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The jaguar in South America – status review and strategy

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For joining the Friends of the Cat Group please contact Christine Breitenmoser at ch.breitenmoser@kora.ch

Original contributions and short notes about wild cats are welcome
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Editors: Christine & Urs Breitenmoser
Co-chairs IUCN/SSC
Cat Specialist Group
KORA, Talgut-Centrum 5, 3063 Ittigen, Switzerland
Tel ++41(31) 951 90 20
Fax ++41(31) 951 90 40
<u.breitenmoser@kora.ch>
<ch.breitenmoser@kora.ch>

Associate editors: Luke Hunter
Stacey Johnson

Cover Photo: Jaguar in the Pantanal
Photo: Patrick Meier

WŁODZIMIERZ JĘDRZEJEWSKI[1*], LEONARDO MAFFEI[2], SANTIAGO ESPINOSA[3,4], ROBERT B. WALLACE[5], NUNO NEGRÕES[6], RONALDO G. MORATO[7], MATHIAS TOBLER[8], GUIDO MARCOS AYALA CRESPO[5], EMILIANO E. RAMALHO[9], ESTEBAN PAYÁN[10,11], RAFAEL HOOGESTEIJN[10], JOSÉ F. GONZALEZ-MAYA[12,13], MARIA VISCARRA[5], KATIA MARIA P. M. B. FERRAZ[14], MARINA PERES PORTUGAL[15], ANGELA PARRA ROMERO[16], JOHN POLISAR[2,10,17,18], CHRISTINE BREITENMOSER[19] AND URS BREITENMOSER[19]

Jaguar conservation status in north-western South America

We analysed the current conservation status of the jaguar *Panthera onca* in north-western South America (7.14 million km² in total). The area is composed of habitats belonging to three eco-regions: the Andes, the Llanos, and the Amazon. Based on a large set of jaguar presence-absence data and a species distribution model, we estimated the current jaguar range at 4.98 million km², which represents 78.6% of the historical jaguar range in this region. The countries where jaguar range has shrunk most are north-western Venezuela, Ecuador and Colombia. Across the region, protected areas cover 27% of the jaguar range and indigenous territories 25%, with Ecuador having the highest and north-west Venezuela the lowest percentage of jaguar range under protection. Jaguar densities vary across the region, from 0.3 jaguars/100 km² in the driest or most degraded parts to 4.0–7.3 jaguars/100 km² in humid, productive, and best-preserved habitats of the Amazon Basin and Venezuelan Llanos. Based on combined density and updated distribution models we estimate a total jaguar population at 105,000 jaguars (95% CRI: 81,200–128,800) for the region, with mean density of 2.1 jaguars/100 km². Jaguar diet varies by habitat, from arboreal mammals and aquatic reptiles (mainly caimans) in the 'varzea' floodplain forests of Central Amazon, to large and medium-sized mammals in upland tropical forests and in the Llanos, with peccaries, capybaras, and occasionally livestock being the most important prey species. The main threats for jaguars in the region are deforestation and fragmentation of habitats, human-jaguar conflict, poaching (increasing due to the growing demand for jaguar parts from the Asian market), infrastructure expansion, and mining. The most important conservation goals are to halt deforestation, reduce the killing of jaguars for retaliation and trade, increase the number of protected areas, protect ecological connectivity, improve law enforcement, and implement a better system of environmental education.

In this chapter, we analyse the current conservation status of the jaguar in north-western South America, an area that encompasses the territories of Colombia, Ecuador, and Peru, and portions of the territories of Venezuela, Bolivia and Brazil (Fig. 1). The total area considered covers 7,137,000 km² and is composed of three main eco-regions: the Andes, the Llanos, and the Amazon (Fig. 1). All three eco-regions are recognised as biodiversity hotspots, and together hold a large portion of the planet's biodiversity (Baillie et al. 2004). The huge Amazon tropical forest is characterised by high primary productivity, which may transform into abundant jaguar prey and locally high jaguar densities (Ramalho 2012). The high Andes are usually covered by treeless páramo, which is not jaguar habitat, but the lower parts of the Andes, especially the Andean foothills, are covered with highly productive tropical forests with many rivers and streams and are known to bear high prey biomass and high jaguar population densities (Emmons 1987, Tobler et al. 2013, 2018). The Llanos is composed of open and partially open seasonally flooded savannas, dry forests, and gallery forests along numerous rivers, which altogether constitute important jaguar habitat with abundant prey and many jaguars (Polisar et al. 2003, Jędrzejewski et al. 2017a, 2017b). However, large areas of NW South America have been transformed for cattle pastures or agriculture, including plantations of soybeans, rice, corn, sugar cane, oil palms, and other crops (Eva et al. 2004, Grasser et al. 2018). Urban areas and road infrastructure are heavily developed in parts of the Andean and sub-Andean regions. Mineral extraction is spreading quickly, especially oil in the Colombian Llanos and gold mining, including the most remote parts of the Amazon (RAISG 2020). Some areas are sparsely populated while others have very high human population densities (e.g. coastal or some Andean areas), with a total of 158.6 million people living in north-western South America (http://sedac.ciesin.columbia.edu/data). Jaguar populations are exposed to various favourable and unfavourable conditions, but detailed jaguar distribution and population density are often unknown for several areas. Additionally, in the last decade there have been several environmental, climatic, industrial, land use, and political changes that may have had a strong impact on jaguar populations in north-western South America.

In this article, we update knowledge on jaguar ecology and its current conservation status for the entire region and each country inside our study area, based on results of the analysis of distribution data sets that we compiled and results presented in other articles in this volume (Jędrzejewski et al. 2023a, 2023b, Morato et al. 2023, Payán et al. 2023, Polisar et al. 2023), as well as other published sources. In particular, we provide an overview of density estimates, current threats, and conservation needs, as well as a detailed description of the current jaguar status, distribution, protection, and population estimate for each country.

Methods

To estimate current jaguar distribution, we compiled jaguar presence and absence data from each country of NW South America between 2000 and 2020, including data from published sources and ongoing monitoring projects. Data were mostly from camera trapping, radio-tracking, recording of tracks, and field interviews. In order to avoid the negative effects of spatial autocorrelation (Dormann et al. 2007, De Angelo et al. 2011), for the distribution analysis we reduced clumped data points, allowing a maximum of one record for each 100 km². In total, we used 568 jaguar presence records from 2000–2009 and 521 records from 2010–2020. We also compiled 377 jaguar absence points that were collected in the field and randomly selected 491 points from known jaguar absence areas, where jaguars have not been recorded recently (Fig. 1).

