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The jaguar in South America – status review and strategy

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Prologue: Why care about jaguars?

Humankind has always been fascinated by carnivores, has always felt and emotional response to them, a response of exaltation or fear, delight or loathing (Schaller 1996). The mammal carnivores, order Carnivora, descend from a monophyletic order of placental mammals consisting of the most recent common ancestor of all cat-like and dog-like animals. The jaguar (*Panthera onca*) is the only extant representative of the *Panthera* species in the Western Hemisphere. Its massive head and powerful bite and muscular limbs are unique among felid species and seems to be an evolutionary adaptation for preying on the large and hard-integumented reptiles of the Neotropics (Emmons 1987). Wozencraft recognised nine subspecies of jaguar (Wozencraft 2005), however, morphometric and molecular analysis did not find evidences of morpho-geographical patterns or major phylogeographical structure, respectively (Larson 1997, Eizirik et al. 2001, Ruiz-García et al. 2006, Ruiz-García & Payán 2013). Therefore, the jaguar is considered a monotypic species (Kitchener et al. 2017). Analysis of the whole jaguar's genome revealed that the species have undergone cycles of demographic fluctuations in the last 1–2 million years (Lorenzana et al. 2021). The same study also reinforced the Amazon as having the largest population while highlighting genomic erosion in the Atlantic Forest population.

Carnivora literally means "eaters of flesh". The jaguar's vernacular name comes from the Tupí-Guaraní indigenous name: yaguará, which can be translated as "the one that kills with one jump". Jaguars have been dancing and killing in our collective minds for millennia, have guided us in dreams and questioned our anthropocentrism by being capable (albeit very infrequently) of killing and eating humans. For example, the pictographs in the Colombian table-top mountains of Chiribiquete National Park depict the jaguar as the most common motifs among 6,000 pictographs portrayed in cliff rocks dating back to at least 15,000 years ago. Archeologists argue that being considered prey is the ultimate fear and challenges violently our supreme consciousness as lords of nature (Castaño-Uribe 2013). The jaguar has always been a strong character in the collective imagery of all of the tropical American ethnic groups, a definitory deity for Olmecs, Mayas and Aztecs, for example, and portrayed as hero or devil, the representation of thunder and lightning, or even as a rapist (Reichel-Dolmatoff 1972, 1978, Saunders 1998), or as vital messengers to the gods in the Yanomamö deities (Chagnon 1973). That is why jaguars are preeminent in nearly all ancient society iconographies.

Jaguar symbolism has shifted through time and humanity, from gods to vermin to conservation icons (Payán & Gomez Garcia-Reyes 2017). The values ascribed to jaguars through human history have shifted from objects of admiration to detestation to – recently – conservation. Alan Rabinowitz named this the Jaguar Cultural Corridor, reckoning a connected admiration from pre-Columbian times along all of Latin America (Rabinowitz 2013). As Spanish, Portuguese and other European colonisers came to the Americas jaguars became demonised by the Christian missionaries (Castaño-Uribe 2016), considered as vermin that should be shot for pelts (Payán & Trujillo 2006) or persecuted and killed in retaliation for attacks on their cattle. This sentiment lives on in many rural communities today (Hoogesteijn et al. 2015, Boron & Payán-Garrido 2016). But now, the jaguar is being seen in a new light – as a conservation icon, as the last stand of wildness and wilderness, and as a top representative of healthy and functional ecosystems.

The International Union for the conservation of Nature (IUCN) lists the jaguar as Near Threatened, but, aside from the Amazonian subpopulation, all other subpopulations have been categorised as Endangered or Critically Endangered due to their small size, isolation and poor protection (de La Torre et al. 2018). Jaguars have been decimated over the years, they have currently lost some 60% of their habitat and today large-scale threats such as man/made fires, deforestation, illegal killing and trade, and other invasive human activities keep pushing them into the last forested corners of the Neotropics (Fig. 1; see this issue). Losing jaguars does not just imply an ethical and aesthetic loss, their absence can cause ecological cascades that can reverberate in less dense forest, less water and of lower quality, more erosion, more pests and more wildlife-transmitted diseases. Habitat destruction represents the main threat for the jaguar long term survival (Bernal-Escobar et al. 2015, Olsoy et al. 2016). In the 20th century, the jaguar's habitat has been reduced from 19,000,000 km^2 to 9,000,000 km^2, a trend that remains in the 21st century with an estimated loss of 1,700,000 km^2 by 2015 (Romero-Muñoz et al. 2020).

