Nayarit's coastal mangroves, in (Nesbitt & Wright 1981).

Thus, one of my primary objectives, covered in Chapter 2, was to assess the present status of jaguars in coastal Nayarit after decades of intensive hunting in their historical stronghold. To further analyze factors contributing to jaguar persistence, I conducted interviews with local people to document sightings and assess perceptions of the species.

In Chapter 3, I evaluate jaguar presence in Colombia's middle Magdalena River valley, in an attempt to elucidate the factors contributing to the species' persistence in a landscape heavily transformed by cattle pasture and oil palm plantations. I analyze 3 years of detection, non-detection data (2013-2016) from 275 camera-trap sites to estimate detection probabilities and measure the associations between jaguar presence and habitat, landscape, and prey covariates.

In Chapter 4, I present results of the first multi-taxon evaluation of the jaguar's umbrella value. I demonstrate how jaguars can serve as an effective umbrella for co-occurring endemics, especially amphibians, in NCA. Substantiation of multi-taxa dependence on the jaguar network could strengthen policy measures and aid the selection of priority areas to maximize conservation benefit.

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CHAPTER 2 ~ DENSITIES AND PERCEPTIONS OF JAGUARS IN COASTAL NAYARIT, MEXICO[2]

Introduction

Jaguars (*Panthera onca*) have been eradicated from approximately 60% of their historical range in Mexico, where they are considered endangered (SEMARNAT 2002, Chávez & Ceballos 2006). The *Marismas Nacionales* (hereafter, *Marismas*) in the state of Nayarit represents the northernmost semiaquatic habitat for jaguars where the species' prey base includes American crocodiles (*Crocodylus acutus*) and freshwater turtles (*Trachemys* spp.; Brown & López-González 2001). Unlike jaguar habitat in the more arid states of Sinaloa and Sonora to the north that have prolonged dry seasons and <800 mm annual rainfall, the *Marismas* has a wetter climate and contains the largest tract of Pacific coast mangroves (*Laguncularia* and *Avicennia* spp.) in North America (Flores-Verdugo et al. 2001).

Extending from the vicinity of Escuinapa, Sinaloa, to San Blas, Nayarit, Mexico, the *Marismas* represents approximately 22% of the total mangrove cover in Mexico (Ruiz-Luna et al. 2010). Designated a Ramsar wetland of international importance in 1995 (Ramsar site no. 732; RSIS 1995), and declared a Biosphere Reserve in 2010 (DOF 2010), the *Marismas* has been an area reportedly associated with robust jaguar populations for more than half a century (Leopold 1959, McCurdy 1979, Carmony & Brown 1991, Brown & López-González 2001, Brown & Thompson 2010). Leopold (1959) identified coastal Nayarit as 1 of 4 areas in Mexico believed to contain the greatest densities of jaguars anywhere in the country.

However, Nayarit's mangroves and tropical dry forests (TDF) have undergone extensive deforestation and its highway network has expanded since Leopold's surveys in the 1950s

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(Kramer & Migoya 1989, Ramírez-García et al. 1998). The opening of an artificial channel—Canal de Cuautla—in 1972 drastically altered salinity in the *Marismas,* from predominantly freshwater–brackish to marine, resulting in the death of 24% of the white mangrove (*Laguncularia racemosa*) and black mangrove (*Avicennia germinans*) forests (Flores-Verdugo et al. 2001). From the 1970s to 2005, the *Marismas* lost >10,000 hectares (ha) of mangroves—about 13% of its total extent (Ruiz-Luna et al. 2010). Much of the southern *Marismas* is now covered by expansive private-sector shrimp farms (Berlanga-Robles & Ruiz-Luna 2006) and construction of a new highway is ongoing.

Despite the loss of mangrove vegetation communities and expansion of paved roads, coastal Nayarit was classified as one of 9 Priority II regions for jaguars in Mexico—areas that contain suitable habitat but where jaguar status has not been systematically evaluated (Chávez & Ceballos 2006). There have been no camera-trap surveys of jaguars in coastal Nayarit since 1987 when jaguar hunting was banned and the species first received legal protection in Mexico.

Our objectives were to 1) estimate jaguar abundance and density using spatially explicit capture–recapture (SECR) methods, 2) test *a priori* hypotheses about the influence of human population densities on jaguar presence, and 3) document human perceptions and sightings of the species in the *ejidos* (government-recognized forms of communal land tenure) of coastal Nayarit. *Ejidatarios (ejido* members) are important stakeholders for jaguar conservation in Mexico because they collectively manage their natural resources and are sole owners of their territories, which overlap approximately 80% of the remaining forest cover in the country (Bray et al. 2006). A 'critical human density index' posited by Woodroffe (2000), estimated a 50% likelihood of extinction for jaguars once human population densities—measured at the state, district, or county level—reach 17.3 people/km^2. Given the relatively high human population densities of 51 people/km^2 in our study area and because humans are the primary cause of large carnivore mortality (Noss et al. 1996, Brown & López-González 2001, Vickers et al. 2015), we sought a better understanding of perceptions and tolerance of jaguars in this diverse landscape.

Methods

Study area

Our study area was in the San Blas Municipality (SBM) in west-central Nayarit, Mexico, at 105°17′W, 21°32′N, in and around the southern border of the 133,854-ha *Marismas Nacionales* Biosphere Reserve, officially declared on May 12, 2010. Encompassing 850 km^2, the SBM had a population of 43,120 inhabitants (INEGI 2010), 24% of who reside in the town of San Blas. Mean annual temperature was 26° C and mean annual rainfall was 1,400 mm, which accumulated mostly during June–October and the driest months were February–April.

Maritime wetland dominants included red mangrove (*Rhizophora mangle*), button mangrove (*Conocarpus erectus*), black mangrove, and white mangrove (Brown et al. 2007); the latter two being most common (Ramírez-García et al. 1998). The corozo palm (*Arecaceae* spp.) was a characteristic tree of the TDF along with figs (*Ficus* spp.), gumbo-limbo (*Bursera simaruba*), cohune palm (*Attalea cohune*), kapok (*Ceiba pentandra*), feather acacia (*Lysiloma divaricatum*), rosa-maria (*Tabebuia* spp.), and other drought-deciduous species (Gentry 1982).

Two of the most important economic activities in the SBM were fishing and shrimp farming, with 1,900 ha of shrimp culture ponds present (CONAPESCA 2010). The SBM was also the top-producing municipality in Nayarit for mangos (*Mangifera* spp.) and bananas (*Musa* spp.). These crops comprised most of the cultivated land, occupying 11,610 ha and 6,084 ha, respectively (SAGARPA 2011). Average plot size was 6.5 ha for mangos and 8 ha for bananas.

Small-scale cattle ranching was practiced in the *ejidos* of La Palma, La Libertad, Las Palmas, and Navarrete.

We selected the SBM as our jaguar study area, in part, because of the species' priority status (Chávez & Ceballos 2006, Zeller 2007); jaguars had not yet been systematically surveyed in the SBM despite historical literature anecdotally documenting robust populations since the 1950s (Leopold 1959, McCurdy 1979, Carmony & Brown 1991, Brown & López-González 2001, Brown and Thompson 2010). The northern SBM is an ecotone, connecting Sinaloan TDF with the mangroves of the *Marismas* (Brown et al. 2007), where jaguars have year-round access to sources of freshwater and reptilian prey biomass unavailable in the upland forests. We wanted to sample the intact mangroves subject to the east–west connections with TDF of the Sierra Madre Occidental severed further north by the construction of the Tepic-Culiacán 4-lane Highway 15D in 2008.

Camera Sets

We deployed digital (Reconyx RC-55, Holmen, WI, USA; and Cuddeback Attack, Green Bay, WI, USA) and film (CamTrakker, Watkinsville, GA, USA; and DeerCam, Park Falls, WI, USA) camera traps at the extreme southern end of the *Marismas Nacional*es ecoregion in accordance with the 'National Census of the Jaguar and its Prey' (CENJAGUAR) (Figure 5). The CENJAGUAR was proposed by Mexican biologists to standardize camera-trap methods for surveying jaguars in the country (Chávez and Ceballos 2006). We followed the CENJAGUAR protocol so study results could be compared with other national survey sites.

The town of San Blas was <3 km west of our 194-km^2 camera-trap polygon within which there were 5 *ejidos* with human populations averaging 579 inhabitants per *ejido* (range = 50–

1,581). To maximize capture rates, we selected camera-trap sites based on jaguar sign recorded during our reconnaissance surveys of the study area. We also placed cameras at sites where *ejidatarios* reported sightings or provided evidence of jaguar presence (e.g., fresh kills, scrape marks on trees, or jaguar pugmarks). We placed camera traps 30–45 cm above the ground at 27 locations. We used stratified sampling to deploy cameras in secondary TDF (n = 12 sites), mangroves (n = 7), banana plantations (n = 4), and mango plantations (n = 4), setting cameras along forest trails (n = 11), dirt roads (n = 9), dry stream beds (n = 5), and at waterholes (n = 2). We did not use baits or lures.

Cameras were active 24 hours/day during a 64-day sampling session that overlapped the dry to wet season transition from 4 April through 7 June 2010. We considered each camera-trap-night as a single trapping occasion. We checked the film cameras for film and battery replacement approximately every 10 days and revised the digital cameras every 3–4 weeks. Camera sites ranged in elevation from sea level to 475 m ($\bar{x}$ = 157 m). To meet a key assumption of closed population abundance estimation (that no individual within the study area has a detection probability of zero; Wilson & Anderson 1985), we set cameras at distances of <3.6 km and >800 m between each camera. This spacing ensured there were no gaps larger than a jaguar's home range where an individual cat could go undetected within the sampling area.

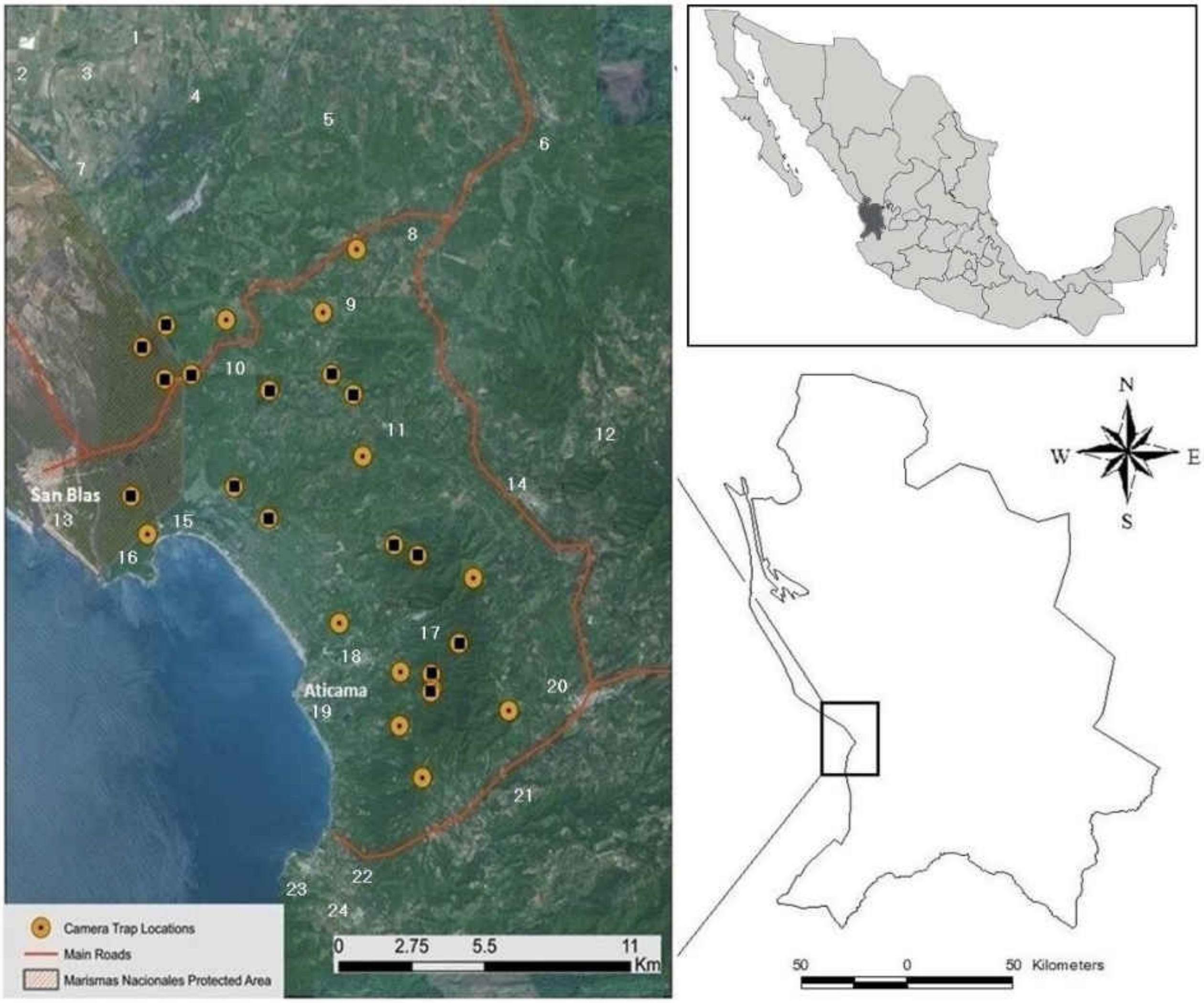

Figure 5. Camera-trap sites and localities of interviews of residents about perceptions of jaguars in the San Blas Municipality, Nayarit, Mexico. The black squares denote jaguar "photo-captures" recorded during 64-day sampling period from April to June 2010. The numbers indicate interview localities (see Appendix A for locality names).

Interviews

For interviews, we applied a 30-question structured interview survey to 82 local residents in 24 SBM localities. We informed interviewees that we had no affiliation with government entities or local agencies and that their responses would be considered anonymous. We conducted all interviews following verbal consent of participants. J.J.F and F.R.G employed ‘snowball’ sampling, a technique where respondents identify other person(s) who may have seen jaguars or have information about jaguars in the area. Snowball sampling is particularly well-suited when specific segments of a population are involved (e.g., hunters; Goodman 1961). Targeting fishermen, hunters, and other individuals who spend a lot of time in the forest can generate more information with less effort than random sampling (Figel 2008).

We selected interviewees based on leads identified during our snowball sample, prioritizing individuals with putative knowledge of jaguars in new localities rather than continuing interviews in any single *ejido*. Before beginning an interview, we showed photographs of native and nonnative felids to test interviewee knowledge. If the participants could not identify a jaguar, referred to any spotted wild cat as a jaguar, or did not understand that >1 species of wild cat was native to the region, we politely and inconspicuously discontinued the interview.

Once interviewees who could correctly identify jaguars were selected, we inquired about any interaction they experienced with jaguars, their attitude or opinion toward jaguars, prey sightings, and present hunting levels. We recorded the type of interaction (sighting, depredation, vocalization), date, place, and time.

Data Analysis

We used the software SPACECAP version 1.1.0 (Gopalaswamy et al. 2012) in R version 3.2.2 (R Core Team 2014) for the SECR analysis. Spatially explicit capture–recapture methods are advantageous to conventional capture–recapture estimation of animal populations because they eliminate the need for an ad hoc estimation of effective sampling area (Noss et al. 2012). Previous jaguar camera-trap studies (e.g., Silver et al. 2004) calculated effective sampling area using the mean maximum distance moved or one-half mean maximum distance moved of jaguars generated from camera-trap survey data, which usually results in overestimation of densities (Soisalo & Cavalcanti 2006, Foster & Harmsen 2011, Tobler and Powell 2013).

Data input files required by SPACECAP include 1) animal capture details (e.g., information on animal identification, trap location, and sampling occasion); 2) trap deployment details (e.g., spatial location, dates when cameras were active, and sampling occasion designation); and 3) state–space details (e.g., a mask of equally spaced points overlapping the trap area and a surrounding buffer, representing potential animal activity centers). We calculated the mask after Royle et al. (2013), who proposed a buffer distance of 2(σ) where σ = the home range radius of the target species. Estimated mean male jaguar home ranges are 36.6 km^2 ± 15.6 km^2 in the Chamela–Cuixmala Biosphere Reserve (Nuñez 2006), roughly 225 km south of our study area. Based on these home range estimates, we used ArcGIS 9.2 (ESRI Inc., Redlands, CA, USA) to create a 12.8-km buffer surrounding the camera-trap polygon to minimize the probability of photo 'capturing' any individual animal outside the buffered area.