To estimate habitat suitability for jaguars and reveal factors driving its distribution, we used logistic regression models with a set of 21 predictive variables, modelling jaguar occurrence probability separately for each eco-region. Finally, we combined the results of these models with a kriging interpolation to estimate the current jaguar status and distribution (Jędrzejewski et al. 2017a). Following the

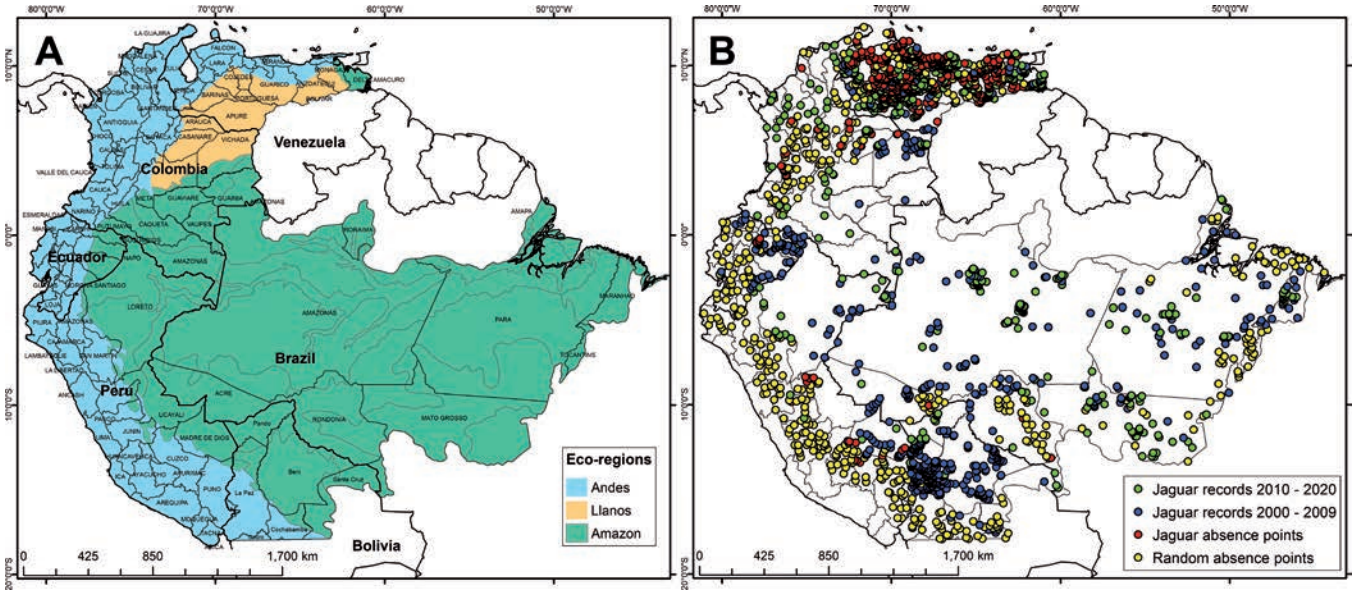

Fig. 1. A: North-western South America and its main eco-regions (after Griffith et al 1998); B: Jaguar records (from 2000–2009 and 2010–2020) and jaguar absence points used for the analysis of jaguar distribution inside the study area.

IUCN guidelines for mapping species distribution (IUCN 2019), we classified jaguar status in four categories: Extinct, Possibly Extinct, Possibly Extant, and Extant. In our classification the class 'Extinct' corresponds to low habitat suitability and no jaguar records; 'Possibly Extinct' to low or medium habitat suitability and no or few jaguar records, 'Possibly Extant' – high habitat suitability and few records or low/medium habitat suitability but several records, and 'Extant' to high habitat suitability and several jaguar records. We defined the current (2020) jaguar range as the combined area of the classes 'Extant' and 'Possibly Extant'. A detailed methodology of all this analysis is given in Jędrzejewski et al. (2023a). Here we present results of the same analysis, however with more details for each country and each eco-region within NW South America.

Additionally, we estimated the jaguar population size by multiplying the potential jaguar population densities (Jędrzejewski et al. 2018) by the probabilities of jaguar occurrence inside the current (2020) jaguar range (Jędrzejewski et al. 2023a), following the methodological approach of Jędrzejewski et al. (2018). We calculated the 95% lower and upper credible limits applying the percentage credible intervals for each country calculated for the same type of estimates by Jędrzejewski et al. (2018).

We also compiled data and information on current threats and conservation achievements and needs, including the most updated information on protected areas and indigenous territories that play important role in jaguar conservation in each country. For this purpose, the co-authors completed a standard questionnaire developed by the IUCN SSC Cat Specialist Group.

Results

Habitats and distribution

Historical distribution of the jaguar in NW South America covered 6.33 million km^2 that was 89% of the total area of the region (Table 1, Fig. 2). It indicates that originally jaguars could occur in almost all types of habitats found throughout the region, except high Andean 'paramos' and bare areas (Sanderson et al. 2002, Jędrzejewski et al. 2017a). However, due to the increase in human population and habitat transformations of the 20th and 21st centuries, vast areas of the region have become fragmented or poorly suitable or unsuitable for jaguars; the only large refuge for jaguars today is the Amazon Forest, although it is also more and more intersected by large clearings and devastations (Fig. 2A). We estimated jaguar status as 'Extant' over 4,32 million km^2 (68% of the jaguar historical range) and as 'Possibly Extant' at 0.66 million km^2 (11%). Jaguars are found as Extinct or Possibly Extinct at 12% and 9% of their historical range, respectively (Table 1, Fig. 2B).

The current (2020) jaguar range (combined categories 'Extant' and 'Possibly Extant') in NW South America covers 4.98 million km², which constitutes 70% of the total area and 79% of the historical jaguar range of this region (Table 1, Fig. 2B). Jaguars disappeared from 21% of their historical range. Regarding the ecoregions, the biggest decline of the jaguar range occurred in the Andes, where the current range constitutes only 29% of the historical range, while in the Llanos the jaguar range dropped to 54% and in the Amazon to 91% of its historical distribution (Table 2). This overall picture is the result of summing up the situation of jaguars in individual countries, where environmental conditions, human impact and the history of human-jaguar relationship are very diverse and often differ from each other.

North-western Venezuela

The Venezuelan part of north-western South America covers 466,000 km² and has about 29 million inhabitants with an average population density of 62 people/km². Historical jaguar distribution (Sanderson et al. 2002) covered about 95% of the territory and jaguars inhabited all large tropical humid and dry forests, scrublands, as well as partially open, flooded savannahs in the Llanos and all other types of swamp areas, including coastal mangrove forests. Only in high mountain areas (approximately over 2,500 m) and in very dry open savannahs they possibly did not occur or occurred at very low densities (Jędrzejewski et al. 2017a).

The current jaguar distribution covers about 38% (172,000 km²) of the historical range in NW Venezuela; during the last 80 years, jaguars disappeared from about 62% of the area (Table 1, Fig. 2). Moreover, only about 68,000 km² (40% of the current range) is still a good jaguar habitat with strong jaguar populations and frequent presence records

(jaguar status classified as 'Extant'), while in the remaining 104,000 km² (60% of the jaguar range) the habitats have lower suitability for jaguars, their presence and absence points are highly interspersed, and the jaguar status is classified as 'Possibly Extant' (Table 1, Figs 1, 2).