In the Brazilian Amazon, the largest jaguar's stronghold, deforestation in recent years (2016–2019) has displaced nearly 1,422 individuals (Menezes et al. 2021). The worldwide increases in soy and beef production, trade and consumption are likely to boost deforestation in Latin America considering that these commodities are the base for the economy of most of the South America countries. Agriculture expansion increases access

Fig. 1. Fire destroying jaguar habitat (Photo: E. Payán/WCS).

Fig. 2. Jaguar tourism (Photo: E. Payán/WCS).

to formerly remote areas (Romero-Muñoz et al. 2020) facilitating the action of hunters and poachers. In addition, close contact between jaguars and livestock may result in a conflict, in which case jaguars are persecuted and killed (Carvalho et al. 2015). For instance, in Brazil just one poacher has killed 200 jaguars in the last four years in a small region of the Acre State. In Bolivia and other countries, the increasing illegal trade of jaguar body parts seems to be a byproduct of retaliatory killing (Romero-Muñoz et al. 2020). Although the creation of protected areas, more efficient law enforcement and human-jaguar coexistence are useful instruments for the species conservation, they are not enough. Conservationists must find new creative ways to protect jaguar populations and promote co-existence actions, mainly through economic incentives and conservation financing for those living in contact with the jaguar (Romero-Muñoz et al. 2020, Menezes et al. 2021).

However, the jaguar may be more valuable alive than dead. Resource economics provides a means of calculating the potential value of a species (Schaller 1996). Jaguar-viewing ecotourism represents a gross annual income of nearly seven million dollars annually in land-use revenue across a representative portion of the northern Brazilian Pantanal, the world's largest wetland (Fig. 2; Tortato et al. 2017). These economic gains compared to projected losses in the same area from depredation (less than 2 percent of losses compared to tourism gross income), reinforce the importance of jaguar tourism as a conservation tool in boosting tolerance of jaguars in private ranches, which is on the increase in the Brazilian Pantanal and in the Colombian Llanos (Hoogesteijn et al. 2015).

The vast distribution of jaguars (but high abundance/density variation) poses challenges and opportunities for jaguar protection and valuation. The great aspect of jaguar conservation is that we have so much occupied range to deal with, with a low percentage of officially and effectively protected areas and large areas under private property and used for cattle-ranching (with high levels of jaguar/cattle conflict). This implies a variety of threats in intensity and scale, and a multitude of stakeholders with varying attitudes and opinions on jaguar conservation. Bringing stakeholders together to promote and ensure jaguar preservation is one of the great challenges for conservationists. Our ability to truly monitor the species is another daunting challenge since it requires significant funding and is dependent on habitat-specific monitoring. For example, the total estimated number of jaguars is in the range of 175,000 individuals (Jędrzejewski et al., 2018), which seems large, but the need for density studies in impacted ecosystems was very apparent and mostly lacking. For example, there are fewer than three density estimates for the Amazon Basin, its stronghold (Payán et al. 2013, Tobler et al. 2013, Mendonça et al. 2023). Most jaguar research has not taken place in high-slope landscapes such as coastal southern Brazil, or the northwest coast of Honduras; and researchers tend to choose areas that are less impacted by human influence. Furthermore, we lack range-wide surveys, and there is significant discrepancy of different "mapping exercises" since there are still some information voids in geographic distribution and potential connectivity. Furthermore, as we further map these uncharted populations, the total number of jaguars estimated on paper increase and affect Red Listing exercises. Another major challenge is jaguar conflict resolution across larger areas of the species' distribution, especially around protected areas and corridors (Castaño-Uribe et al. 2016).

Many of the big cats, like lions, tigers and leopards, have range-wide population survey results, but not jaguars. This volume probably contains the most up to date body of knowledge on the species.

Why care? We present this chapter, and this volume, to make the case for the jaguar as an ideal species for conservation focus for South America, and for the Americas. As a large carnivore, the jaguar is the quintessential focal species and thus the ultimate conservation target for many conservation programs (Rabinowitz & Zeller 2010). Focusing on jaguar conservation will enable large scale conservation given their landscape species needs (Coppolillo et al. 2004) and umbrella effects (Thornton et al. 2016). Part of the stability of ecosystems is due to the presence of large carnivores such as jaguars that contribute to the stability of ecosystems because they maintain healthy prey species populations and they impose a landscape of fear. This landscape is the primordial, healthy forest, where rich tropical biodiversity has flourished for hundreds of thousands of years. Given the jaguar's focal species position, areas with conserved populations will also protect entire wildlife communities. This, coincidentally, is biodiversity conservation's ultimate purpose! Thus, to conserve the jaguar epitomises an important goal for humanity: Saving this species has become one of the most difficult tests we face in the race against extinction.