A key assumption of the SPACECAP model is that animals occupy randomly dispersed and circular home ranges, and successive trapping occasions are independent. The program does not rely on the assumption of geographic closure, unlike traditional non-spatial capture–recapture models (Otis et al. 1978). We used SPACECAP rather than other SCR packages in R because SPACECAP is less sensitive to sparse data sets (Noss et al. 2012).

We considered jaguar photographs taken at each camera station to be independent if images were obtained >1 hour apart. We used χ^2 tests to determine detection differences between male and female jaguars at camera-trap sites. Five observers and 2 additional jaguar researchers identified individuals from their unique pelage patterns. We discarded 4 blurry photos from the analysis and only included individuals where unequivocal agreement among the 7 reviewers was reached that each jaguar was a distinct individual. Observer agreement was 100% for the sampling timeframe although there was uncertainty about individuals (min. of 1, max. of 3, depending on the observer) photographed during our 2009 reconnaissance and 2012 monitoring surveys (but not during our 2010 sampling period). This observer uncertainty did not affect our density estimate, however, because all unidentifiable jaguar(s) were photographed outside the 64-day window of the 2010 data set.

For interviews, we classified responses about sightings of jaguars and prey species into 4 sub-categorical variables after Zeller et al. (2011): undetected (not seen), rare (observed once/year), moderate–sometimes (seen twice/year to once/month), and frequent (observed > once per month). We used Kruskal–Wallis and χ^2 tests to differentiate perceptions of jaguars among livestock owners and other *ejidatarios* who reported jaguar sightings. We set α at <0.05 for all statistical tests.

Results

We accumulated 90 photographs of 9 individual adult jaguars—2 males, 5 females, and 2 individuals of unknown sex during a total sampling effort of 1,575 trap-nights (Table 1). One of the females was pregnant and another female was accompanied by a cub at a waterhole. We photographed jaguars at 16 of the 27 camera-trap sites, at elevations from 8 to 446 m ($\bar{x}$ = 143 m ± 131 SD). We obtained 30 jaguar photographs on dirt roads, 41 at waterholes, and 19 on trails in secondary TDF (n = 8 sites), mangrove (n = 5), banana plantations (n = 2), and mango plantations (n = 1) (Figure 6). The number of photographs recorded on roads, waterholes, and trails did not differ between male and female jaguars ($\chi^2_1 = 0.77$, P = 0.68). We did not photograph jaguars at the dry-stream-bed sites.

The greatest straight-line distance between detections of the same individual jaguar was 12.4 km and the mean maximum distance moved of individuals photographed more than once was 2.75 km. Using SPACECAP, we estimated a density of 2.04 (SE = 0.45) jaguars/100 km^2, within the range of other density estimates calculated across the species' distribution (Table 2).

Table 1. Capture histories of the 9 jaguars identified in San Blas, Nayarit, México, during the 9-week sampling period from April 2010 to June 2010. An entry of 1 indicates a photographic 'capture' of the individual. 'F' signifies female, 'M' male, and 'U' denotes individual of unknown sex.

Individual	Week								
	1	2	3	4	5	6	7	8	9
F1	0	0	0	0	0	1	1	0	1
F2	1	1	0	0	0	0	0	0	0
F3	0	0	0	1	1	1	1	0	0
F4	1	0	0	0	0	0	0	0	0
F5	0	0	0	0	0	0	0	0	1
M1	0	1	0	0	0	0	0	0	0
M2	0	1	1	1	0	0	1	0	0
U1	1	0	0	0	0	0	0	0	0
U2	0	0	0	0	0	0	0	1	0

Figure 6. Female jaguar photographed in *ejido* banana plantation in the San Blas Municipality, Nayarit, Mexico, in June 2010.

Interviews

We completed 82 structured interviews with *ejidatarios* at 24 localities ($\bar{x}$ = 3.42 interviews/locality; range = 2–10). Males comprised 95% of the interviewees; the youngest respondent was 20 years old, the oldest was 94 years, and the mean age was 43 years. Twenty-two percent of respondents claimed to have seen jaguars within the past year (at time of interview) albeit at varying frequencies, and 75% stated a positive perception of jaguars (Appendix A). There was no association between whether individuals had seen a jaguar within the previous year and their perception of jaguars (χ^2_2 = 0.478, P = 0.80) and no association between interviewee age and their perception of jaguars ($\chi^2_2 = 0.35$, P = 0.86). Respondents who held a negative opinion of jaguars said they were harmful to livestock and/or dangerous. Livestock owners held the mostly negative perception of jaguars (Kruskal–Wallis $\chi^2_1 = 6.49$, P = 0.02).

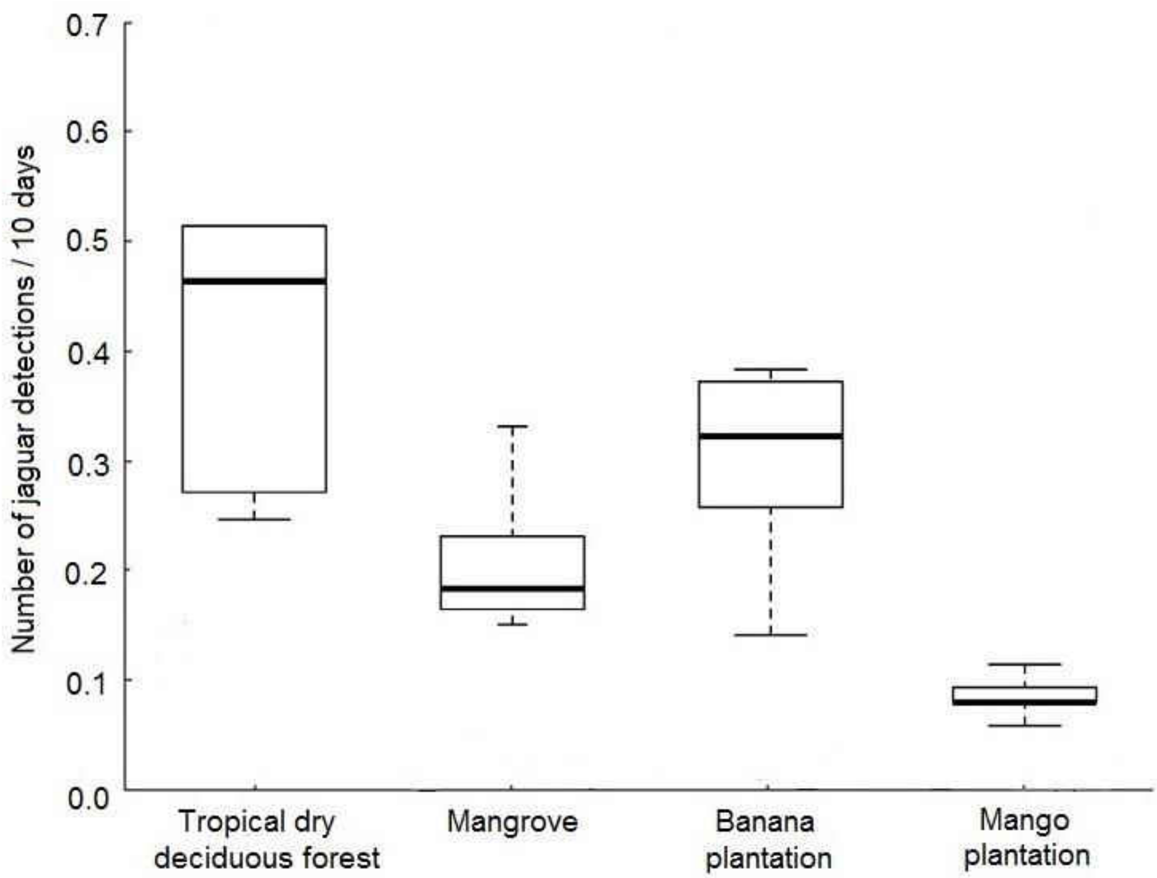

Figure 7. Number of jaguar camera-trap detections/10 days in natural and agricultural habitats in San Blas, Nayarit, Mexico, during April–June 2010.

Some respondents (13 of 82; 16%) stated they tolerated jaguars because they thought these cats limited agricultural depredations. Animals such as collared peccaries (*Pecari tajacu*) and coati (*Nasua nasua*) are considered pests in some parts of Mexico because of their foraging raids into cultivated *milpas* (Figel 2008). In response to the open-ended question, “What is your opinion about jaguars living on your community's land?", 15% of all positive answers described jaguars as *espantaparajos* (scarecrows). Other positive answers related to the jaguars beauty (37%), as an animal deserving of respect or protection (30%), or because they were viewed as a symbol of the country's natural heritage (18%).

Respondents reported killing 6 jaguars during 2000–2012. Four killings were in retaliation for livestock depredation in a single *ejido*. We obtained photographs to document 1 of the killings and observed 2 mounted jaguars and 3 jaguar skins in San Blas (Figure 8). Seven percent of respondents claimed to have hunted jaguar prey animals in the past year and 12% of the respondents believed that collared peccaries—an important prey species for jaguars (Foster et al. 2010)—had been extirpated from the region due to overhunting.

Figure 8. These mounted specimens represent 2 of the ≥ 6 jaguars killed from 2000–2012 in the San Blas Municipality, Nayarit, Mexico.

Table 2. Density estimates (D̂) for jaguars (individuals/100 km²) from camera-trap surveys in municipalities of varying human population densities (HPD) (per 1 km²) across the species' distribution. Surveys were conducted from 2003 – 2012. Methods are CCRC=conventional capture-recapture or SECR = spatially explicit capture-recapture. Effort = number of trap nights and *n*=number of individuals photographed.

Country	Municipality (state)	Munic. area	Munic. pop	Year	Method/effort	n	$\hat{D} \pm SE$	HPD[a]	Reference
Argentina	Puerto Iguazú	759	42,849	2006	CCRC/2,059	11	0.93 ± 0.2	56.45	Paviolo et al. (2008)
Mexico	San Blas (Nayarit)	850	43,120	2010	SECR/1,575	9	2.04 ± 0.45	50.73	This study
Mexico	Ocosingo (Chiapas)	9,447	198,877	2007–2008	CCRC/1,792[b]	5[b]	2.13 ± 1.03[b]	21.05	de la Torre and Medellín (2011)
Guatemala	Melchor de Mencos	2,098	21,409	2009	CCRC/1,035	9	2.91 ± 0.72	10.20	Moreira et al. (2010)
Brazil	Canto do Buriti, Coronel José Dias, São João do Piauí, São Raimundo Nonato	2,548[c]	19,985[c]	2007	CCRC/1,249	12	1.28	7.84[c]	Silveira et al. (2010)
Mexico	Lazaro Cardenas (Quintana Roo)	3,288	25,333	2008–2012	SECR/1,610[b]	7[b]	1.95 ± 0.76[b]	7.7	Ávila-Nájera et al. (2015)
Brazil	Mineiros	8,896	52,964	2008	SECR/—	10	0.29 ± 0.10	5.95	Sollmann et al. (2011)
Panama	Chepigana	7,309	27,461	2006	CCRC/1,100	4	2.69	3.76	Moreno-Ruiz (2006)
Brazil	Aquidauana	16,958	44,094	2003	CCRC/960[b]	28[b]	5.75 ± 0.89[b]	2.6	Soisalo and Cavalcanti (2006)
Peru	Manu	27,835	17,297	2005–2010	SECR/2,612[b]	13[b]	4.40 ± 0.7[b]	0.62	Tobler et al. (2013)

*Averaged because data were collected from multiple surveys.

‡ Averaged across municipalities.

Data sources by country for HPD: Instituto Nacional de Estadística y Censos – INDEC (Argentina) http://www.indec.gov.ar/, Instituto Nacional de Estadística y Geografía - INEGI (Mexico) http://www.inegi.org.mx/, Instituto Brasileiro de Geografia e Estatística - IBGE (Brazil) http://www.ibge.gov.br/home/, Instituto Nacional de Estadística y Censo – INEC (Panama) https://www.contraloria.gob.pa/inec/, Instituto Nacional de Estadistica – INE (Guatemala) http://www.oj.gob.gt/estadisticaj/files/poblacion-total-por-municipio1.pdf, Instituto Nacional de Estadística e Informatica – INEI (Peru), https://www.inei.gob.pe/estadisticas/indice-tematico/poblacion-y-vivienda/.

Discussion

Except for a camera-trap survey in northern Argentina that could be considered an outlier given its setting near an internationally visited tourist attraction (Paviolo et al. 2008), our study is the first to estimate jaguar densities among human population densities >50 inhabitants/km^2. Our results fail to support the Woodroffe (2000) 'critical human density index' model, which estimated a 50% likelihood of extinction for jaguars once human population densities reach 17.3 people/km^2, a figure 3 times less than the human population densities in our study area. An occupancy study using interviews in México's Yucatán Peninsula also found lower susceptibility of jaguars to critical human densities, predicting jaguar presence at human population densities of up to 130 people/km^2 in areas (including ejidos) with extensive forest cover, although the species was consistently absent from heavily settled areas (>290 people/km^2; Urquiza-Hass et al. 2009).

The ability of some large carnivores to inhabit heavily altered landscapes is widely recognized in many temperate ecosystems (Linnell et al. 2001, Basille et al. 2009, Vickers et al. 2015), but is virtually undocumented in the Neotropics. Our results add to an increasing body of evidence demonstrating the value of multiuse landscapes as complements to protected areas for large carnivore conservation. Identification of these landscapes and their ecological components has notable implications for the functioning of large-scale conservation initiatives such as the range-wide jaguar corridor (Rabinowitz & Zeller 2010).

Collectively, the *ejidos* in our study area comprise a potential corridor between jaguar populations in the *Marismas* and the Sierra de Vallejo Biosphere Reserve, 130 km to the south. Each *ejido* has an agreed division of land uses with defined areas for permanent agriculture, shifting cultivation, small-scale cattle ranching, as well as areas of forest. Areas designated for forest are often correlated with topography—in Jalisco *ejidos*, a statistical model developed by Morales-Barquero et al. (2015) predicted a 0.84% decrease in the probability of forest degradation for every 1% increase in slope. In our study area, we detected 6 of the 9 jaguars in hilly terrain around La Bajada and La Libertad, which remained heavily forested because these areas were unsuitable for any agriculture besides the approximately 3-ha plots of shifting cultivation embedded in TDF. The maintenance of early successional stages in forests and access to crops provided by shifting cultivation may enhance habitat for ungulates and other jaguar prey, thus offsetting some deleterious effects of human disturbance (Basille et al. 2009). Further work is needed to quantify prey distribution and abundances in varying SBM habitats to test this hypothesis.

The activities of small-scale farmers and fishermen in coastal Nayarit may not be compatible with strict protection, but they can present favorable alternatives to large-scale development projects. Since 2006, the Mexican government and private investors have allocated several billion U.S. dollars into infrastructure for the 'Riviera Nayarit' (ECLAC 2009), a 110-km stretch of coastline extending from San Blas to Punta Mita, 20 km northwest of Puerto Vallarta. In January 2010, as part of plans to develop the coastline's infrastructure to support tourism, construction of a new 38-km 2-lane highway connecting Tepic (Nayarit's capital) with San Blas was begun. The projected route of the highway bisects our camera-trap polygon, threatening the persistence of jaguars in the SBM. Jaguars, especially females, in southeastern Mexico displayed strong aversion to paved roads (Colchero et al. 2010), which are one of the greatest threats to large carnivores because they increase mortality through vehicle collisions and cause demographic isolation by inhibiting movement between populations (Noss et al. 1996, Vickers et al. 2015).