The highest rate of jaguar range decline occurred between 1970 and 2000 (Jędrzejewski et al. 2017a) coinciding with very extensive deforestations conducted during this period. Today, jaguar populations in NW Venezuela are highly fragmented and mostly found in the areas with low human population density (<4 persons/km²). Larger populations are still found at the Atlantic coast (Sucre and Monagas states) and in the Delta of the Orinoco (Fig. 2). Partially isolated populations are found in the forested parts of Barlovento region (Miranda state, east of Caracas) and in Guatopo NP. In the eastern (drier) part of the Llanos (Anzoátegui and Guárico states) jaguars are mostly gone, while in the western Llanos they still occur in parts of Cojedes, Barinas, and Apure states, mostly in seasonally flooded and forested areas. Very fragmented populations are found in the foothills of the Andes (Portuguesa, Mérida, Trujillo, Táchira), in the Perijá mountains, and south-west of the Maracaibo Lake in Zulia (Fig 2). Although jaguar range and population numbers tend to decline in Venezuela, there have been reports of recent population increase in some regions, such as the less populated parts of the western Llanos (Jędrzejewski et al. 2017a).

Colombia

Colombia covers 1.14 million km² and has 50 million inhabitants with an average density of 44 people/km². In the past, jaguars were spread all over Colombia except the highest mountains over 2,000 m (Payán et al. 2016). Today, jaguar's range covers 652,000 km², which constitutes 57% of the country area and 63% of the historic distribution (Table 1, Fig. 2B). The area with jaguar status classified as 'Extant', which corresponds to the most suitable habitats and fairly well documented jaguar presence, covers 531,000 km², or 81% of the current jaguar range (Table 1, Fig. 2B).

The Colombian jaguar population is divided by the Andes into two main sub-populations: the western population in the Chocó biogeographic region, which spreads along the Pacific coast, and the south-eastern population in the Amazon and Orinoco basins (Fig. 2; Payán et al. 2013a, 2016). Ruíz-García et al. (2006), based on the analysis of DNA micro-

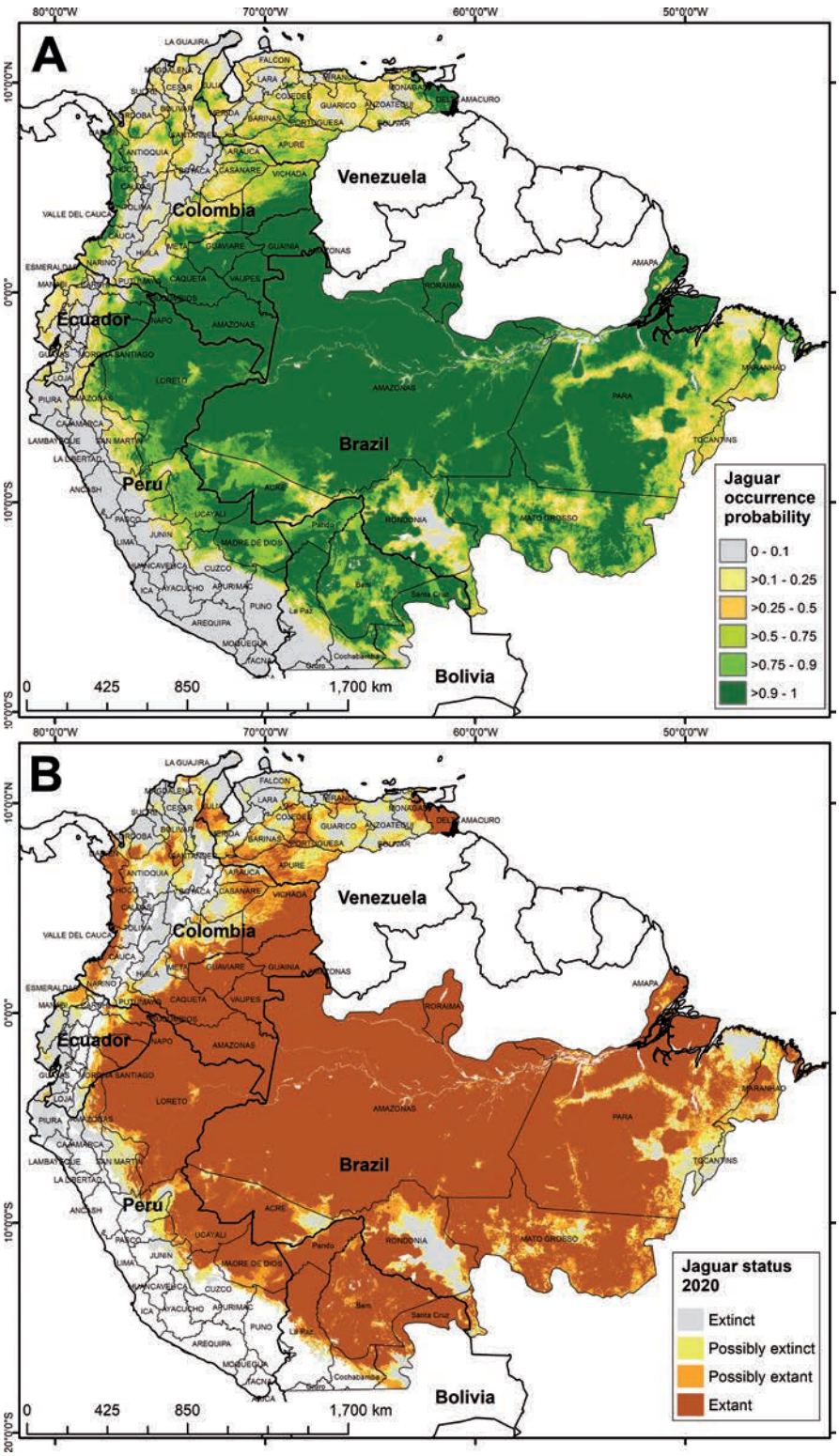

Fig. 2. A: Probability of jaguar occurrence (indicating also habitat suitability for jaguars) estimated with the logistic regression model of jaguar presence and absence. B: Jaguar status in north-west SA classified into four IUCN categories: Extinct, Possibly Extinct, Possibly Extant and Extant; assessment resulting from the combination of logistic regression and kriging interpolation models based on a large set of jaguar presence and absence data. Brown (Extant) and orange (Possibly Extant) indicate the current jaguar distribution, while yellow (Possibly Extinct) and grey (Extinct) indicate an extent of the historical jaguar range (Sanderson et al. 2002) outside the current jaguar range. White areas inside our study area denote territories that historically have never been occupied by the jaguar (Sanderson et al. 2002). For methodological details see Jędrzejewski et al. (2023a).

satellites, have found significant genetic heterogeneity between these two sub-populations; however, they also found some (rather low) level of gene flow between them and concluded that they do not constitute different sub-species, contrary to earlier suggestions (Pocock 1939).

In addition to these two main jaguar populations, there are some smaller, increasingly fragmented ones (Fig. 2): in Paramillo, along the central Cauca and Magdalena rivers, in the Serranía de San Lucas Mountains, in the northern region of Sierra Nevada de Santa Marta, and along the Venezuelan border in the Perijá and Catatumbo regions (Figel et al. 2019, Boron et al. 2020). These populations are key in gene flow since they constitute the only possible connection between west and east of the Andes (Jędrzejewski et al. 2023b). The main habitats occupied by the western (Chocó) population are mostly inaccessible, very humid, flooded and dense tropical forests, as well as mountain forests (González-Maya & Jiménez-Ortega 2015). This population is connected with jaguar populations in Central America through the Darién Gap and Panama, with the Ecuador population in the south, and likely also with Paramillo, central Magdalena and San Lucas populations (Fig. 2). The south-eastern population occupies large tracts of tropical rain forests extending over the Amazon and Orinoco basins and the more open, seasonally flooded habitats of the Llanos. The tropical forests are fairly well preserved, with numerous protected areas and indigenous and afro-descendant territories, although suffering from increasing deforestation pressures in recent years. The Llanos, once important jaguar habitat, have been largely transformed to cattle pasture and agriculture, or oil exploitation areas (Payán & Díaz-Pulido 2016).

Ecuador

Ecuador covers 256,400 km² and has a population of 18 million people, with a mean population density of 70 people/km². Jaguars in Ecuador occur below 2,000 m on both the western and the eastern sides of the Andes (Fig. 2), although some sporadic records at higher altitudes also exist (Espinosa et al. 2016, Griffith et al. 2022). The current jaguar range has been estimated at 87,000 km², which constitutes 46% of the historic jaguar range (Table 1). In 72% (63,000 km²) of the current range, the jaguar status has been classified as 'Extant', indicating good habitat quality, and in the remaining 28% as 'Possibly Extant' (Table 1, Fig. 2B).

In western Ecuador (Andean eco-region), the historic jaguar range (areas below 2,000 m above sea level) covered approximately 91,000 km². Land cover in this region has been strongly transformed and as a consequence, the distribution of the species has been drastically reduced (Fig. 2A). Based on the most recent information on natural land cover (MAAE 2018), we calculated that only 26% of tropical forest in western Ecuador remains natural and it is highly fragmented, limiting the jaguar presence. Most of the recent records of jaguars are limited to the north-west (Fig. 1), where the largest patches of the humid Chocó biogeographic region remain, and within protected areas such as Cotacachi Cayapas Ecological Reserve and Pambilar Wildlife Refuge (Zapata-Ríos & Araguillin 2013). In south-western Ecuador, one individual was photo-captured between 2008 and 2011 in the tropical dry forest of Cerro Blanco Protected Forest, located on the Chongón-Colonche mountain range and on the outskirts of Guayaquil city (Saavedra-Mendoza et al. 2017). Due to the large degree of habitat fragmentation and human encroachment, the jaguar population of western Ecuador is likely no larger than 100 individuals, posing it to the risk of genetic drift (Eizirik et al. 2002). However, at least some parts of this population are likely connected with the Colombian Chocó jaguar population (Fig. 2).

In eastern Ecuador, jaguar distribution originally corresponded to an area of ca. 100,000 km² and currently about 80% of that area still maintains its natural forest cover (Fig. 2). Eastern Ecuador possesses large protected areas, such as Yasuní National Park (10,227 km²) and Cuyabeno Wildlife Refuge (5,901 km²) which fall entirely within the current jaguar range (Fig. 3). In addition to protected areas, indigenous lands such as the Waorani, Kichwa, Sápara, Shiwar, Achuar and Shuar territories (Fig. 3), also protect a large part of remaining jaguar habitat in Ecuador's Amazon (Table 1, Fig. 2).

Peru

Peru covers 1,285,000 km² and has a population of 32.8 million people with a mean population density of 25 people/km². The majority of the population lives along the coast and in the Andes, with the Amazonian lowlands having a much lower population density and few urban centres. The historical jaguar range in Peru covered about 61% of the country and was distributed mainly on the eastern side of the Andes, except the most

Table 1. Area of the jaguar historic range (in thousands km²; Sanderson et al. 2002), area corresponding to the categories of the current jaguar status (Jędrzejewski et al. 2023a, Chapter 6, this volume), and area of protected areas and indigenous territories inside the current (2020) jaguar range in NW South America inside the countries of NW South America. The current jaguar range is defined as the combined area of 'Extant' and 'Possibly Extant' categories. All areas are in thousands km².

Country	Total area	Hist. jag. range	Current (2020) jag. range (% of hist. range)	Current jaguar status area (% of hist. range)				Protected areas inside jag. range (% of curr. jag. range)	Indigenous territories in jag. range (% of curr. jag range)
				Extinct	Poss. Extinct	Poss. Extant	Extant		
Venezuela (NW)	466	451	172 (38)	142 (32)	137 (30)	104 (23)	68 (15)	26.5 (15)	0.0 (0)
Colombia	1,142	1,030	652 (63)	253 (24)	125 (12)	121 (12)	531 (52)	122.1 (19)	246.4 (38)
Ecuador	256	190	87 (46)	70 (37)	33 (17)	24 (13)	63 (33)	20.0 (23)	50.0 (57)
Peru	1,285	787	617 (79)	106 (13)	64 (8)	69 (9)	548 (70)	171.4 (28)	190.7 (31)
Bolivia (Amazon)	548	449	417 (92)	16 (4)	16 (4)	47 (10)	370 (82)	164.1 (39)	72.8 (17)
Brazil (Amazon)	3,440	3,420	3,031 (89)	180 (5)	209 (6)	290 (9)	2,741 (80)	849.9 (28)	697.9 (23)
Total NW South America	**7,137**	**6,327**	**4,976 (79)**	**767 (12)**	**584 (9)**	**655 (11)**	**4,321 (68)**	**1,354 (27)**	**1,258 (25)**

Table 2. Jaguar historical and current (2020) range (in thousands km²) and jaguar population estimates (in thousands) with 95% credible intervals CRI, as well as percentages of jaguar range and population size inside protected areas PAs, indigenous territories IT, and in unprotected areas UAs within the three main eco-regions in NW South America.

Eco-region	Hist. jag. range	Jag. range 2020	Jag. range 2020 % of hist. range	% jag. range in PAs	% jag. range in ITs	% unprotected jag. range	Pop. est. 2020 (CRI)	% pop. PAs	% pop. ITs	% pop UAs
Andes	1,001	286	29	29	17	54	5.3 (4.1–6.4)	33	17	50
Amazon	4,922	4,472	91	28	27	45	96.9 (75.0–118.7)	30	26	44
Llanos	403	218	54	7	7	86	3.0 (2.3– 3.7)	8	5	87
Total	**6,327**	**4,976**	**79**	**27**	**25**	**48**	**105.2 (81.2– 128.8)**	**30**	**26**	**44**

north-western parts (department of Piura) close to Ecuador, where the jaguar was possibly also found in the dry lower mountain forests close to the coast (Sanderson et al. 2002). The dry areas of the Pacific coast, and the higher Andean elevations (often over 4,000 m) have sparse vegetation (grasslands or dry scrublands) with few potential prey species, and are not suitable for jaguars. Today, jaguars occur only on the eastern side of the Andes, below 2,000 m (Figs 1, 2). They are found in the Amazonian tropical forests (ca. 90% of their current distribution) and Peruvian Yungas or montane forest of the Andean foothills (ca. 10%, Olson et al. 2001; Brack-Egg & Mendiola 2004). Based on the analysis of actual forest cover in Peru, Maffei et al. (2021a) estimated jaguar range at 602,000 km².