Although measuring response of jaguars to the new highway will require long-term monitoring, our data do not support a high likelihood of jaguar extinction in coastal Nayarit at present. The rugged topography, mangrove–upland connectivity, prey habitat maintained by the dynamic mosaic of shifting cultivation within TDF, and overall tolerance among *ejidatarios* have apparently given jaguars some refuge in the SBM. The small-scale livestock ranching is also noteworthy because it decreases the probability of widespread human–jaguar conflict, which is typically spurred by livestock depredation and results in retaliatory killing of jaguars (Brown and López-González 2001, Figel 2008). However, additional research is needed on the relationship between the killing of jaguars by humans and jaguar depredation on cattle in areas with varying livestock densities and herd sizes.

Our results suggest that jaguars may, at least in some areas, be less sensitive to human presence than previously believed, given tolerance of the animal's presence by residents (75% of respondents stated positive perceptions of jaguars) and sufficient access to prey and cover. Figel et al. (2011) documented positive perceptions of jaguars in community-conserved areas in Oaxaca; and studies in jaguar-occupied forests in the Yucatán found lower deforestation rates in community-managed areas, compared with bordering protected areas (Bray et al. 2004, Ellis and Porter-Bolland 2008). Yet data on human perceptions of jaguars in Mexico are lacking and more information is needed on the comparative status of jaguars and their prey in *ejidos* and protected areas beyond the tropical forests of southeastern México. Our deficiency of reptilian prey data in the mangroves and limited sampling of agricultural plots precluded wider inference on prey, populations of which are often functionally related with large carnivore abundance (Karanth et al. 2004). These limitations aside, our study demonstrates the importance of social–ecological research that accounts for human perceptions of large carnivores in unprotected areas. Future studies examining jaguar presence in relation to biogeographic variables, human infrastructure, and finer scale human population densities will allow for a better understanding of the mechanisms that facilitate jaguar persistence in human-dominated landscapes.

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CHAPTER 3 ~ SWAMP CATS: JAGUARS PREFER WETLANDS WITHIN AN INTERCONTINENTAL CORRIDOR THREATENED BY PASTURE AND OIL PALM DEVELOPMENT[3]

Introduction

A global analysis of forest cover change from 2000-2012 found the highest rates of deforestation in South American rainforests (Hansen et al. 2013). Large carnivores in the Neotropics may be especially susceptible to the effects of habitat loss and fragmentation due to their occurrence at low densities (Sollmann et al. 2011, Ripple et al. 2014), propensity for conflict with humans (Goldstein et al. 2006, Quiroga et al. 2016), and requirement for extensive tracts of habitat (Foster et al. 2010, de la Torre et al. 2017). Yet, empirical data on the response of large carnivores to habitat loss and fragmentation in the Neotropics is scarce and, in the case of jaguars (*Panthera onca*), most studies have not been conducted at sufficient scales necessary to accurately estimate population parameters and assess the species' habitat requirements (Tobler & Powell 2013).

Corridors have been the primary strategy to minimize the deleterious effects of fragmentation on populations of large carnivores (Carroll et al. 2001, Wikramanake et al. 2004, Proctor et al. 2015), including jaguars (Sanderson et al. 2002, Rabinowitz & Zeller 2010, Silveira et al. 2014). Corridors are intended to facilitate dispersal and establish connections between suitable habitat patches, putatively contributing to maintenance of genetic diversity, disturbances, and other ecological processes (Noss & Daly 2006, Gilbert-Norton et al. 2010). Mounting evidence suggests positive effects on species movements between patches for most

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taxa (Noss 1987, Beier & Noss 1998, LaPoint et al. 2013), including jaguars (Zeller et al. 2011, Wultsch et al. 2016).

Jaguars are the largest felid in the Americas and the largest terrestrial carnivore in the Neotropics. They favor lowland tropical habitats where their presence is strongly associated with water (Crawshaw & Quigley 1991, Cullen Jr. et al. 2013). Although >85 species have been recorded in jaguar diet (Sunquist & Sunquist, 2002), armadillos (*Dasypus novemcinctus*) and peccaries (*Tayassu pecari* and *Pecari tajacu*) are favored (Rabinowitz & Nottingham 1986, Scognamillo et al. 2003, Foster et al. 2010). Reptiles are important prey in the wetter parts of jaguar distribution (Emmons 1987, Zuloaga 1995, Da Silveira et al. 2010, Ramalho 2012).

Extirpated from approximately 54% of their historic range, jaguar distribution presently spans 18 countries from Mexico to Argentina (Rabinowitz & Zeller 2010). Core populations are severely fragmented and jaguar status remains unknown throughout significant portions of their distribution (Zeller 2007). Jaguars are considered a vulnerable species in Colombia (Rodríguez-Mahecha et al. 2006) where populations in the fragmented middle Magdalena River valley were assigned a 'medium probability of long-term survival' (Sanderson et al. 2002). A recent study in a 154.8 km^2 area of Colombia's Magdalena River valley recorded jaguars at moderately high densities of $2.52 \pm 0.46 - 3.15 \pm 1.08$ adults/100 km^2 (Boron et al. 2016). However, analyses in Brazil suggest that the species is highly sensitive to habitat fragmentation, especially in human-dominated landscapes (Roques et al. 2016).

The range-wide jaguar conservation network (JCN) aims to preserve populations (jaguar conservation units - JCUs) and maintain connectivity using corridors in fragmented, human-use landscapes (Rabinowitz & Zeller 2010). JCUs were defined as either: (1) areas with a stable, diverse prey base and adequate habitat capable of maintaining at least 50 breeding jaguars or (2) areas with less than 50 breeding jaguars but with sufficient habitat and prey to support jaguars if their populations increased under favorable conditions (Sanderson et al. 2002).

The Colombian Magdalena segment of the JCN is one of the most critical linkages because it represents part of an intercontinental connection between Mesoamerican and South American JCUs. Embedded in the northeastern portion of the Tumbes-Choco-Magdalena hotspot (Mittermeier et al. 2011), the middle Magdalena River valley is part of one of the most degraded and least protected biogeographic regions in Colombia (Etter et al. 2006, Forero-Medina & Joppa 2010). It has also long been recognized as a key linkage connecting jaguar populations east and west of the Andes Mountains (Melquist 1984).

The permeability of the inter-Andean linkage is threatened by highway construction, infrastructure associated with oil palm plantations, and widespread deforestation attributable to ongoing pasture expansion. There is significant overlap between areas targeted for oil palm (*Elaeis guineensis*) expansion and the middle Magdalena portion of the JCN in Colombia, which has the second-greatest area of palm oil in Latin America (FAO 2014) (Figure 9).

Globally, most palm oil is produced in Indonesia and Malaysia where its destructive impacts on biodiversity have been well documented (Maddox et al. 2007, Wilcove & Koh 2010, Sulai et al. 2015). However, oil palm cultivation is projected to increase in Latin America (Garcia–Ulloa et al. 2012, Dinerstein et al. 2015). Development threatens critical linkages of the JCN in Mesoamerica where oil palm monoculture supports low species richness and decreased abundances of birds, invertebrates, and herpetofauna (Nájera & Simonetti 2010, Gilroy et al. 2015). However, data on mammalian ecology in Neotropical oil palm is virtually nonexistent. The potential contribution of plantations to serve as habitat or movement corridors for jaguars remains largely unknown.

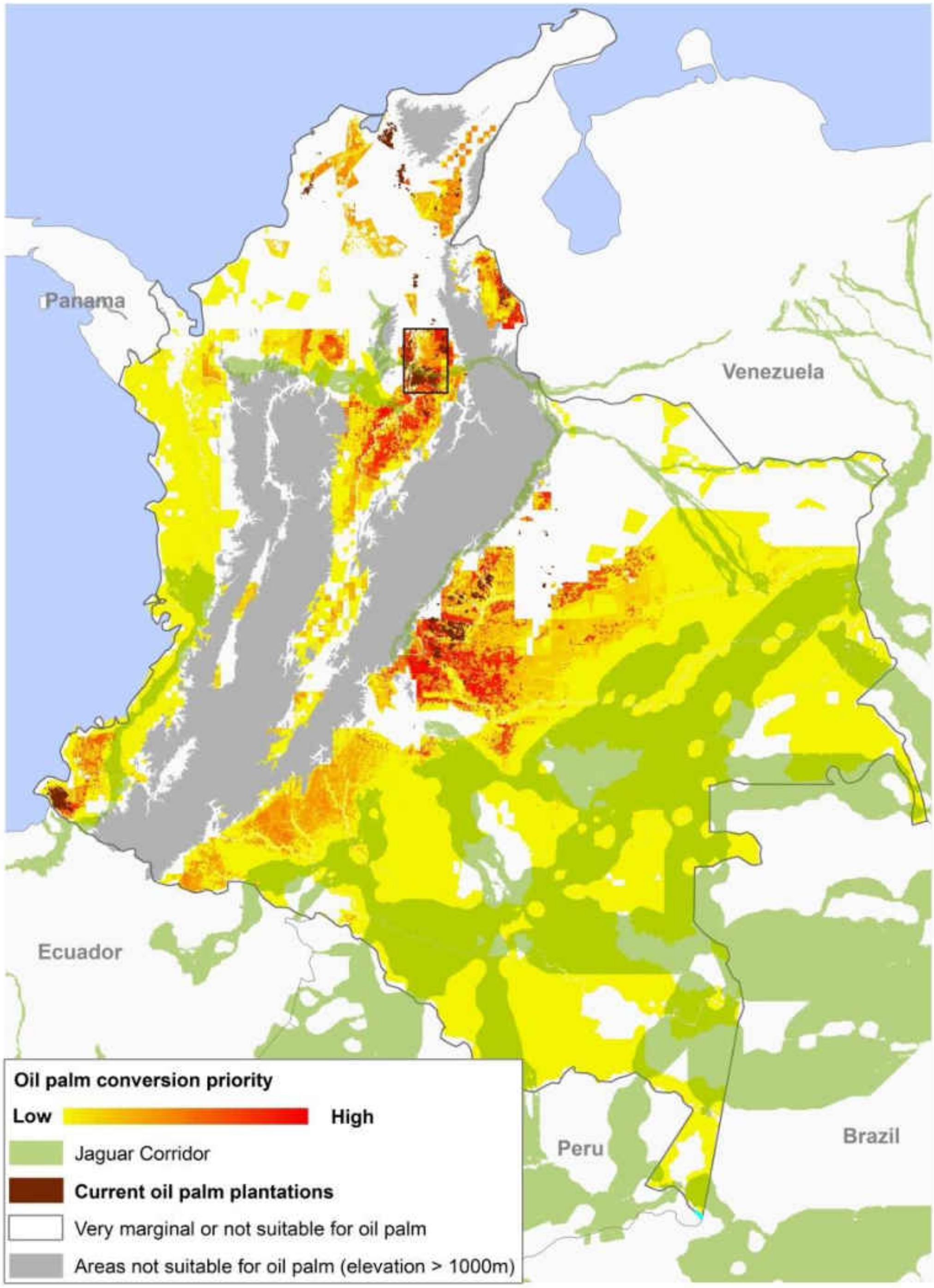

Figure 9. The Jaguar Corridor in relation to current and projected oil palm plantations in Colombia. My study area is framed by the rectangle. Land cover data is based on 30 m-resolution satellite imagery (Landsat TM and ETM+) for 2001, which is the best available and most widely used land cover data set for Colombia (IDEAM et al. 2007).

Our study evaluated the presence of jaguars in Colombia's middle Magdalena River valley, in an attempt to elucidate the factors contributing to the species' persistence in this transformed landscape. We hypothesized that jaguar occupancy would increase as the proportion of forest cover and wetlands (locally known as ciénagas) increased and oil palm decreased in buffers of 1, 3, and 5 km around each camera site. We further hypothesized higher jaguar occupancies nearer to wetlands and potential source populations in the Serranía de San Lucas and Serranía de los Yariguies. We also predicted a positive correlation between jaguar detections and detections of their main prey species and greater likelihood of occupancy in wetlands and forests than in oil palm plantations.

Methods

Study area

Located 400 km east of the intercontinental Colombia/Panama border, our study area spanned 2,196 km² across ten municipalities within four *departmentos* (provinces)–Antioquia, Bolívar, Cesar, and Santander – from 6.5° to 7.9° N and -74.5° to -73.4° W. The altitudinal range of sampled sites is 40–202 m a.s.l. Mean annual temperature is 27°C and precipitation is 2500–2800 mm, with most rainfall occurring in a bimodal pattern from April–May and September–November. There is a distinct dry season from December–February when precipitation averages < 130 mm/month. January is the driest month and October is the wettest.

Two large forest blocks are located at the southeastern and western borders of our study area: The Serranía de los Yariguíes National Park, a 790 km² protected area established in 2005 and the Serranía San Lucas, a 15,000 km² forested massif that represents the largest block of primary rain forest in the middle Magdalena River valley. A 3,770 km² portion of the Serranía San Lucas was under evaluation for a new national park in 2014 but extensive mining and occupation by armed guerilla groups has complicated the declaration process and the park has not yet been formally established.

Sampling design

We used detection, non-detection camera-trap surveys to estimate jaguar occupancy (ψ) and detection probability (p) from April 2013 – April 2016 (Figure 10). To address imperfect detection, we conducted multiple surveys of the sampling units to minimize the possibility of recording false absences (MacKenzie & Royle 2005), which are one of the greatest sources of biases in occupancy surveys (Moilanan 2002).

We analyzed the detection/non-detection data in an occupancy framework to estimate the probability of occurrence by incorporating an additional parameter of detection probability (MacKenzie et al. 2002). We defined detection probability as the probability that jaguars were detected in a survey period, given the site was used by jaguars (*sensu* MacKenzie et al. 2006). We then created single season occupancy models defining each camera trap location as the site and five consecutive day blocks as an occasion. We created individual models for each covariate and also used combinations of covariates for those that outperformed the null model.

To provide data that can be applied to design future jaguar occupancy surveys, we calculated the required sample size (i.e. camera-trap sites) using Eq. 1 (MacKenzie et al. 2006):

$$s = \frac{\Psi}{Var\,(\hat{\Psi})}\left[(1 - \Psi) + \frac{(1-p^{*})}{p^{*} - Kp(1-p)^{K-1}}\right] \qquad (1)$$

Where p^{*} is the expected probability of detecting jaguars at least once, and K is the optimum number of surveys to conduct at each site. Through a simulation study, MacKenzie et al. (2002) estimated that ≥ 5 sampling occasions were necessary to obtain unbiased results of ψ given detection probabilities ≥ 0.3. Considering a naïve occupancy of 0.57 and a detection probability of 0.28 (estimates obtained from the only other jaguar occupancy survey in oil palm/cattle pasture/tropical lowland forest mosaics, Zeller et al. 2011), and assuming p = 0.28 and K = 5, the optimum number of sites to survey to achieve SEs of 0.05, 0.075, and 0.10 (where ψ=0.57) was estimated to be 157, 70, and 39 camera-trap stations, respectively.

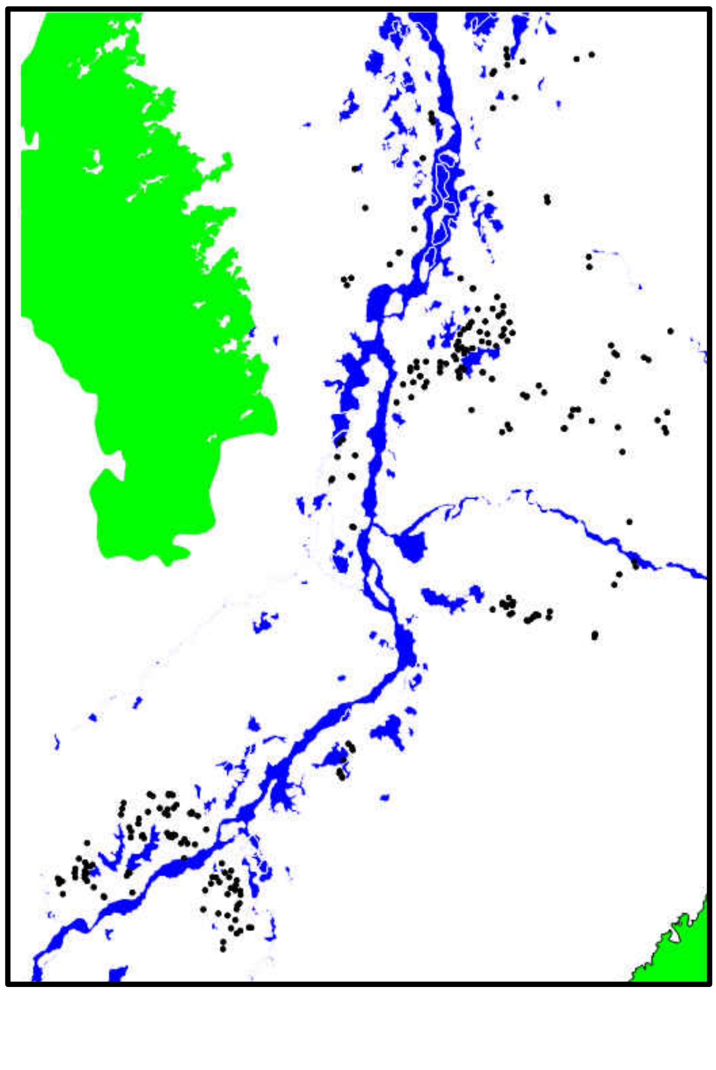

Figure 10. Camera-trap sites (n=275) from 2013–2016 in the middle Magdalena River valley, Colombia.

Most of our cameras were placed on private lands and required permission for access. Land cover within buffers surrounding each camera station varied in percentages of forest cover ($\bar{x}$ = 36.6 ± 31.6 SD), oil palm ($\bar{x}$ = 9.7 ± 16), and ciénaga coverage ($\bar{x}$ = 10.7 ± 19 SD) (Table 3). The average distance between cameras and the nearest wetland was 3.27 km (range 0.0 – 15.5 km).

Table 3. Mean values of covariates at camera sites (n=275) in the middle Magdalena River valley, Colombia. SSL = Serranía San Lucas, SYNP = Serranía de los Yariguíes National Park.

Covariate	Average	Range
Forest cover – 1 km buffer	41.9	0 – 100
Forest cover – 3 km buffer	35.8	0 – 97.3
Forest cover – 5 km buffer	32.1	0 – 95.7
Oil palm – 1 km buffer (%)	10.7	0 – 99.1
Oil palm – 3 km buffer (%)	9.6	0 – 66.6
Oil palm – 5 km buffer (%)	8.8	0 – 67.3
Wetland – 1 km buffer (%)	7.9	0 – 100
Wetland – 3 km buffer (%)	11.4	0 – 100
Wetland – 5 km buffer (%)	12.8	0 – 96.4
Distance to wetland (km)	3.25	0 – 15.5
Distance to SSL (km)	41.57	10.2 – 64.2
Distance to SYNP (km)	72.99	32.2 – 116.7

We hypothesized that jaguar habitat use would be influenced by six GIS-based landscape covariates: distances to the Serranía San Lucas (D_SSL), Serranía de los Yariguíes National Park (D_SYNP), and nearest wetland (wetland). Using ArcGIS 9.2 (ESRI, Inc.), we also included proportions of forest cover (P_forest), oil palm (P_palm), and wetland (P_wetland) in buffers of 1, 3, and 5 km around each camera site. We used varying buffer sizes because species respond to biogeographical variables at different scales (Pusparini et al. 2015, Nagy-Reis et al. 2016).

We also included three additional camera-derived sampling covariates related to principal mammalian prey: relative abundances of collared peccaries (RA_CP), spotted paca (*Cuniculus paca*) (RA_SP), and armadillos (RA_ARM). We defined principal mammalian prey as species found to comprise >0.10 of consumed biomass in jaguar diet in tropical lowland forest and floodplain habitats (Emmons 1987, Scognamillo et al. 2003, Azevedo & Murray 2007, Foster et al. 2010). Another primary mammalian jaguar prey species at forested floodplain sites – lesser capybara (*Hydrochoerus isthmius*) – was not included in the analysis due to scarcity of detections.

Prior to running the analyses, we standardized the data using Z scores (difference between each value and the mean, divided by the standard deviation) (Hines 2010). To avoid over-parameterizing the models, we ensured that each covariate used in the models had at least 10–15 events in the sampled cells, which also reduces the probability of a Type II error (Babyak 2004). Each covariate was selected *a priori* based on our knowledge of jaguar ecology.

Camera-trap surveys

We strategically placed remotely triggered camera-traps (Bushnell Trophy Cam®, Overland Park, KS, Cuddeback® Attack, Green Bay, WI, Pantheracam® V4., New York, NY, and Reconyx® HC500, Holmen, WI) 30 - 40 cm above the ground (Figure 10). Camera placement depended, in part, on permission from private landowners and accessibility, which was constrained by seasonal flooding in some areas flanking the Magdalena River. We maximized detection probability by placing cameras at locations where jaguar sign had been observed by local informants and during our reconnaissance surveys of the study area. We did not use scents or baits to attract animals. We selected camera sites using a stratified, systematic sampling design, based on land cover categories. The stratification of camera sites was intended to represent the dominant land-cover types, which allowed for better inference about non-surveyed locations.

Data analysis

We treated each camera site as an individual sampling unit for which we constructed detection histories of jaguars, comprising ≤ 75 sampling occasions. Each occasion corresponded to a camera operational in a 5 day period. We used the R package Unmarked (Fiske et al. 2011) to estimate jaguar occupancy in the middle Magdalena River valley. All models were fit using maximum likelihood. 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 site) is independent of detection at other sampling units (MacKenzie et al. 2006).

We tested all possible univariate model combinations of habitat variables on Ψ and p where each covariate is represented equally among the candidate model set (maximum of one covariate in each of occupancy and detection components). Two occupancy states were possible for each camera: occupied (corresponding probability is Ψ) and unoccupied ($1 - \Psi$). We incorporated covariates into the occupancy and detection components using the logit-link function. Estimated effect sizes can be interpreted in a manner similar to a logistic regression analysis.

We used Akaike's information criterion corrected for small sample sizes (AICc, n=275 cameras) and weighted the support of each model using AICc weights, with lower values indicating greater parsimony (Burnham & Anderson 2002). We computed jaguar detection probabilities as a function of predictor variables using a logit link function. We used the R package AICcmodavg (Mazerole 2016) to perform a goodness-of-fit test for single season models to further assess the fit of the selected models (MacKenzie & Bailey 2004).

Our data could not meet the population closure assumption of the modeling because we placed camera-traps over a 3-year 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 study area). Relaxation of these conditions changes the interpretation of (Ψ) from 'proportion of area occupied' (e.g. true occupancy) to 'proportion of area used' by jaguars. Thus, our results should be interpreted as 'likelihood of habitat use (Ψ)" (MacKenzie & Nichols 2004, Nagy-Reis et al. 2016).

Results

We set camera-traps at 275 sites where cameras were operational for an average of 239 days. The sampling effort was 15,798 trap nights. We photo-captured 21 distinct adult jaguars 230 times (9 males, 6 females, and 6 individuals of unknown sex) (Appendix B). We photo-captured jaguars at 51 (21.3%) of the 275 camera stations and detected the species an average of 1.31 km from the nearest ciénaga (wetland) (Figure 11). We never detected jaguars at camera sites where oil palm comprised > 25% of the surrounding 5 km buffer or <24% forest cover, except for one outlier of a male jaguar photographed in a 93-ha forest patch in a 5 km buffer > 90% deforested. We photographed females with cubs at 5 camera trap sites.

The covariates contributing the most to jaguar habitat use were proportion of wetland coverage in the 5 km buffers and distance to wetland ($\Sigma w = 0.86$; Table 4, 5). Jaguar habitat use strongly increased in the 5 km buffers that included greater wetland coverage ($\beta = 1.18$, 0.347 SE). Jaguar habitat use was also associated with camera sites at closer proximity to protected areas ($\beta = -0.57$, 0.188 SE; Table 6; Figure 12). The most plausible model for jaguar habitat use– psi(wetland_5)p(wetland_3)–was consistent with our *a priori* expectations of higher jaguar presence in buffers with greater spatial extent of wetlands.

The model-averaged probability of detecting jaguars in a sampling grid cell, given jaguar presence in the cell, was 18% (95% CI = 0.11, 0.32). However, detection probability varied according to wetland proximity (Figure 13). Among principle terrestrial prey, the collared peccary had the highest detection probability and the lesser capybara had the lowest (Table 7).

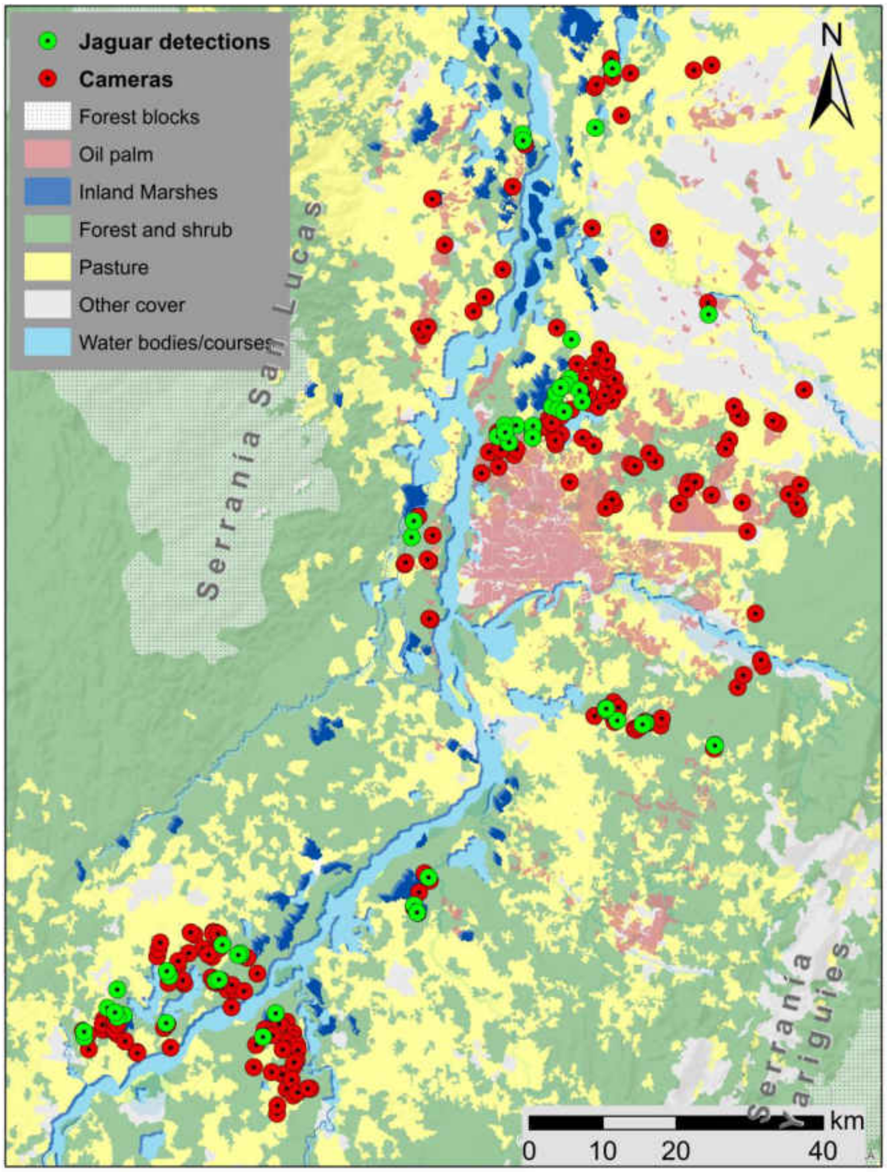

Figure 11. Sites of jaguar detections from 2013–2016 in the middle Magdalena River valley, Colombia.

Table 4. Top single-season site-covariate models for jaguars in the middle Magdalena River valley, Colombia, ranked in ascending order of AIC_c

Model	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
psi(wetland_5)p(wetland_3)	4	934.4876	0	1	0.70268	-463.17	0.703
psi(dist_wetland)p(wetland_3)	4	937.5027	3.015104	0.22145	0.15561	464.677	0.858
psi(wetland_3)p(wetland_3)	4	938.7104	4.222886	0.12106	0.08507	465.281	0.943
psi(dist_PA)p(wetland_3)	4	939.6627	5.175146	0.07520	0.05284	465.757	0.996
psi(wetland_1)p(wetland_3)	4	947.8767	13.38915	0.00124	0.0009	469.864	0.997
psi(palm_3)p(wetland_3)	4	948.1445	13.65692	0.00108	0.00076	469.998	0.998
psi(palm_1)p(wetland_3)	4	948.7389	14.25131	0.00080	0.00057	470.295	0.998
psi(forest_5)p(wetland_3)	4	948.9816	14.494	0.00071	0.00050	470.417	0.999
psi(palm_5)p(wetland_3)	4	949.5237	15.03612	0.00054	0.00038	470.688	0.999
psi(forest_1)p(wetland_3)	4	949.5879	15.10035	0.00053	0.0004	-470.72	0.999
psi(forest_3)p(wetland_3)	4	949.7144	15.22684	0.00049	0.00035	470.783	0.999
psi(dist_wetland)p(.)	3	958.5781	24.09054	5.87E-06	4.13E-06	476.245	0.999
psi(dist_PA)p(.)	3	960.4369	25.94932	2.32E-06	1.63E-06	477.174	0.999
psi(.)p(.)	2	963.4279	28.94032	5.20E-07	3.65E-07	479.692	0.999
psi(wetland_5)p(dis_wetland)	4	963.6544	29.16679	4.64E-07	3.26E-07	477.753	0.999
psi(palm_3)p(.)	3	964.1569	29.66936	3.61E-07	2.54E-07	479.034	0.999
psi(palm_1)p(.)	3	964.3512	29.86359	3.27E-07	2.30E-07	479.131	0.999
psi(wetland_5)p(.)	3	964.5096	30.02201	3.03E-07	2.13E-07	479.211	0.999
psi(forest_1)p(.)	3	965.0091	30.52151	2.36E-07	1.66E-07	-479.46	0.999
psi(forest_5)p(.)	3	965.1627	30.67514	2.18E-07	1.53E-07	479.537	0.999
psi(wetland_1)p(.)	3	965.2519	30.76436	2.09E-07	1.47E-07	479.582	1
psi(wetland_3)p(.)	3	965.3161	30.82853	2.02E-07	1.42E-07	479.614	1
psi(forest_3)p(.)	3	965.3388	30.85126	2.00E-07	1.40E-07	479.625	1
psi(palm_5)p(.)	3	965.3717	30.88414	1.97E-07	1.38E-07	479.642	1

*Site covariates: wetland_1, wetland_3, wetland_5=percentage of wetland coverage in 1, 3, or 5 km buffers around camera, respectively; palm = percentages of oil palm coverage in 1,3, or 5 km buffers around each camera, respectively; forest_1, forest_3, forest_5 = percentage of forest cover in 1,3, or 5 km buffers around each camera site, respectively; dist_PA=Distance to the Serranía de los Yariguíes or Serranía San Lucas.

Table 5. Top single-season sampling-covariate models for jaguars in the middle Magdalena River valley, Colombia, ranked in ascending order of AICc.