We estimate the current jaguar range in Peru at 617,000 km² (78% of the historical range, Table 1, Fig. 2). The jaguar status is classified as 'Extant' in 89% of the area of the current jaguar range and as 'Possibly Extant' in 11% (Table 1, Fig. 2B).

The core habitat for jaguars in Peru is the lowland Amazonian humid forest in the departments of Loreto, Ucayali and Madre de Dios (Fig. 2A). These large departments make up 43% of the countries' total area and have low human population densities (1.3–4.2 people/km², INEI 2018). These forests are intersected by numerous rivers and streams flowing down from the nearby Andes, and are characterised by very high primary productivity and a high biomass of potential jaguar prey (Emmons 1987). The other departments with jaguar populations are in central Peru, along the eastern slopes of the Andes: Amazonas, San Martin, Huánuco, Pasco, Junín, Cusco, and Puno (Fig. 2). Human population in these departments is higher (mean density: 16.8 people/km²), however given that all larger cities are located in the Andes, lower elevations where jaguars occur have rather lower human population densities (INEI 2018).

Amazonian Bolivia

The Bolivian part of NW South America (Amazonian Bolivia; Fig. 1) covers 548,000 km² and has a population of 7 million people, with an average population density of 12.8 people/km² and most inhabitants living in Andean cities. Jaguars originally occurred throughout the Bolivian lowlands below 2,000 m (Fig. 2), including all forms of tropical humid forests, tropical dry forests, natural savannas and wetlands including the flooded savanna-forest mosaics of the Beni Department in the Llanos de Moxos (Noss et al. 2010, Wallace et al. 2010, 2013).

Before 2000, there was no jaguar research in the Bolivian Amazon. Since then, several studies using track records, camera trapping, and occupancy modelling (Wallace et al. 2003, 2010, 2013, 2020, Silver et al. 2004, Arispe et al. 2007, Ayala et al. 2020, 2022) largely increased knowledge on jaguar distribution in the northern portions of the La Paz Department, and less so in the departments of Beni (WCS, unpubl. data), Chuquisaca (E. M. Peñaranda, unpubl. data), Pando (N. Negrões, unpubl. data) and Tarija (X. Velez-Liendo, unpubl. data).

We estimate the current jaguar range in Amazonian Bolivia at 417,000 km² (92.9% of its historic range; Table 1, Fig. 2). Populations with the 'Extant' status, indicating high suitability of habitats for jaguars and/or frequent jaguar records, occupy 370,000 km² (89% of the current jaguar range) while those with the 'Possibly Extant' status occupy 47,000 km² (11%; Table 1, Fig. 2).

Brazilian Amazon

The Brazilian portion of NW South America (Brazilian Amazon, Fig. 1) covers 3,440,000 km² and has a population of 22.3 million people (6.5 people/km²); however, most of its area has very low human population with densities between 0 and 2 people/km². Originally, jaguars were found throughout the region (Sanderson et al. 2002, de Oliveira et al. 2012), but currently we estimate that the species occupies only 89% of the area, i.e. 3,031,000 km² (Fig. 2, Table 1).

Jaguar status is classified as 'Extant' in 90% of the current jaguar range (Fig. 2, Table 1). The two habitats of the Brazilian Amazon that are most important for the jaguar are the 'varzea' floodplain forests (10% of the total jaguar range) and the upland 'terra firme' forests (90% of jaguar range, Alvarenga et al. 2018). Although jaguars use both types of habitats, they have higher population density in the 'varzea' (Ramalho 2012, Von Mühlen 2018). In Mamirauá Sustainable Development Reserve, a protected area of 11,240 km² entirely composed of 'varzea' in Central Amazon, during the high-water season jaguars live an arboreal and semi-aquatic lifestyle, staying in trees or swimming (Ramalho et al. 2021).

Home range size, densities, and population estimate

Jaguar home range size and jaguar population densities are inversely related parameters because with the smaller home ranges more individual jaguars can live in the same area leading to higher population density of jaguars. Both parameters are driven by factors related to primary productivity of habitats which in turn determine prey density and biomass (Jędrzejewski et al. 2018, Thompson et al. 2021, Morato et al. 2023). So far, there have been only six studies that aimed at estimating jaguar home range size in NW South America. In the Venezuelan Llanos mean female home ranges were estimated at 65 and 79 km² and mean male home ranges at 100 and 167 km², respectively by two independent studies that used VHF radio-tracking and spatial capture recapture models based on camera trapping data (Scognamillo et al. 2002, 2003, Jędrzejewski et al. 2017b). Four other studies conducted in NW South America used GPS collars and 95% kernel or autocorrelated kernel to estimate home range size. In the Colombian Llanos, the home range size of a female was 35 km², and of a male

100 km² (Thompson et al. 2021). In Madre de Dios in Peru (G. Powell & M. Tobler, unpubl. data) mean home range size of females was 138 km² (N=4, range: 70–192 km²) and that of males 272 km² (N=5, range: 175–351 km²). In Mamirauá Reserve in Brazilian Amazon mean estimate for females was 87.75 km² and for males 158 km² (Ramalho et al. 2021). All these results indicate that in general jaguar home ranges in NW South America tend to be rather small or medium compared to estimates from the drier and less productive areas across the species range (Thompson et al. 2021).

In contrast to home range size estimates, there have been numerous studies estimating jaguar population densities based on camera trapping and spatial capture-recapture models. In Venezuela, high population densities (4.4 adult jaguars/100 km²) were found in a protected area in the seasonally flooded habitats of the Venezuelan Llanos (Jędrzejewski et al. 2017b). Similar high densities were documented for the very humid and productive habitats of southern Maracaibo Lake (Puerto 2012). In the tropical forests of Guatopo National Park and in the upper Caura, jaguar densities were lower (2.2–2.3 jaguars/100 km², Isasi-Catalá 2012, 2013, Perera-Romero et al. 2012).

In the Colombian Llanos, rather low densities (1.9 and 3.2 jaguars/100 km²) were found in cattle production areas along tributaries of the Orinoco and Magdalena rivers, where jaguars are often persecuted by ranchers (Boron et al. 2016). In the Amazonian tropical forests in Colombia (Calderón river valley and Amacayacu National Park) jaguar population densities were estimated between 2 and 3 individuals/100 km², respectively (Payán 2009, recalculated with spatial capture-recapture models).