Model	K	AICc	Delta AICc	ModelLik	AICcWt.	LL	Cum.Wt
Psi(.)p(wetland_3)	3	947.6549	0	1	0.648241	470.783	0.648241
Psi(.)p(wetland_5)	3	949.4883	1.83342	0.399832	0.259188	-471.7	0.907429
Psi(.)p(wetland_1)	3	951.7363	4.081436	0.129935	0.084229	472.824	0.991658
Psi(.)p(forest_1)	3	956.842	9.187149	0.010117	0.006558	475.377	0.998216
Psi(.)p(palm_1)	3	962.6954	15.04057	0.000542	0.000351	478.303	0.998568
Psi(.)p(PA)	3	962.9554	15.3005	0.000476	0.000309	478.433	0.998876
psi(.)p(.)	2	963.4279	15.77302	0.000376	0.000244	479.692	0.99912
Psi(.)p(d_village)	3	963.4338	15.7789	0.000375	0.000243	478.673	0.999363
Psi(.)p(forest_3)	3	963.4998	15.8449	0.000363	0.000235	478.706	0.999598
Psi(.)p(palm_5)	3	964.6911	17.03626	0.0002	0.00013	479.301	0.999727
Psi(.)p(palm_3)	3	965.3413	17.68643	0.000144	9.36E-05	479.626	0.999821
Psi(.)p(forest_5)	3	965.3825	17.72763	0.000141	9.17E-05	479.647	0.999912
Psi(.)p(dis_Wetland)	3	965.4712	17.81632	0.000135	8.77E-05	479.691	1

Table 6. Site covariates influencing jaguar habitat use in the middle Magdalena River valley, Colombia. Covariates are ranked according to their summed model weights, β-coefficients and standard errors (SE).

Model	Site Cov.	*B*	SE	Z	P
psi(wetland_5)p(wetland_3)	wetland_5	**1.18**	**0.347**	3.4	6.67E-04
psi(dist_wetland)p(wetland_3)	Dist_wetland	**-0.79**	**0.274**	-2.89	3 .87E-03
psi(wetland_3)p(wetland_3)	wetland_3	**1.091**	**0.383**	2.85	4.39E-03
psi(dist_PA)p(wetland_3)	Dist_Forest_block	**-0.57**	**0.188**	-3.05	2.30E-03
psi(wetland_1)p(wetland_3)	wetland_1	0.387	0.315	1.23	2.19E-01
psi(palm_3)p(wetland_3)	palm_3	-0.22	0.182	-1.21	2.28E-01

± sign indicates direction of influence; bold entries indicate robust impact - β confidence intervals (estimate - 2*std error, estimate + 2*std error) do not overlap zero.

Table 7. Naïve occupancy* rates and detection probabilities‡ for principal mammalian jaguar prey detected by camera-traps from 2013–2016 in the middle Magdalena River valley, Colombia.

Common Name	Scientific name	Naïve occupancy	Detection probability
Lowland paca	*Cuniculus paca*	0.330	0.25
Collared peccary	*Pecari tajacu*	0.326	0.26
Armadillo	*Dasypus novemcinctus*	0.230	0.16
Lesser capybara	*Hydrochoerus isthmius*	0.070	0.06

*Naïve occupancy was calculated as the proportion of cameras where each species was detected ((total sites occupied/(total sites sampled)).

‡ Detection probability was calculated as the probability that the prey species was detected during a survey period at a camera site, given the site was used by the species.

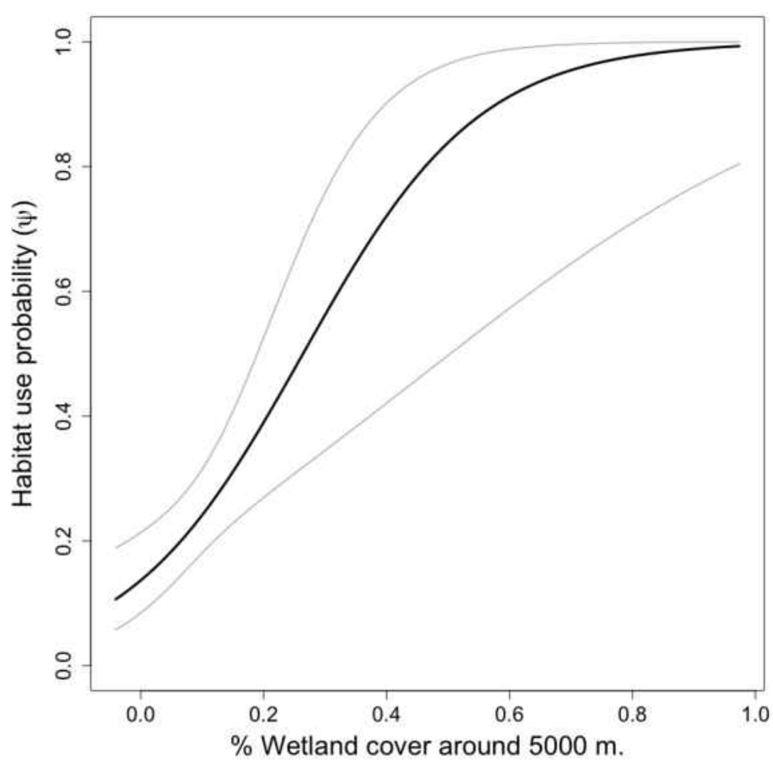

Figure 12. Probability of jaguar habitat use in the middle Magdalena River valley, Colombia.

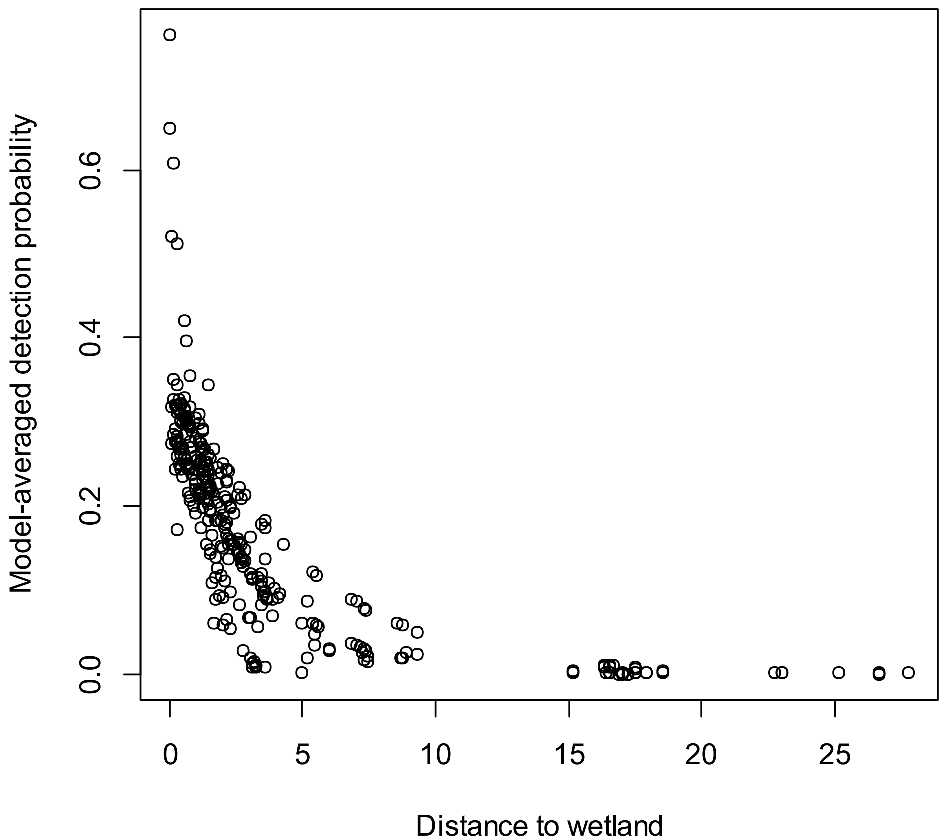

Figure 13. Model-averaged estimates of the relationship between jaguar detection probability and distance (km) to nearest wetland in the middle Magdalena River valley, Colombia.

Discussion

Colombia targets a six-fold increase in palm oil production by 2020, a goal that would require a total of 7,300 km² countrywide, double the land area that was cultivated when we began our study in 2013 (Garcia-Ulloa et al. 2012). One primary zone targeted for palm expansion is the middle Magdalena River valley, where the extent of palm cultivation is presently 1,291 km² (FEDEPALMA 2014). Beyond the middle Magdalena, oil palm plantations are also projected to expand in the tropical savannahs of the Orinoco region (Garcia-Ulloa et al.

2012), which contains 55% of Colombia's wetlands (IDEAM 2001). The persistence of jaguars in these transformed regions may depend on the extent to which dynamic landscape configurations preserve key features essential for the species.

Our results demonstrate the importance of landscape-scale perspectives for identifying key habitat features for jaguars. We show that survival of jaguars in the fragmented landscapes of the middle Magdalena River valley is likely to depend on the preservation of wetlands, although further investigation is needed to determine the status of the region's JCUs. The Serranía San Lucas and Serranía de Los Yariguíes National Parks, both considered JCUs (Sanderson et al. 2002), are separated by 170 km of entirely unprotected land, much of which is slated for oil palm plantation expansion. The Serranía San Lucas experienced the fourth-greatest extent of habitat loss among JCUs range-wide, losing 1,590 km^2 of forest cover from 2000–2012 (Olsoy et al. 2016). Without secure core areas in heavily modified landscapes, most corridors have minimal value (Noss & Daly 2006).

Our naïve estimates of jaguar occupancy (0.21) were lower than those reported from interview-based surveys in Nicaragua (0.57), which found jaguar presence to correlate with lower elevations and higher proportions of surface water (Zeller et al. 2011). Based on analyses from 119 camera trap sites, Sollmann et al. (2012) also noted a strong association between jaguar occurrence and surface water in the Brazilian Cerrado, where oil palm plantations do not occur. Our data indicate the potential ability of jaguars to persist in a dynamic landscape comprised of oil palm, pasture, and forest, given access to wetlands and adequate forest cover.

Consistent with jaguars' association with water (Crawshaw & Quigley 1991, Cullen Jr. et al. 2013), the most plausible model of jaguar habitat use was based on proportion of wetland in the 5 km^2 buffers. Many wetland areas in the Magdalena River basin are unsuitable for intensive development (e.g. large-scale oil palm plantations) due to seasonal flooding. The resulting hydroperiod (up to six months/year) may create favorable conditions by giving jaguars refuge from the relatively high human disturbance rates in surrounding pastures and plantations. Oil palm is one of the most labor-intensive agricultural land-uses (Corley & Tinker 2015) and plantations in the middle Magdalena typically employ 20-30 workers per km^2 of cultivated area, which is 5-10 times greater than the workforce employed in pastures of similar size (Figel unpublished data). We recommend that future studies on jaguars in oil palm landscapes estimate the response and thresholds of jaguar tolerance to human densities and disturbance, an important subject that has received minimal study (but see Foster et al. 2010, Figel et al. 2016).

To our knowledge this study was the largest (in terms of spatial coverage and sampling effort) occupancy-based survey of jaguars with camera-traps. Evaluation of occupancy and habitat use at large spatial scales is necessary to identify the ecological needs of wide-ranging species (Karanth et al. 2011). We stress the importance of long-term monitoring – resampling the same sites during consecutive years – to better evaluate occupancy and persistence of any wide-ranging species, including jaguars. Habitat may prove far less suitable for jaguars as the proportion of oil palm and pasture increases relative to forest and wetlands. Wetlands, for example, are commonly drained to meet the palm industry's demanding water footprint of 5,000 m^3 ton^{-1} (Mekonnen & Hoekstra 2011) and plantation operations can cause severe water contamination (Sulai et al. 2015).

Species extirpations often occur progressively over decades following such habitat loss or degradation (Brook et al. 2003, Vellend et al. 2006) and the extinction debt of jaguars in the middle Magdalena is not yet estimated. Fragmented landscapes can carry high extinction debts (Metzger et al. 2009), although empirical evidence on mammals is sparse (Kuussaari et al. 2009).

Reptilian prey

The strong association of jaguars with wetlands and lack of support for an influence of terrestrial mammalian prey on habitat use raises the hypothesis that jaguars in the middle Magdalena selectively prey on aquatic/semi-aquatic reptiles such as spectacled caimans (*Caiman crocodilus*), American crocodiles (*Crocodylus acutus*), and freshwater turtles (*Podocnemis lewyana* and *Trachemys callirostris*). Spectacled caiman can obtain a biomass of 2,000 kg/km^2 (Rueda-Almonacid et al. 2007) in Colombia, where their habitat preferences are similar to those we observed for jaguars (Moreno-Arias et al. 2013).

Caiman, crocodiles, and turtles were undetected by our terrestrial camera-traps and should be surveyed in subsequent studies of jaguars in the Magdalena because they can comprise significant portions of jaguar diet (Emmons 1987, Azevedo & Verdade 2008, Da Silveira et al. 2010). In the Amazon *varzea* (flooded forest), spectacled caiman were recorded in 41% of jaguar scat samples (Ramalho 2012), and reptiles comprised 36% of jaguar diet in the floodplains of the San Jorge and Cauca rivers (Zuloaga 1995), located 150 km northwest of our study area. We observed evidence of jaguar depredation on Colombian sliders *T. callirostris* in southern Bolívar, where preliminary surveys indicate robust populations of this species (Figel, pers. observ.).

Conclusion

Our findings have mutual implications for the conservation of jaguars and planned expansion of oil palm plantations. The Colombian National Federation of Oil Palm Growers (Fedepalma) has directed palm cultivators to avoid plantation establishment in forests and in areas with poor drainage prone to flooding, where pathogens destructive to the palms occur naturally. Responsible for the spread of a destructive disease known as bud rot, the pathogen

Phytophthora palmivora has decimated 350 km² (~27%) of the oil palm plants in the middle Magdalena since 2006 (Torres et al. 2016). Likewise, greater enforcement of forest preservation in riparian buffers–already required under Colombian law (Rubiano 2011)–is likely to benefit ecosystem health without sacrificing gains in palm oil production. Finally, jaguars use riparian areas as corridors in fragmented areas within other floodplain habitats (Crawshaw & Quigley 1991). These ecological, legal, and phytopathological factors (e.g. jaguar habitat use, riparian buffer law, and palm pathogens) oppose expansion of oil palm in riparian areas of Colombia's fragmented middle Magdalena River valley.

Habitat fragmentation is intensifying throughout the Neotropics (Link et al. 2010, Benchimol & Peres 2013, Zahawi et al. 2015), further threatening critical linkages of the jaguar network in southeastern Mexico, eastern Guatemala, and northern Honduras, all of which are targeted for oil palm expansion (Aguilar-Gallegos et al. 2015, Cajas-Castillo et al. 2015, Figel 2011). Investigating jaguar habitat use in these transformed landscapes is increasingly relevant because population isolation, deterioration of genetic diversity and local extirpation of the species has already occurred in several heavily-fragmented regions (Cullen 2006, Mazzolli 2008, Haag et al. 2010) and the effects of fragment size and connectivity in determining the species' persistence in fragmented forests is still poorly understood (but see De Angelo et al. 2011). Future research in the high priority, intercontinental corridor of the middle Magdalena should target wetland preservation, examine multi-season occupancy dynamics, and investigate finer-scale habitat configurations that may support jaguar persistence in one of the most important yet vulnerable areas of their distribution.

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CHAPTER 4 ~ AN EVALUATION OF JAGUARS AS AN UMBRELLA SPECIES FOR ENDEMIC HERPETOFAUNA IN NUCLEAR CENTRAL AMERICA[4]

Introduction

The umbrella species concept is based on the assumption that habitat preservation for species with large spatial requirements should simultaneously protect sympatric species with smaller home ranges (Frankel & Soulé 1981, Hurme et al. 2008, Branton & Richardson 2011). Presumptive umbrella species are selected by identifying the most demanding species with respect to area, resources, dispersal, and process (Lambeck 1997). Despite widespread application on a multitude of taxa in diverse ecosystems across five continents, the effectiveness of the umbrella approach and benefit for co-occurring species (hereafter beneficiary species) remains equivocal (Berger 1997, Simberloff 1998, Dunk et al. 2006).

Surprisingly few studies have systematically evaluated the umbrella effectiveness of large carnivores. Even fewer used appropriate methods, study areas of sufficient scales, and adequate sample sizes to sufficiently test umbrella effectiveness. Thus, empirical evidence of the utility of large carnivores as umbrella species is scarce (Noss et al. 1996, Sergio et al. 2008). One notable exception concluded that jaguars (*Panthera onca*) were an effective umbrella species for co-occurring mammals in Latin America (Thornton et al. 2016).