In the Yasuni Biosphere Reserve in Ecuador jaguar density estimates varied from 0.3 to 5.4 jaguars/100 km², being clearly negatively related to the level of human access to an area and proximity to roads (Espinosa et al. 2018). At the border between Ecuador, Peru, and Colombia, mean density was 2.2 jaguars/100 km² (Mena et al. 2020).

Density estimates from several sites in the lowland Amazon Forest of Madre de Dios in Peru ranged from 4.0 to 4.9 jaguars/100 km² (means from two studies 4.4 and 4.5 jaguars/100 km²; Tobler et al. 2013, 2018). Maffei et al. (2021b) estimated 2 to 2.5 jaguars/100 km² for Manu National Park.

Population density estimates in Amazonian Bolivia were conducted around the Madidi National Park and Natural Area of Integrated Management, in northern La Paz Department, and in El Encanto, Santa Cruz (Wallace et al. 2003, Silver et al. 2004, Arispe et al. 2007, Ayala et al. 2020, 2022). More recent camera trapping efforts in Pando (N. Negrões, unpubl. data) and Tarija (X. Velez-Liendo, unpubl. data) have resulted in additional population density estimates. These estimates widely varied: 3.0 jaguars/100 km² in El Encanto, Santa Cruz (Arispe et al. 2007, recalculated using spatial capture-recapture SCR models), and 1.4 jaguars/100 km² in Tacana II indigenous territory, La Paz (ACEAA, N. Negrões, unpubl. data, SCR models). Other study conducted at five sites across the Kaa-Iya landscape in Bolivian Chaco resulted at great variation of jaguar density estimates: from 0.3 to 1.9 jaguars/100 km² (Noss et al. 2012). In Madidi, jaguar populations have gradually recovered from lower densities at the beginning of the century (0.9–1.5 jaguars/100 km² Wallace et al. 2003, Silver et al. 2004, Ayala et al. 2022), to 6.9–7.2 jaguars/100 km² between 2014 and 2019 (G. Ayala et al., unpubl. data).

There are very few studies providing jaguar density estimates from the Brazilian Amazon. In the 'varzea' of Mamirauá Sustainable Development Reserve, Ramalho (2012) found as much as 11.6 jaguars/100 km² while Montanarin (2016) estimated 7.3–11.9 jaguars/100 km² between 2012 and 2015 with average density of 9.54 jaguars/100 km² at the same site. There are no estimates from the 'terra firme' upland tropical forests.

Based on the combination of the jaguar density model (Jędrzejewski et al. 2018) and the jaguar distribution and probability of occurrence assessed in this study, we estimated the total jaguar population within NW South America at 105,200 jaguars (95% credible interval: 81,200–128,800), with a mean density of 2.1 jaguars/100 km² (Tables 2 and 3). Of the total population, the largest number of jaguars are found in the Brazilian Amazon (62,200), then in Peru (18,600), Colombia (11,300), and Amazonian Bolivia (8,700). The smallest numbers are found for NW Venezuela (2,600) and Ecuador (1,800). Regarding the eco-regions of NW South America, the biggest number of jaguars was estimated for the Amazon (96,900), then for the Andes (5,300), and then for the Llanos (3,000).

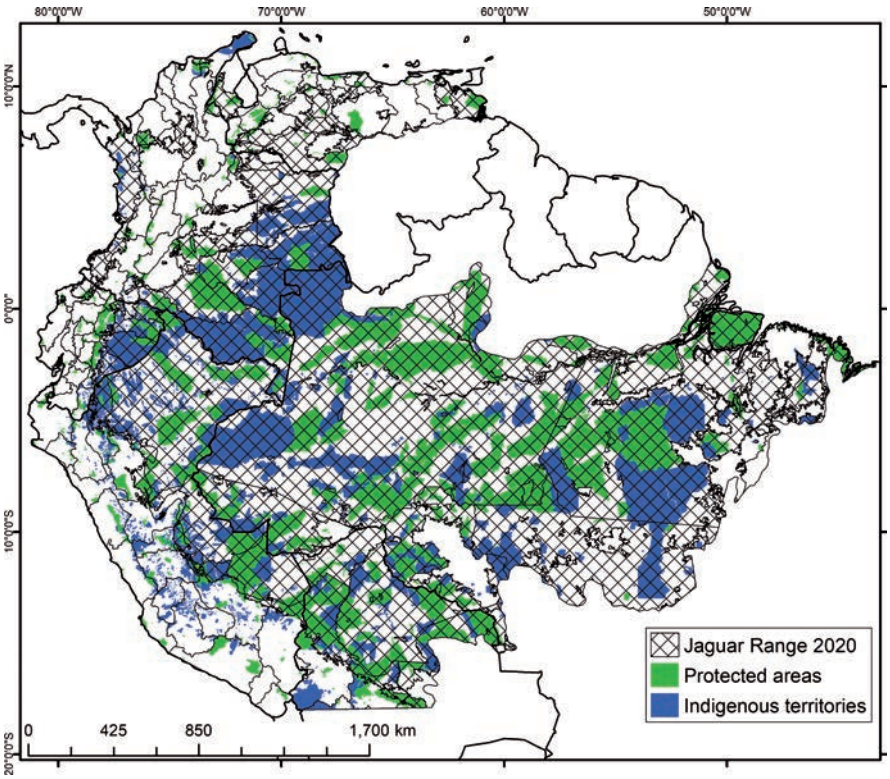

Fig. 3. Protected areas and indigenous territories within NW South America compared with the current (2020) jaguar range. Sources of data on protected areas and indigenous territories: World map of protected areas, http://www.protectedplanet.net/, Amazonia Socioambiental RAISG 2019, https://www.amazoniasocioambiental.org/es/mapas/#!/areas, and SERNANP (2020), https://www.gob.pe/sernanp.

Diet

The few studies on jaguar diet in NW South America show that jaguars may hunt for a wide variety of large to medium-sized vertebrate prey, which usually includes forest

Table 3. Jaguar population estimates for each country and percentages of jaguar population inside protected areas PAs, indigenous territories ITs, and outside these two management categories. To estimate jaguar population size, we multiplied jaguar potential population densities (Jędrzejewski et al. 2018) by probabilities of jaguar occurrence inside the current (2020) jaguar range (Jędrzejewski et al. 2023 a).