Due to their presence in diverse habitats and requirement for large connected landscapes, areas designated for large carnivore conservation would presumably meet the space requirements for numerous beneficiary species (Sergio et al. 2008, Branton & Richardson 2011). Among attributes positively correlated with size of habitat tract are the diversity of vegetation types, the

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[4] Prepared as: Figel JJ, E García-Padilla, F Castañeda, AP Calderón, RF Noss. An evaluation of jaguars (*Panthera onca*) as an umbrella species for endemic herpetofauna in Nuclear Central America.

likelihood of occurrence of rare or specialized habitats, overall biological diversity, the size of populations, and the sustainability of natural disturbance regimes (Bennett 2003, Noss 2012).

Nuclear Central America's (NCA) status as part of the Mesoamerican biodiversity hotspot (Myers et al. 2000) and geographical setting as a land bridge between North and South America has spawned multiple regional connectivity initiatives beginning with Paseo Pantera (Path of the Panther), launched in 1990 as a cooperative agreement between the United States Agency for International Development, the Wildlife Conservation Society, and the Caribbean Conservation Corporation (Jukofsky 1992). Succeeding Paseo Pantera was the Central American System of Protected Areas, created in 1992, the Mesoamerican Biological Corridor (MBC) in 1997 (Carr et al. 1994), and most recently, the jaguar conservation network (hereafter referred to as the jaguar network) (Rabinowitz & Zeller, 2010).

Identified by a least-cost corridor analysis, the jaguar network aims to preserve jaguar populations (categorized as jaguar conservation units - JCUs) and maintain connectivity using corridors in fragmented, human-use landscapes (Rabinowitz & Zeller 2010, Olsoy et al. 2016). JCUs are defined as either 1) areas with a stable, diverse prey base and adequate habitat capable of maintaining at least 50 breeding jaguars; or 2) areas with less than 50 breeding jaguars but with sufficient habitat and prey to support the species if their populations increased under favorable conditions (Sanderson et al. 2002). The mean distance of corridor length between JCUs range-wide is 331.78 km (Rabinowitz & Zeller 2010).

The corridors connecting JCUs are intended to maintain connectivity and facilitate jaguar dispersal between suitable habitat patches (JCUs), increasing the likelihood of gene flow and maintenance of genetic diversity (Rabinowitz & Zeller 2010). The Rabinowitz & Zeller (2010) least-cost corridor analysis identified corridors connecting all JCUs range-wide with one notable exception: a disconnection was identified between the Sierra de las Minas JCU in southeast Guatemala and the Pico Bonito-Texiguat JCU in northern Honduras. The urgency for conservation measures in this region is increasing because JCUs in Guatemala and Honduras experienced the highest rate of habitat loss among Mesoamerican countries between 2000–2012 (Olsoy et al. 2016) (Table 8). Consequently, only one-third of the Honduras-Guatemala transboundary connection is believed to support jaguar movement (Wultsch et al. 2016).

The Guatemala-Honduras transboundary segment of the NCA corridor is one of the most critical linkages of the range-wide jaguar network because it comprises part of a highly threatened segment of the connection between the two largest JCUs in Mesoamerica: the trans-national Maya Forest JCU spanning the Mexico-Guatemala-Belize border and the Rio Platano-Bosawas JCU along the Honduras-Nicaragua border (Sanderson et al. 2002). This transboundary corridor is vulnerable due to extensive habitat loss, which is accelerating because of road construction, pasture expansion, and agricultural conversion (including oil palm) (Olsoy et al. 2016, Wultsch et al. 2016, de la Torre et al. 2017).

The history of agricultural conversion along the transboundary corridor and Caribbean coasts of Honduras and Guatemala is extensive. In the 1930s and 1940s, widespread habitat conversion – largely to banana plantations – was noted by naturalists (Standley 1931, Yuncker 1940). Accelerating habitat conversion to widespread oil palm plantations, which have largely replaced lands formerly supporting banana plantations, is occurring at critical linkages of the NCA jaguar network, e.g. southern Mexico (Aguilar-Gallegos et al. 2015), eastern Guatemala (Cajas-Castillo et al. 2015) and northern Honduras (Figel 2011) (Table 9).

Table 8. Area, protection level, deforestation rates, and endemism in Nuclear Central American JCUs.

JCU	Area (km²)	Area and (%) of JCU protected	Annual deforest. rate	Endemic amphibians	Endemic reptiles	Total herp. endemics
Chimalapas	10,777	1907 (17.7)	2.5 - 5 %	25	30	55
Montes Azules	7,324	5127 (70)	5 - 10 %	9	9	18
Santa Cruz	1,063	0 (0)	> 10 %	20	11	31
Sierra de las Minas	2,085	1,687 (80.9)	1.5 - 2.5 %	22	20	42
Texiguat/Pico Bonito	1,715	1,715 (100)	1.5 - 2.5 %	21	15	36
Bosawas/Rio Platano	25,210	23,496 (93.2)	5 - 10 %	7	9	16
Total	48,174	33,932 (70.4)	-	104	94	198

Table 9. Area, protection level, deforestation rates, and endemism in Nuclear Central American corridors.

JCU	Area (km²)	Area of corridor protected (%)	Annual deforestation rateǂ	Endemic amphibians	Endemic reptiles	Total herp. endemics
North Chiapas	8,485	224 (2.6)	2.5 - 5 %	16	30	46
W Lake Izabel	551	156 (28.3)	5 - 10 %	6	9	15
East. Guatemala	3,007	1,398 (46.5)	> 10 %	16	11	27
West Honduras	3,392	1108 (32.7)	1.5 - 2.5 %	18	20	38
East Honduras	3,150	508 (16.1)	1.5 - 2.5 %	18	15	33
Total	18,585	3394 (18.3)	-	74	85	159

ǂ From Olsoy et al. 2016, supplementary data.

The jaguar network provides a unique opportunity to evaluate the effectiveness of a large carnivore as an umbrella species in a heterogeneous tropical landscape. Jaguars inhabit diverse habitats across a broad elevational gradient in NCA (McNab & Polisar 2002, Castañeda et al. 2011, Briones-Salas et al. 2012, de la Torre et al. 2017) where a recent study, from Chiapas, estimated their home ranges up to 431.6 ± 152.6 km^2 (de la Torre et al. 2017).

Jaguars are most commonly present in wetter lowlands but they are sporadically recorded at higher elevations, including one recent record at 2,200 meters in Honduras (Castañeda, 2016). Mitigating the species' sensitivity to habitat fragmentation (Roques et al. 2016, de la Torre et al. 2017) will require strategic zoning, enforcement of hunting laws, and collaboration with local communities (ICF 2011, Calderón-Quiñónez 2013). However, evidence of tangible conservation outcomes for jaguars due to zoning regulations is presently nonexistent within the NCA portion of the jaguar network. Substantiation of multi-taxa dependence on habitat under the 'umbrella' of the jaguar network could strengthen policy measures and aid the selection of priority areas for zoning and preservation.

The objective of our study was to quantify co-occurrence of jaguars and sympatric herpetofauna endemic to NCA. More specifically, we sought to compare the distributions of reptile and amphibian species overlapping a sample of three networks: the Rabinowitz & Zeller (2010) modeled network, the ground-truthed jaguar network, and a random selection of corridors and protected areas in NCA. We restricted our analysis to endemic herpetofauna (rather than including mammals) because taxonomic similarity may positively influence conclusions of umbrella effectiveness (Fleishman et al. 2001, Hurme et al. 2008, Branton & Richardson 2011) and NCA is a global hotspot for population declines of amphibians, which are the most threatened class of vertebrates worldwide (Stuart et al. 2008, Hoffmann et al. 2010). For reptiles, NCA contains a greater density of threatened species than any other region in the Western Hemisphere (Tingley et al. 2016). Our expertise on amphibians and reptiles allowed us to verify distributions mapped by the IUCN and compare international and regional status assessments of these threatened taxa in NCA.

Methods

Study area

We defined NCA as the mainland area between the Isthmus of Tehuantepec in southern Mexico and the Nicaraguan Depression in northern Nicaragua, excluding Belize and the Yucatan Peninsula (Schuchert 1935). Within this region, our study area spanned ~370,000 km² across four countries: Mexico, Guatemala, Honduras, and Nicaragua. We evaluated umbrella coverage in three networks, each ~103,370 km² in spatial extent: the ground-truthed network, Rabinowitz & Zeller (2010) network, and a random network. The ground-truthed network was comprised of 14 Nuclear Central America ecoregions (Table 10). Central American Atlantic moist forests and Petén-Veracruz moist forests account for ~78% of the broadly classified habitat, whereas uplands and montane ecoregions are not well represented.

NCA is a topographically and ecologically diverse region (Fig 14) with biogeographic barriers (e.g. volcanoes, mountain ridges, valleys) recognized to influence herpetofaunal distributions and increase the likelihood of high endemism (Carr 1950, Campbell 1999, Townsend 2014, Suárez-Atilano et al. 2014). The Isthmus of Tehuantepec and Nicaraguan depression, which represent the northern and southern limits of our study area, are recognized to act as geographical barriers restricting gene flow (Hardy et al. 2013, Pérez-Consuegra & Vásquez-Domínguez 2015).

We selected NCA as our study area due to the combination of the region's high endemism of herpetofauna, classification as part of the Mesoamerican biodiversity hotspot (Myers et al. 2000), priority status for the jaguar network (Rabinowitz & Zeller 2010), as well as our experience ground-truthing the corridor (Castañeda et al. 2011, Figel 2012, Calderón-Quiñónez 2013) and familiarity with the region and taxa analyzed in this study (McCranie & Castañeda 2007, García-Padilla & Mata-Silva 2014).

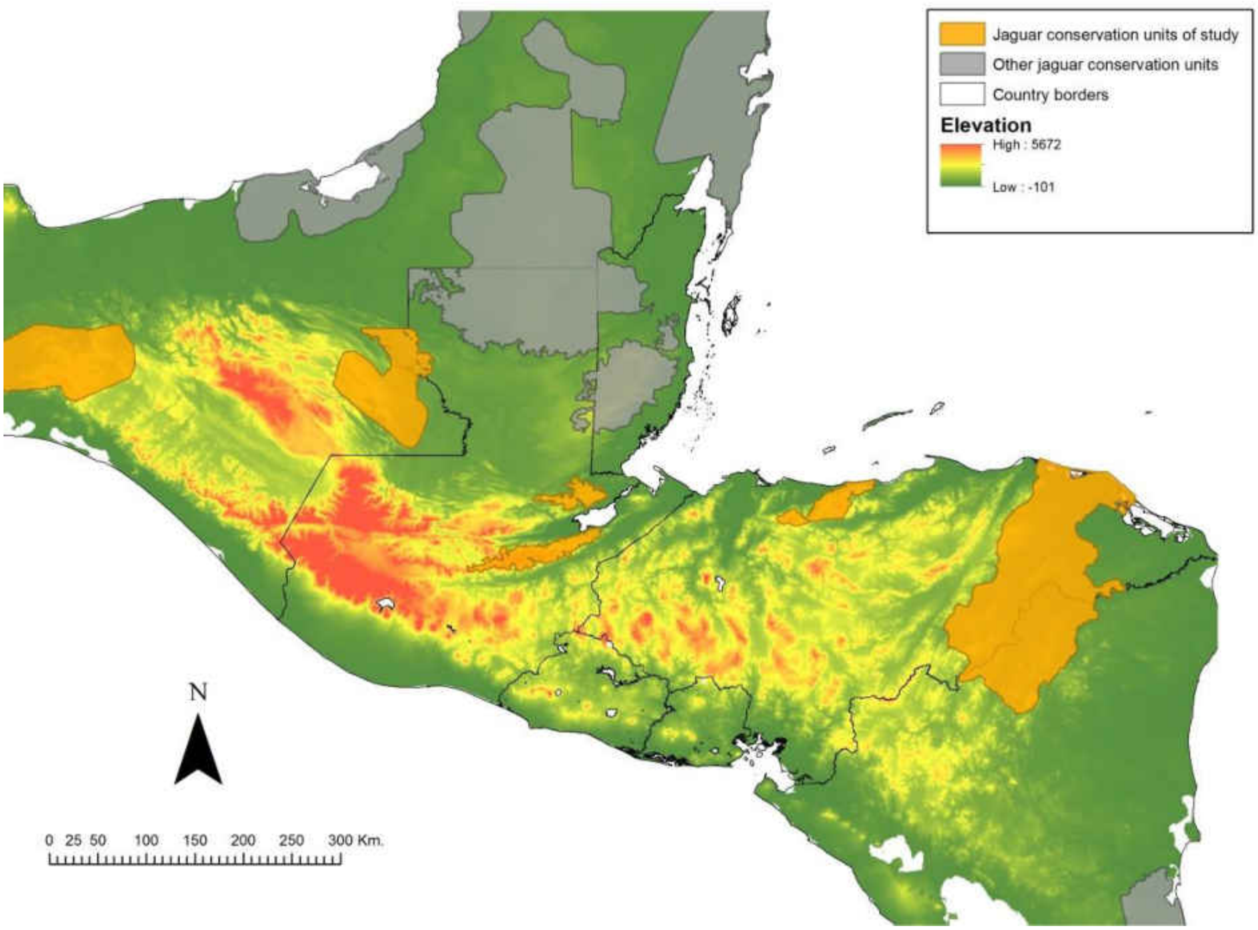

Figure 14. Jaguar conservation units and elevational gradients in Nuclear Central America.

Table 10. Ecoregion coverage of the ground-truthed jaguar network in Nuclear Central America.

Ecoregion	km²	% of NCA jaguar network
Central American Atlantic moist forests	31,757	52%
Petén-Veracruz moist forests	15,628	25.70%
Central American pine-oak forest	3,206	5.30%
Central American montane forest	1,820	3%
Miskito pine forests	1,727	2.80%
Chiapas montane forest	1,608	2.60%
Chimalapas montane forests	1,583	2.60%
Mesoamerican Gulf-Caribbean mangrove	1,518	2.50%
Pantanos de Centla	668	1.10%
Sierra Madre de Oaxaca pine-oak forests	516	0.85%
Southern Pacific Dry Forests	337	0.55%
Motagua Valley thornscrub	269	0.44%
Chiapas Depression dry forests	183	0.30%
Central American dry forests	93	0.15%

Ground-truthing the Jaguar Conservation Network

Our umbrella analysis of the NCA jaguar network included field-validated (ground-truthing) portions of putative jaguar corridors in Guatemala and Honduras (Calderón-Quiñónez 2013, Castañeda et al. 2011) and Chiapas, Mexico (Figel 2012) where we systematically conducted interview-based field surveys to estimate the probability of jaguar presence in 36 km² sampling units. We conducted the interviews with local people living or working in forests and rural areas believed to be occupied by jaguars (*sensu* Zeller et al. 2011). For Nicaragua, we only included the Rio Platano-Bosawas JCU in the analysis because all corridors in this country are located south of our study area.

We analyzed the detection/non-detection interview data in an occupancy framework to estimate the probability of occurrence by incorporating an additional parameter of detection probability (MacKenzie et al. 2002, Zeller et al. 2011). We defined detection probability as the probability that jaguars were detected in a survey period, given the cell was used by jaguars (*sensu* MacKenzie et al. 2006).

Evaluating jaguars as umbrella species

To estimate the umbrella effectiveness of jaguars, we downloaded species distribution vector polygons (shapefiles) from the IUCN Red List of Threatened Species website (IUCN 2012) and imported them into GoogleEarth Pro as raster images. We excluded all historical range, polygons where the species' presence is uncertain, and polygons comprised of ≤ 5 presence points. We then overlapped the Rabinowitz & Zeller (2010) jaguar network, the ground-truthed jaguar network, and the random network with shapefiles of herpetofauna distributions (Figure 15, 16, 17).

The IUCN defines these distributions as "extent of occurrence" (EOO) and IUCN range maps are generally 'extent of occurrence' maps. EOO is defined as "the area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon, excluding cases of vagrancy" (IUCN 2012). EOO is measured by a minimum convex polygon (MCP; "the smallest polygon in which no internal angle exceeds 180 degrees and which contains all the sites of occurrence" (IUCN 2012). Thus, EOO maps represent range boundaries, not occupancy.