Country	2020 jag. pop. est. (95% CRI)	mean jag. pop. density (jag./100 km^2)	% of jag. pop. in PAs	% of jag. pop. in ITs	% of jag. pop. not in PAs or ITs
NW Venezuela	2.6 (2.0–3.2)	1.5	20	0	80
Colombia	11.3 (8.0– 14.5)	1.7	21	40	39
Ecuador	1.8 (1.5– 2.2)	2.1	26	63	11
Peru	18.6 (15.0–22.5)	3.0	30	29	41
Bolivia (Amazon)	8.7 (6.9–10.4)	2.1	44	20	36
Brazil (Amazon)	62.2 (47.9–76.0)	2.1	31	24	45
Total	105.2 (81.2–128.8)	2.1	30	26	44

dwellers, aquatic species, and often livestock. In the Venezuelan Llanos, Scognamillo et al. (2002, 2003) identified 198 jaguar prey items of which peccaries (collared peccary *Pecari tajacu* and white-lipped peccary *Tayassupecari*) constituted 28%, capybaras *Hydrochoerus hydrochaeris* 21%, cattle 20%, caimans *Caiman crocodilus* 12%, giant anteaters *Myrmecophaga tridactyla* 5%, turtles (*Geochelone denticulata*, *Podocnemys unifilis*, *Platemys platycephala*) 4%, agouti 4%, and deer *Odocoileus virginianus* 3%, while other small and medium prey constituted the remaining 5%. In an interview study conducted across Venezuela, Jędrzejewski et al. (2017c) documented 387 records of livestock killed by jaguars, of which 79% were cattle, 12% horses, 11% pigs, 9% donkeys, 3% mules, 4% sheep, and 1% goats. In the same study 37 records of dogs (mostly hunting dogs) killed by jaguars were collected.

Emmons (1987) found that in Manu NP in Peru jaguars hunted for several prey species, of which the most important were collared peccary, brocket deer *Mazama americana*, agouti *Dasyprocta variegata*, paca *Cuniculus paca*, turtles and caimans. They hunted also for birds, smaller mammals, and fish. An analysis of 34 scats from Madre de Dios, Peru (S. Carrillo-Percastegui, unpubl. data) showed that the main prey items were collared peccary (32%) and white-lipped peccary (21%). Other prey species included coati *Nasua nasua*, lowland tapir *Tapirus terrestris*, nine-banded armadillo *Dasypus novemcinctus*, collared anteater *Tamandua tetradactyla*, grey four-eyed opossum *Philander opossum*, and Kinkajou *Potos flavus*.

In Amazonian Bolivia, studies in the lower Tuichi, Hondo (PNANMI Madidi) and Quiquibey (RB Pilón Lajas) river valleys revealed a high consumption of the white-lipped peccary (Flores-Turdera et al. 2020).

In floodplain 'varzea' forests of Mamirauá Reserve, Brazilian Amazon, the jaguar's main prey are arboreal mammals (51% of biomass consumed) and aquatic reptiles (47%). Mammal species included sloths (*Bradypus variegatus, Choloepus didactylus*), tamanduas *Tamandua tetradactyla*, red howler monkeys *Alouatta seniculus* while reptiles included spectacled caimans, black caimans *Melanosuchus niger*, and some snakes and turtles. Jaguars there occasionally killed also cattle (1% of biomass) and birds (Silveira et al. 2010, Ramalho et al. 2012). An additional study conducted in Mamirauá using interviews showed that among livestock killed in the region (125 cases), pigs constituted 50%, cattle 17%, dogs 10%, sheep 6%, buffalo 2%, and poultry 15% (Ramalho 2012). In the study conducted at four sites of 'terra firme' in Brazilian Amazon, both species of peccaries constituted 57% of prey biomass, deer *Mazama* sp. 13%, armadillos (*Cabassous unicinctus, Dasypus* sp.*, Euphractus sexcinctus*) 15%, agouti *Dasyprocta* sp. 7%, paca *Cuniculus paca* 6%, along with some smaller mammals and birds (Prado 2010).

All these studies show that jaguars are highly versatile hunters, adapted to hunting large and medium-sized prey both on the ground, in the water, and even in trees.

Threats

Jaguar populations are still declining in every country in this region, with the highest overall rate of jaguar range decline documented for NW Venezuela, then Ecuador, and Colombia (Table 1). Major threats vary by country (see Supplementary Online Materials SOM Text T1), but deforestation made for agriculture and cattle ranching has the greatest negative impact on jaguar distribution throughout the area of NW South America (SOM Table T1, Jędrzejewski et al. 2023a). Deforestation, often carried out at high speed by large man-made forest fires, causes direct habitat loss for jaguars, but may also lead to a catastrophic collapse of the whole Amazon system through changes in hydrological cycles and climate (Marengo et al. 2011, Lovejoy & Nobre 2018, Damasio 2019, Romero-Muñoz et al. 2020, Menezes et al. 2021). As the Amazon Forest and nearby oceans have a large impact on the global climate, conservation actions targeting the jaguar also have global implications.

Conflicts with cattle ranching and retaliatory killing of jaguars are important factors of jaguar decline in NW Venezuela, Colombia, and in some areas of Brazilian Amazon and are likely increasing in other countries too, as the agricultural frontier advances (Ramalho 2012, Aconcha-Abril et al. 2016, Jędrzejewski et al. 2017c; SOM Table T1). The rates of jaguar predation on livestock and retaliatory killing of jaguars can be occasionally very high in the Llanos and cause local extirpations of jaguars (Hoogesteijn et al. 1993, 2002, González-Fernández 1995, Jędrzejewski et al. 2014, 2017c).

Hunting by regular hunters (mostly illegal) in forests, other natural areas, and even in the protected areas has moderate impact in NW Venezuela, Peru, and Brazil, and lower impacts in Ecuador and Bolivia and possibly in Colombia (e.g. Jędrzejewski et al. 2017c, Braczkowski et al. 2019, Carvalho 2019, SOM Table T1), although data is generally missing on this topic. However, hunting impact is likely growing due to increasing international trade of jaguar parts driven by Asian market demands, particularly in China (Morcatty et al. 2020, Arias et al. 2021,

Mena et al. 2021, Morcatty 2022, Polisar et al. 2023).

Other important threats are expansion of human settlements, increased road density (Espinosa 2018), habitat fragmentation, and loss of ecological connectivity (Jędrzejewski et al. 2023b). Mining, both legal and illegal, is a growing problem all over the region, but especially in Colombia, Peru, Bolivia, and Brazil (e.g. Finer & Mamani 2018a, Davalos 2001, Payán et al. 2016, SOM Table T1). Mining converts forests and soil into unrecoverable, polluted swamps and causes mercury poisoning of waters, which can have a direct effect on jaguar survival (May Junior et al. 2018); it also stimulates road constructions, opens access to jaguar core areas, and increases hunting rate for jaguars and their prey (Espinosa et al. 2014). Poor law enforcement is a general problem in all countries, but particularly in Venezuela, Peru, and Brazil. Prey depletion is most important in Ecuador (SOM Table T1).

See the Supplementary Online Materials for more detailed information on threats for jaguar conservation in each country of the region.

Conservation status and goals

In the countries of NW South America, jaguars are either fully legally protected (Brazil, Colombia, Ecuador, Venezuela) or partially protected (Peru; Kretser et al. 2022, Payán et al. 2023). In the national red books, the jaguar is categorised as Critically Endangered and Endangered in western and eastern Ecuador respectively, it is listed as Vulnerable in Bolivia, Brazil, Venezuela and western Colombia, and Near Threatened in eastern Colombia and Peru (see SOM for details).