Contrary to 'area of occupancy' (AOO), the EOO is not intended to represent an estimate of the amount of occupied or potential habitat (Gaston & Fuller 2009). AOO is defined as "the area within (the species') extent of occurrence which is occupied….excluding cases of vagrancy" (IUCN 2012). Whereas EOO is more inclusive, AOO accounts for unsuitable or unoccupied habitats throughout the EOO where the taxon will not usually occur.

We defined a regional endemic as any species with >50% of its EOO inside our predetermined NCA study area. Any habitat for species that fell outside the boundaries of our NCA study area was not included in our estimates of umbrella overlap. For species with >50% of their EOO inside the NCA, we excluded all portions of the EOO in the Yucatan Peninsula, southern Nicaragua, or northwest of the Isthmus of Tehuantepec. Thus, our umbrella analysis was restricted to the region between the Isthmus of Tehuantepec in southern Mexico and the Nicaraguan Depression, excluding Belize and the Yucatan Peninsula.

For each sampled network, we estimated 1) total numbers of species' EOOs overlapped; 2) overlap for herpetofauna species classified by their IUCN risk status (CR=Critically endangered, EN=Endangered, VU=Vulnerable, NT=Near threatened, DD=Data deficient, LC=Least concern); and 3) the proportion of the species' EOO overlapped by the network. For species with EOOs that extended beyond our study area (i.e. west of the Isthmus of Tehuantepec), we only included the percentage of its EOO in our NCA study area.

To evaluate the umbrella effectiveness of the NCA jaguar network, we measured the extent of spatial overlap, comparing results from the JCUs and ground-truthed corridors with the Rabinowitz & Zeller (2010) network and a randomly selected portion of the Mesoamerican Biological Corridor (MBC), under the assumption that such ecologically-based analyses could be more informative from a management perspective. To generate the random network, we randomly selected portions of the MBC until its total area equaled the spatial extent of the JCUs and corridors. Thus, our final sample of networks included: 1) the Rabinowitz & Zeller (2010) corridor and JCUs; 2) the ground-truthed corridor and NCA JCUs; and 3) a randomly selected portion of the MBC.

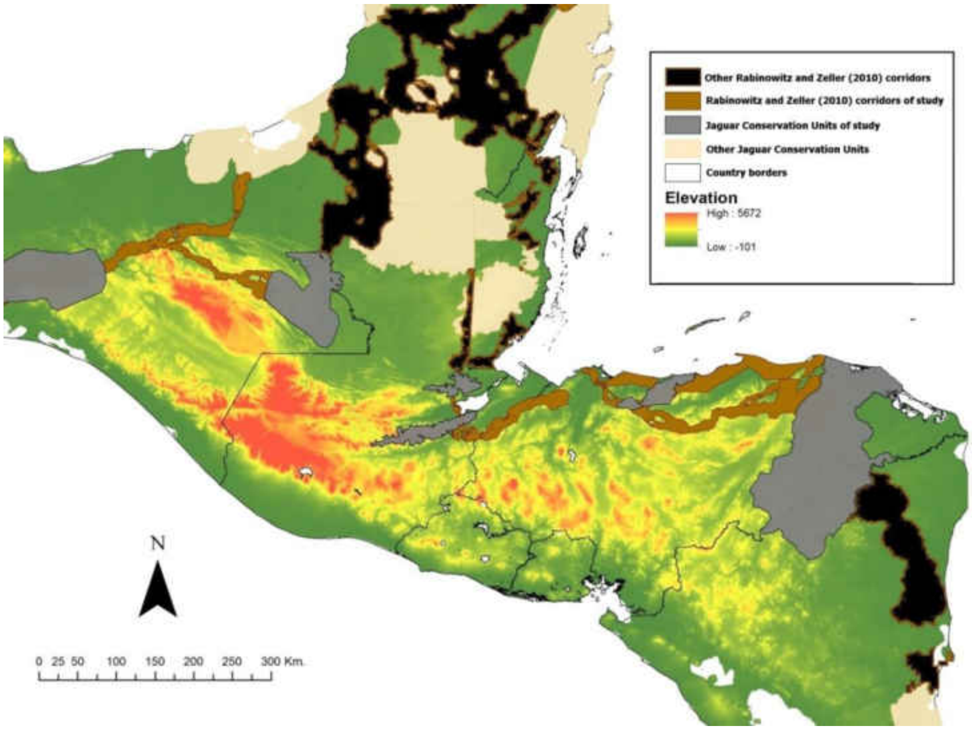

Figure 15. The Rabinowitz and Zeller (2010) modeled jaguar network in Nuclear Central America.

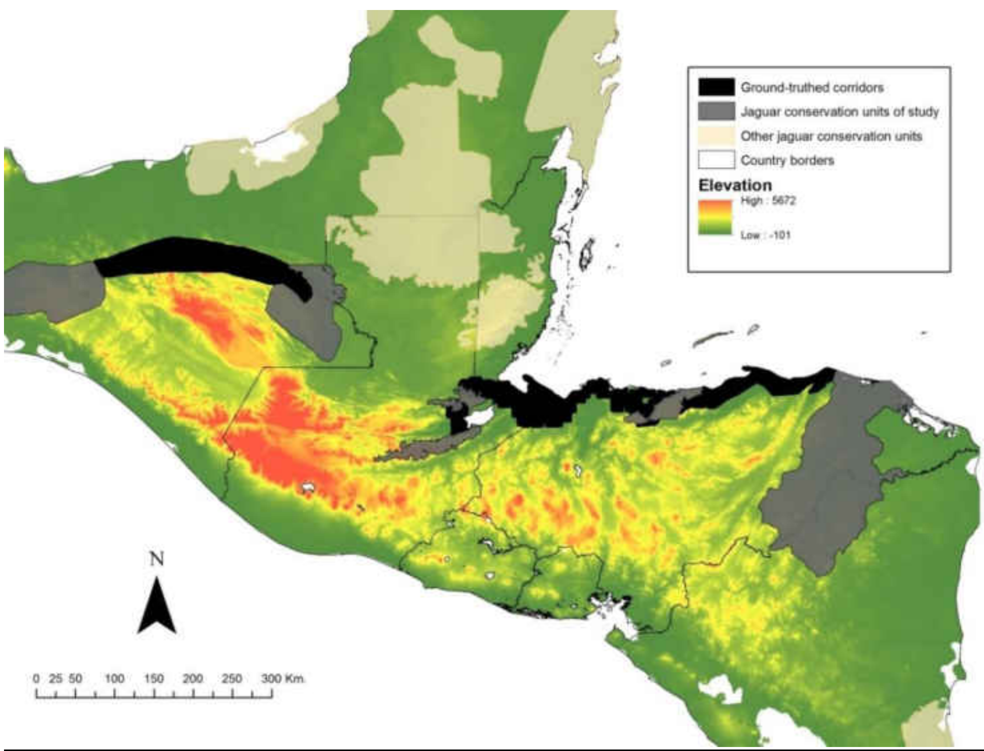

Figure 16. The ground-truthed jaguar network in Nuclear Central America.

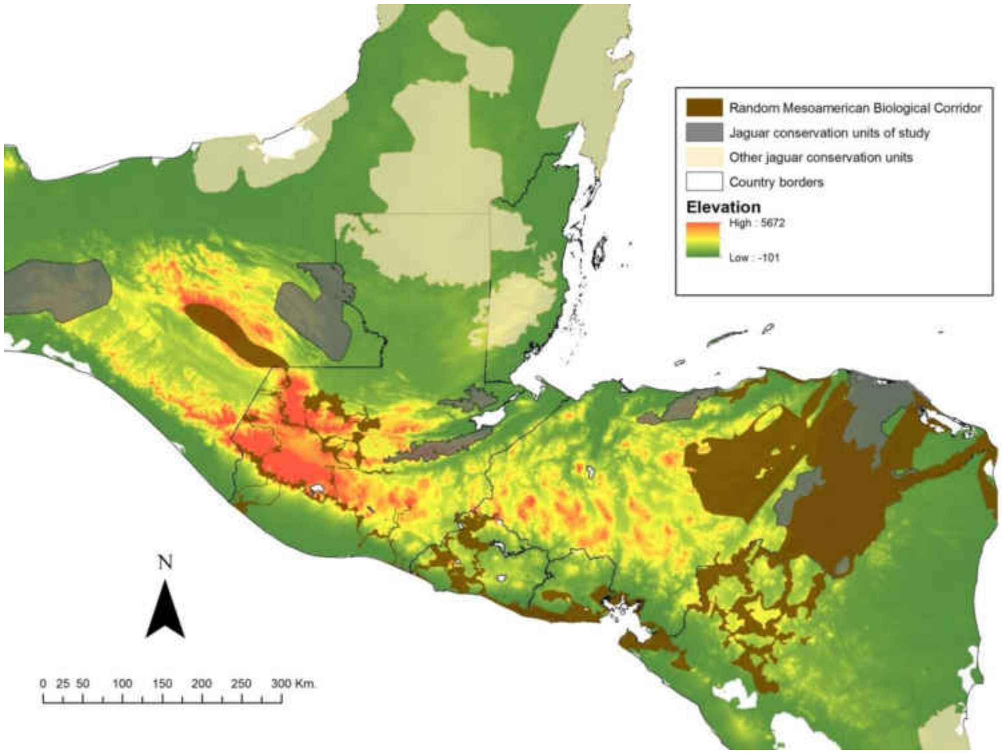

Figure 17. The randomly selected Mesoamerican Biological Corridor in Nuclear Central America.

Results

Ground-truthing results

Our ground-truthing results significantly redefined corridor boundaries in Honduras, Guatemala, and the Mexican state of Chiapas. Whereas the modeled corridor proposed by Rabinowitz & Zeller (2010) included corridors in the highlands of Guatemala and Honduras, the ground-truthed corridor was found to extend parallel to the Caribbean coastline in both countries. Ground-truthing in southern Mexico resulted in the identification of a single, east-west corridor ~40–50 km north of the cities of Tuxtla Gutiérrez and San Cristóbal de las Casas (Figel 2012). That corridor, roughly double the width of the modeled Rabinowitz & Zeller (2010) corridor, now extends directly from the Chimalapas JCU in Oaxaca to the Lacandona JCU in Chiapas, a distance of 220 km.

Umbrella results

Jaguars were more effective as an umbrella species for amphibians than for reptiles in NCA. The ground-truthed occurrence of jaguars in NCA was associated with high species richness of amphibians of conservation concern (Figure 18). The ground-truthed NCA jaguar network had significantly higher coverage for amphibians than the randomly generated MBC corridor (one-way ANOVA, $P < 0.003$).

The greatest benefit was observed for *Craugastoridae*; an average of 40.3% overlap was recorded between the EOO of species in this family and the jaguar network. Jaguars served as a less effective umbrella for amphibian families *Bufonidae* and *Plethodontidae*. *Bufonidae* was the family with the lowest average overlap ($\bar{x}$ = 19.3%) (Figure 19). Seventeen amphibians, including ten critically endangered species (*Bolitoglossa diaphora*, *Craugastor cruzi*, *Craugastor fecundus*, *Craugastor trachydermus*, *Isthmohyla insolita*, *Ixalotriton parvus*, *Oedipina tomasi*, *Plectrohyla chrysopleura*, *Plectrohyla exquisita*, *Ptychohyla sanctaecrucis*) and two endangered species (*Charadrahyla chaneque*, *Exerodonta chimalapa*) occur exclusively within the NCA jaguar network (Figure 20, Appendix C).

For reptiles, *Dactyloidae* was the beneficiary family with the greatest average overlap ($\bar{x}$ = 39.9%). The least overlap was observed for *Colubridae* ($\bar{x}$ = 9.05% of species' EOO overlapping the NCA jaguar network). Twelve reptiles, including two critically endangered species (*Bothriechis guifarroi*, *Rhadinella tolpanorum*) and three endangered species

(*Lepidophyma lipetzi*, *Norops amplisquamosus*, *Norops cusuco*) occur exclusively within the ground-truthed NCA jaguar network (Appendix D).

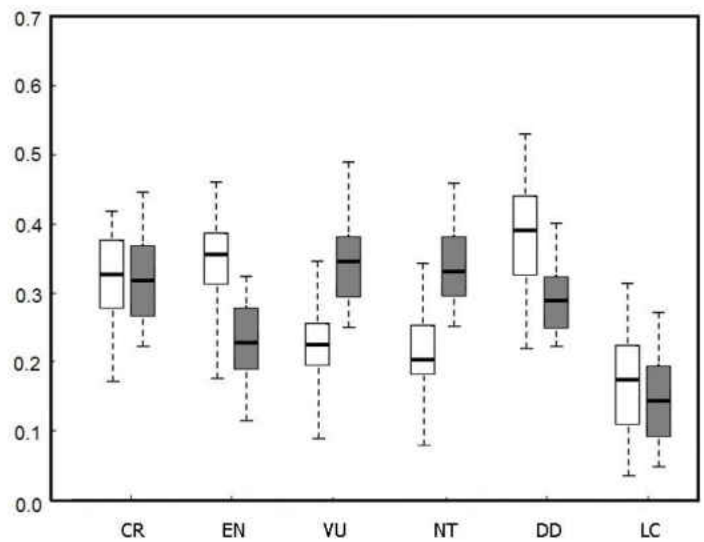

Figure 18. Proportion of the extent of occurrences of endemic amphibians (white boxes) and reptiles (shaded boxes) overlapped by the ground-truthed jaguar conservation network in Nuclear Central America. CR=Critically endangered, EN=Endangered, VU=Vulnerable, NT=Near threatened, DD=Data deficient, LC=Least concern.

Reptiles were less represented than amphibians in terms of number of species despite their EOO being 4 times larger, on average. The spatial overlap for threatened amphibians showed marked differences compared to that of threatened reptiles (Table 11). More threatened amphibians occurred in the ground-truthed jaguar network where a larger proportion of amphibians' EOO was found. The JCUs with the highest totals of endemic herpetofauna species richness in the NCA jaguar network were the Sierra de las Minas in Guatemala and Chimalapas in Mexico.

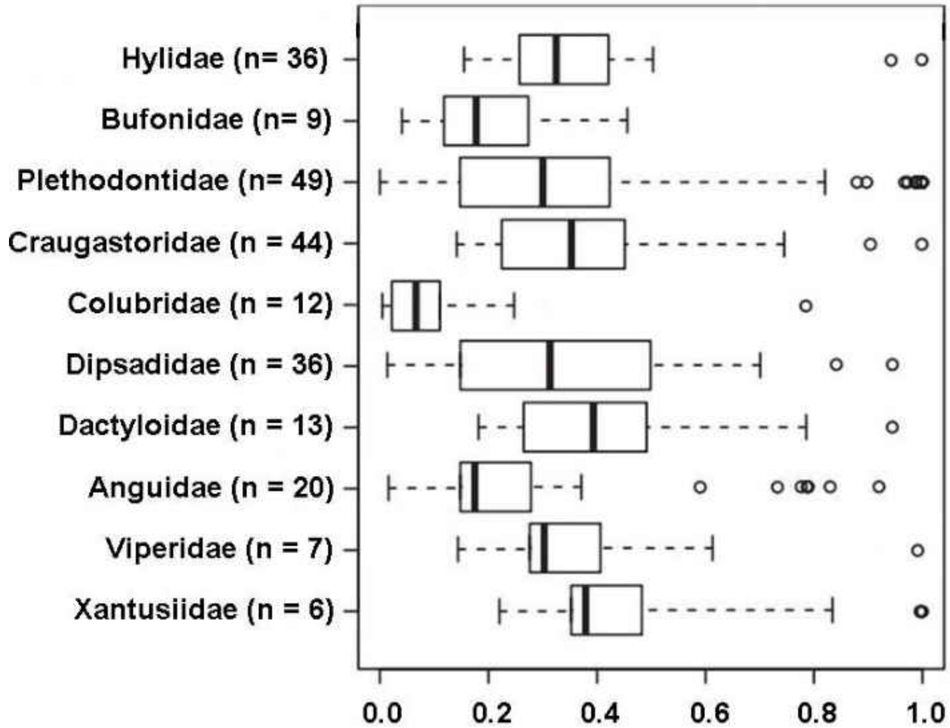

Figure 19. Proportion of the extent of occurrences of endemic herpetofauna overlapped by the ground-truthed jaguar conservation network in Nuclear Central America.

Figure 20. *Plectrohyla exquisita*, a critically endangered hyliade endemic to the Jaguar Conservation Network in northwest Honduras. Photo provided by F. Castañeda.

Table 11. Summaries of the amphibian and reptile species overlapped by each network in Nuclear Central America.

Amphibians (n=135)	Ground-truthed Network	Rabinowitz/Zeller Network	Random MBC Network
Species overlap (% of total)	83 (61.4%)	81 (60%)	63 (46.7%)
# of species with 100% overlap	17	8	5
Average proportion of species' range inside corridor	54.5	51.7	33.7
# of CR species partially inside corridor	23	26	13
# of EN species partially inside corridor	28	27	22

Reptiles (n=112)	Ground-truthed Network	Rabinowitz/Zeller Network	Random MBC Network
Species overlap (%)	70 (62.5%)	66 (58.9%)	63 (56.3%)
# of species with 100% overlap	12	10	5
Avg. proportion of species range inside corridor	37.70%	37.20%	33.70%
# of CR species partially inside corridor	6	6	2
# of EN species partially in side corridor	8	10	10

Discussion

This analysis represents the first multi-taxon evaluation of the jaguar's umbrella value. Our results demonstrate how a single-species conservation strategy can effectively serve as an umbrella for co-occurring herpetofauna, especially threatened amphibians. Exceptionally high reptilian diversity exists in NCA (Tingley et al. 2016) but amphibians were clearly more reliant on habitat in the jaguar network. JCUs and corridors managed for jaguars could provide ancillary conservation benefits for endemic amphibians because habitat loss and degradation are a major threat for ~63% of all amphibian species (and 87% of all threatened species) (Chanson et al.

2008). Globally, 41% of amphibian species are at risk of extinction, which is the highest proportion of any class of vertebrate (Hoffmann et al. 2010).

Within the Mesoamerican biodiversity hotspot, NCA is the epicenter for amphibian and reptile species richness and threat (Tingley et al. 2016). Given deforestation trends and intensifying habitat fragmentation throughout jaguar distribution (Hansen et al. 2013), our study area may provide a window into the future of the intensifying threats likely to face jaguars in degraded land mosaics advancing across the Mesoamerican jaguar network (Jordan et al. 2016, Wultsch et al. 2016) where corridors, in particular, are increasingly fragmented (Olsoy et al. 2016). Forest loss is especially severe in Nicaragua where unprotected parts of jaguar corridors lost 10.8% of their forest cover from 2000-2012 (Olsoy et al. 2016) and widespread agricultural conversion is ongoing (Jordan et al. 2016).

In Guatemala, the Sierra de Santa Cruz experienced the greatest extent of habitat loss among JCUs range-wide, losing 11.37% of its forest cover between 2000–2012 (Olsoy et al. 2016 – supplementary information). Recent findings of pronounced genetic subdivision among jaguars from Honduras, Guatemala, and Belize currently support potential limitations in jaguar connectivity through the Guatemala-Honduras connection (Wultsch et al. 2016).

In Honduras, the jaguar network is threatened due, in large part, to its proximity to San Pedro Sula, which is the largest city (1.4 million inhabitants) at the closest proximity to any part of the NCA jaguar network. San Pedro Sula poses a formidable barrier to corridor permeability because of its setting in a landmass at a 90 degree angle along the borders of Guatemala, Belize, and the Caribbean Sea. Human population density, measured at the municipality/department level, in the Honduran side of the ground-truthed corridor is 410 people/km^2 and 46 people/km^2 in Guatemala (IARNA 2012, INE 2012).

Our findings highlight the need to prioritize jaguar conservation in NCA including sites of projected oil palm development at critical linkages of the jaguar network, e.g. southern Mexico (Aguilar-Gallegos et al. 2015), eastern Guatemala (Cajas-Castillo et al. 2015) and northern Honduras (Figel 2011). We identify priority areas where proactive implementation of the jaguar network would have the greatest benefit for threatened and endemic herpetofauna in NCA. The Sierra de las Minas in Guatemala and Chimalapa region in southern Mexico, in particular, harbor important jaguar habitat and extremely high species richness of endemic herpetofauna.

Conclusion

Since the IUCN distributions represent EOO, not occupancy, our ability to assess umbrella effectiveness at finer scales was limited. Many IUCN Red List species lack adequate data to accurately determine their distributions (Ficetola et al. 2014). Inadequate data on rare or infrequently detected species can also limit inferences about occurrence and bias assessments of conservation status (Sandoval-Comte et al. 2012, Tracewski et al. 2016).

These limitations aside, the IUCN EOO maps used in our analysis represent the best available data and management decisions should include all species, not simply datasets on the most easily detected species (Zipkin et al. 2010). The jaguar's umbrella value could increase as more corridors are ground-truthed and further surveys are conducted on cryptic amphibian and reptile species.

Evaluating the umbrella effect of jaguars elsewhere in their range is of increasing relevance because population isolation, deterioration of genetic diversity and local extirpation of this imperiled carnivore has already occurred in several heavily-fragmented regions (Mazzolli 2008, Haag et al. 2010, Wultsch et al. 2016) where herpetofauna (especially reptiles) face greater extinction risk (Keinath et al. 2017). Mountainous regions and other areas with high endemism, such as the western Sierra Madres of Mexico (Jenkins & Giri 2008) and Tropical Andes (Sarkar et al. 2009), should be prioritized for more in-depth analyses of the jaguar's umbrella value. Results could aid the justification of strengthened policy measures and selection of priority areas to maximize simultaneous conservation of jaguars, herpetofauna, and other threatened taxa in Latin America.

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CHAPTER 5 ~ CONCLUSIONS

My study areas represent a 'window into the future' of the imminent threats to the jaguar network as deforestation advances. Jaguar corridors range-wide lost 45,979 (4.4%) of their forest cover between 2000 and 2012 (Olsoy et al. 2016) and many connections are now only partially functional for jaguar movement (Wultsch et al. 2016). My research at sites in North, Central, and South America highlights the importance of multiple study areas for (1) identifying site-specific threats faced by jaguars and (2) properly evaluating strategies to support habitat connectivity and conservation. I demonstrate the need to reevaluate extirpation thresholds of jaguars in human-dominated areas, prioritize research on wetlands as keystone sites for jaguars (especially in oil palm landscapes), and further assess the utility of holistic conservation planning using this wide-ranging large carnivore as a focal species.

Results from the western Mexico JCU fail to support the 'critical human density' index model, which estimated a 50% likelihood of jaguar extinction once human population densities reach 17.3 people/km^2 (Woodroffe 2000). It is important to note, however, that Woodroffe's (2000) calculation of the 'critical human density' estimate is potentially biased because it omitted data from all jaguar-range countries besides Brazil, where data from 21 states were considered. Results from Nayarit (Chapter 2) demonstrate the importance of considering other variables (i.e. water sources, prey availability, local tolerance of large carnivores) when evaluating jaguar presence and persistence in human-use landscapes.

However, in a recent attempt to estimate the global jaguar population, de la Torre et al. (2017) assumed jaguar densities declined linearly as human population densities increased (de la Torre et al 2017), without accounting for habitat type, ecosystem productivity, or other variables.

Their over-simplistic assumption is unfounded and likely to result in erroneous inference. de la Torre et al. (2017) applied the critical human density index range-wide, excluding significant areas of jaguar distribution (i.e. coastal Nayarit), to estimate the global jaguar population. For their estimates, they used the linear regression formula:

$$y = xm + b,$$

where y is the estimated jaguar density, x is the human population density, m is the constant rate at which jaguars decline as human population densities increase, and b is the jaguar density defined for the biomes in each >2,000 km polygon across jaguar distribution.

The formula used by de la Torre et al. (2017) is flawed for two key reasons: (1) Data on the rate at which jaguars decline as human population densities increase is grossly limited; and (2) More than 90% of jaguar density estimates, based on obsolete closed population capture-recapture models, are biased due to improper study designs and incorrect analyses (Tobler & Powell 2013).

Occupancy estimation can be a valid alternative to density because of the shortcomings inherent to camera-trapping when calculating density estimates across large spatial scales (Linkie et al. 2007, Foster & Harmsen 2012, Tobler & Powell 2013). Applying occupancy models to assess jaguar habitat use, my research in Colombia's middle Magdalena River valley provides valuable insight into the habitat characteristics (i.e. wetlands) that may support jaguar persistence in transformed landscapes. As reviewed in Chapter 3, enforcement of riparian forest preservation–already required under Colombian law (Rubiano, 2011)–is likely to benefit jaguars without sacrificing gains in palm oil production because the palms are susceptible to bud rot and other diseases in soils with poor drainage and in areas prone to flooding (Corley & Tinker 2015, Torres et al. 2016).

Jaguars, in turn, can extend disproportionate benefits to other species as demonstrated by my umbrella species evaluation in Nuclear Central America (Chapter 4). Substantiation of multi-taxa dependence on habitat within the jaguar network could strengthen policy measures and refine the selection of priority areas to maximize simultaneous conservation of jaguars, herpetofauna, and other threatened taxa in Latin America.

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APPENDIX A: REPORTS OF JAGUAR SIGHTINGS OBTAINED FROM INTERVIEWS OF RESIDENTS IN 24 TOWNS AND *EJIDOS* IN NAYARIT, MEXICO, FROM 2009 - 2013. FREQUENCIES OF SIGHTINGS ARE GIVEN IN PERCENTAGES: FREQUENT SIGHTINGS WERE ASSIGNED FOR JAGUARS OBSERVED GREATER THAN ONCE/MONTH. MODERATE=SEEN TWICE/YEAR TO ONCE/MONTH, RARE=OBSERVED ONCE/YEAR, AND UNDETECTED=NOT OBSERVED

Locality[a]	*Ejido*/town name	*Ejido*/town pop.	No. interviews (*n*)	% Jaguar sightings			
				Frequent	Moderate	Rare	Undetected
1	Aután	1,890	2	50	0	50	0
2	El Ciruelo	636	2	0	50	0	50
3	Guadalupe Victoria	2,932	3	0	33.3	33.3	33.3
4	El Capomo	188	2	0	0	0	100
5	Reforma Agraria	561	2	0	0	0	100
6	Navarrete	1603	2	0	0	0	100
7	Chacalilla	486	4	100	0	0	0
8	Las Palmas	191	2	0	0	50	50
9	La Libertad[b]	1,581	5	0	0	80	20
10	Singaita[b]	140	5	80	20	0	0
11	José María Mercado	202	2	0	0	50	50
12	Huaynamota	201	2	0	0	50	50
13	San Blas[c]	10,187	6	33.3	33.3	33.3	0
14	Mecatán	2,657	2	0	0	50	50
15	Mantanchén[b]	50	3	100	0	0	0
16	Ceboruco[b]	50	4	0	50	50	0
17	La Bajada[b]	537	10	70	20	0	10
18	La Palma[b]	1113	6	83.3	16.7	0	0
19	Aticama	1404	4	0	50	0	50
20	Jalcocotán	4,207	3	0	0	33.3	66.7
21	El Cora	335	2	0	50	0	50
22	El Llano	1,184	3	0	0	100	0
23	Santa Cruz	1,564	4	0	0	50	50
24	Jolotemba	297	2	0	50	0	50
Averages		1,425	3.42	21.53	15.55	26.25	36.67

[a] Numbers refer to *ejido* locations in Figure 1.

[b] *Ejido* present within camera-trap polygon.

[c] San Blas is a town.

APPENDIX B: TWO OF THE TWENTY-ONE ADULT JAGUARS PHOTOGRAPHED DURING 2013-2016 IN THE MIDDLE MAGDALENA RIVER VALLEY OF COLOMBIA. INDIVIDUAL JAGUARS CAN BE IDENTIFIED BY THEIR UNIQUE SPOT PATTERNS

APPENDIX C: AMPHIBIAN SPECIES RESTRICTED (100% OVERLAP) TO THE NUCLEAR CENTRAL AMERICAN JAGUAR NETWORK

Species	Country[a]	Class	Order	Family	Status[b]	EOO[c,d]
Bolitoglossa diaphora	HON	Amphibia	Caudata	Plethodontidae	CR	43.7
Charadrahyla chaneque	MX	Amphibia	Anura	Hylidae	EN	308
Craugastor adamastus	GTM	Amphibia	Anura	Craugastoridae	DD	5
Craugastor campbelli	GTM	Amphibia	Anura	Craugastoridae	DD	6
Craugastor cruzi	HON	Amphibia	Anura	Craugastoridae	CR	7.2
Craugastor fecundus	HON	Amphibia	Anura	Craugastoridae	CR	141.5
Craugastor taylori	MX	Amphibia	Anura	Craugastoridae	DD	49
Craugastor trachydermus	GTM	Amphibia	Anura	Craugastoridae	CR	51
Cryptotriton sierraminensis	GTM	Amphibia	Caudata	Plethodontidae	DD	27
Dendrotriton megarhinus	MX	Amphibia	Caudata	Plethodontidae	VU	41
Exerodonta chimalapa	MX	Amphibia	Anura	Hylidae	EN	252
Isthmohyla insolita	HON	Amphibia	Anura	Hylidae	CR	91.1
Ixalotriton parvus	MX	Amphibia	Caudata	Plethodontidae	CR	12.9
Oedipina tomasi	HON	Amphibia	Caudata	Plethodontidae	CR	9.9
Plectrohyla chrysopleura	HON	Amphibia	Anura	Hylidae	CR	109.8
Plectrohyla exquisita	HON	Amphibia	Anura	Hylidae	CR	131.8
Ptychohyla sanctaecrucis	GTM	Amphibia	Anura	Hylidae	CR	74

[a] HON=Honduras, GTM=Guatemala, MX=Mexico.
[b] CR=Critically endangered, EN=Endangered, VU=Vulnerable, NT=Near threatened, DD=Data deficient, LC=Least concern.
[c] EOO = Extent of occurrence.
[d] IUCN. 2012. IUCN Red List Categories and Criteria: Version 3.1. Second edition. Gland, Switzerland and Cambridge, UK: IUCN. iv + 32pp.

APPENDIX D: REPTILE SPECIES RESTRICTED (100% OVERLAP) TO THE NUCLEAR CENTRAL AMERICAN JAGUAR NETWORK

Species	Country[a]	Class	Order	Family	Status[b]	EOO[c,d]
Abronia bogerti	MX	Reptilia	Squamata	Anguidae	DD	446
Abronia ornelasi	MX	Reptilia	Squamata	Anguidae	DD	354
Bothriechis guifarroi	HON	Reptilia	Squamata	Viperidae	CR	1
Geophis nephodrymus	HON	Reptilia	Squamata	Dipsadidae	VU	24.3
Lepidophyma lipetzi	MX	Reptilia	Squamata	Xantusiidae	EN	267
Norops amplisquamosus	HON	Reptilia	Squamata	Dactyloidae	EN	313
Norops cusuco	HON	Reptilia	Squamata	Dactyloidae	EN	313
Omoadiphas aurula	HON	Reptilia	Squamata	Dipsadidae	VU	46
Rhadinella anachoreta	GTM/ HON	Reptilia	Squamata	Dipsadidae	LC	116
Rhadinella pegosalyta	HON	Reptilia	Squamata	Dipsadidae	VU	3.15
Rhadinella rogerromani	NIC	Reptilia	Squamata	Dipsadidae	NT	3.15
Rhadinella tolpanorum	HON	Reptilia	Squamata	Dipsadidae	CR	82.2

[a] HON=Honduras, GTM=Guatemala, MX=Mexixo, NIC=Nicaragua.

[b] CR=Critically endangered, EN=Endangered, VU=Vulnerable, NT=Near threatened, DD=Data deficient, LC=Least concern.

[c] EOO = Extent of occurrence.

[d] IUCN. 2012. IUCN Red List Categories and Criteria: Version 3.1. Second edition. Gland, Switzerland and Cambridge, UK: IUCN. iv + 32pp.