Protected areas inside the jaguar range of NW South America cover in total 1.4 million km² (27% of the jaguar range area) and indigenous territories an additional 1.3 million km² (25%; Fig. 3, Table 1). About 30% of the total estimated jaguar population of this region lives inside the protected areas and about 26% inside the indigenous territories, while 44% are found in unprotected areas (Table 3). The fairly large proportions of jaguar range (52% in total) and population numbers (56%) found inside the protected areas or indigenous territories are so far an important conservation result. However, the conservation success measured by the proportion of the jaguar range area under legal protection varies between countries: it is highest in Ecuador (80%), then in Peru (59%), Colombia (57%), Amazonian Bolivia (56%), Amazonian Brazil (51%), while in NW Venezuela it is only 15% (Fig. 3, Table 1). Regarding eco-regions, the worst situation is in the Llanos, both in Venezuela and Colombia, where in total only 14% of jaguar range and 13% of jaguar population is found within any kind of protected areas. In the Andes, 46% of the current jaguar range is under protection and in the Amazon 55% (Fig. 3, Table 2).

As the jaguar population is still declining across the region, more conservation actions are needed. All countries need to reduce deforestation rates, protect ecological connectivity, improve law enforcement to stop illegal killing and trade, and implement a better system of environmental education (SOM Table T2). Stopping deforestation can be achieved by improving legal systems and law enforcement, but also by increasing the proportion of area under legal protection. Creating new protected areas is most urgent in NW Venezuela and Colombia (and generally in the Llanos and the Andes), while strengthening existing protected areas is important in all countries (SOM Tables T1 and 2). Protecting/improving connectivity and protecting ecological corridors is important in all countries, but especially in Colombia, Ecuador, and Venezuela (SOM Table T2). Designing a corridor network at a continental scale followed by an international agreement to protect such network across the whole South America is an urgent starting point for other actions that could stop fragmentation of habitat and jaguar populations (Zeller et al. 2013, UNDP 2018, Jędrzejewski et al. 2023b).

Environmental education with the goal of lowering public acceptance for jaguar hunting, can substantially reduce jaguar killing rates, both by subsistence hunters and by cattle ranchers. Conservation education conducted at the grammar school level is an effective way of lowering acceptance of killing protected species in rural areas (Baruch-Mordo et al. 2011, Marchini & Macdonald 2012, St. John et al. 2015, Engel et al. 2016). Education aimed at improving husbandry practices and implementation of protective methods that can reduce rates of cattle predation by jaguars (Hoogesteijn & Hoogesteijn 2010, 2011, Quigley et al. 2015, Castaño Uribe et al. 2016) is important in areas where jaguar range and cattle production are overlapping, e.g. in Colombian and Venezuelan Llanos, the Llanos de Moxos in Bolivia, as well as several lower elevations in the Andes and in Brazilian Amazon (SOM Table T2).

A key factor for success in achieving all of these goals is international cooperation, especially important for monitoring jaguar populations and controlling illegal trade. Unification of monitoring system and research methods to make them more reliable and comparable between countries is also important. An international fund should be created to carry out such monitoring and other conservation and research activities in poorer countries and in less accessible regions. More genetic studies are needed to examine genetic variation and population genetic structure at a large scale (e.g. Lorenzana et al. 2020). High-level agreements between countries of this region, such as the Jaguar 2030 Roadmap (UNDP 2018) and the inclusion of jaguars in Appendices 1 and 2 of the Convention on Migratory Species (CMS 1979) can help intensify collaboration and unify conservation actions.

Finally, joint and decisive actions should be taken to ensure the safety of conducting conservation activities in this area. Any activities and commitment to protect nature in NW South America are becoming increasingly difficult, given political and economic instability, and more and more dangerous due to increasing threats to environmental activists from business corporations or guerrilla and criminal groups conducting illegal mining, deforestation, timber extraction, and drug production in this region. The number of documented cases of environmental activists murdered in the countries of this region in 2016 were as follows: 49 in Brazil, 37 in Colombia, 2 in Peru, and in 2019, 24 in Brazil, 64 in Colombia, 8 in Venezuela, 1 in Bolivia, and 1 in Peru (Global Witness 2017, 2020). Other sources show that in Peru there were 12 murders in 2015, and 8 in 2017 (Statista 2018). Efforts in each country and international help are necessary to improve the safety of conservation activities.

See SOM for more detailed and country-specific information on jaguar conservation issues and goals in each country of the region.

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Supporting Online Material SOM Text T1 and SOM Tables T1 and T2 are available at www.catsg.org.

[1] Centro de Ecología, Instituto Venezolano de Investigaciones Científicas (IVIC), Caracas 1020A, Venezuela
* <wjedrzej1@gmail.com>
[2] Biosfera Consultores Ambientales, Lima, Peru
[3] Facultad de Ciencias, Universidad Autónoma de San Luis Potosí, SLP, México
[4] Facultad de Ciencias Exactas y Naturales, Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Quito, Ecuador
[5] Wildlife Conservation Society; Edificio Torre Soleil, #987 Calle Jaime Mendoza, San Miguel, La Paz, Bolivia
[6] ACEAA-Conservación Amazónica, Calacoto, Calle 16 Nro. 8230, La Paz, Bolivia
[7] Departamento de Conservação e Uso Sustentável da Biodiversidade, Secretaria Nacional de Biodiversidade, Floresta e Direito dos Animais Ministério do Meio Ambiente e Mudança do Clima, Brasilia, DF, Brazil
[8] San Diego Zoo Wildlife Alliance, Conservation Science and Wildlife Health, Escondido, California, USA
[9] Instituto de Desenvolvimento Sustentável Mamirauá, - MCTI-OS, Bairro Fonte Boa - Tefé, Amazonas, Brazil
[10] Panthera, 8 West 40th Street, 18th Fl. New York, NY 10018, USA
[11] Wildlife Conservation Society (WCS), 2300 Southern Boulevard, Bronx, New York, NY 10460, USA
[12] Departamento de Ciencias Ambientales, CBS, Universidad, Autónoma Metropolitana Unidad Lerma, Lerma de Villada, Estado de México, México
[13] Proyecto de Conservación de Aguas y Tierras – ProCAT Colombia, Bogotá, Colombia
[14] Wildlife Ecology, Management and Conservation Lab, Forest Science Department, University of São Paulo, Piracicaba, SP, Brazil
[15] Centro Universitário UNA - Ecossitema Ânima; Belo Horizonte, Minas Gerais, Brazil
[16] Florida Fish and Wildlife Conservation Commission, ProCAT Colombia. 3900 Drane Field Road, Lakeland, FL 33811-1207 USA
[17] Department of Environment and Development, Zamorano Biodiversity Center, Zamorano University, Tegucigalpa, Honduras
[18] Sierra National Forest, Clovis, California 93611, USA
[19] Foundation KORA, Talgut-Centrum 5, Ittigen, Switzerland