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Biology and ecology of the jaguar

In recent years, advances in equipment and analytical tools have provided opportunities to unveil several aspects of the jaguar *Panthera onca* biology and ecology. Here, we made use of the most recent publications to update the knowledge about this iconic species. From Arizona to Northern Argentina, the jaguar "accommodates" its behaviour to survive in a large variety of habitats. However, human modified landscapes have posed a threat for the species' long-term survival. A deep understanding of the species' biology and ecology is crucial for the species conservation planning.

The jaguar evolved 1.8–2.0 million years ago in Europe and western Asia, where fossils of the Eurasian jaguar *Panthera onca gombaszoegensis*/*P. gombaszoegensis* have been reported from many localities between northern Africa, Arabian Peninsula, western and central Europe, Caucasus mountains and Tadjikistan (Argant et al. 2007, Hemmer et al. 2010, Marciszak 2014). The jaguar colonised North America about 800,000 years ago, possibly through the Bering Bridge and later South America through the Isthmus of Panama (Kurtén & Anderson 1980, Seymour 1989, 1993, Marshall & Sempere 1991, Turner & Anton 1997, Arroyo-Cabrales 2002, Webb 2006). Recent phylogenetic analyses confirm these paleontological findings and indicate that evolutionarily the jaguar is most closely related to the lion *P. leo* and the leopard *P. pardus* (Johnson et al. 2006). However, an exact determination of the sequence of speciation (whether the latest split was between jaguar and lion or jaguar and leopard) proved to be difficult because of complex mechanisms of speciation that involved gene flows (introgressions) between already separated species. The newest studies that take into account this post-speciation gene flow and variation in recombination rates across the genome indicate the most likely scenario to be that leopard split first and then jaguar and lion (Figueiró et al. 2017, Li et al. 2019). The jaguar's historic range included Arizona, New Mexico and Texas in the South-western USA to central Argentina. Currently, the jaguar is distributed from southern Arizona and New Mexico to northern Argentina, but is extinct in Uruguay and El Salvador (Sanderson et al. 2002, de la Torre et al. 2017). The jaguar is the largest felid in the Neotropics, its body length (without tail) is usually 120–160 cm and tail length is 50–70 cm. It weighs between 60–158 kg, with males around 30% larger than females (Nowell & Jackson 1996, Eisenberg & Redford 1999, Hunter 2015). The largest individuals are from forested flooded savannas in Pantanal (Azevedo & Murray 2007) and Los Llanos in Venezuela (Hoogesteijn & Mondolfi, 1996), with males averaging 110 kg (76 to 158 kg) and females 83 kg (65 to 110 kg), while in forested habitats of South America they tend to be smaller. The smallest jaguars are found in Central America and Mexico; for example, in Belize males average 57 kg and in Mexico females average 42 kg (Rabinowitz & Nottingham 1986, Aranda 1990). These differences have been attributed to adaptations to habitat and prey types (Kiltie 1984, Seymour 1989, Hoogesteijn & Mondolfi 1996, Sunquist & Sunquist 2002).

Fig. 1. Camera trap record of a male and a female jaguar sharing a large prey carcass. This carcass was shared by several individuals within 48 hours (Tortato et al. 2016; Photo Panthera Brasil).

The jaguar coat has a uniform yellow to orange colour scattered with black spots/rosettes organised in extremely variable, often geometric patterns, different for each individual and with marked differences between populations (Hoogesteijn & Mondolfi 1992, Jędrzejewski et al. 2011). Its ventral part is white. Melanism in jaguars is determined genetically (Eizirik et al. 2003) but occurs in different grades of darkness. No jaguars are completely dark; the black spots can always be seen in sunlight. Melanistic individuals are found in several jaguar populations with average frequency of about 10%, this, however, varies between regions and habitats. For example, melanism occurs at a high frequency in jaguar populations in rain forests of the Amazon Basin and in the Cerrado biome, while in Los Llanos and Pantanal no melanistic individuals have been recorded (da Silva 2014).

Sexual behaviour resembles that of other felid species with an elevated number of copulations likely to induce multiple ovulations (Jorge-Neto et al. 2018). Gestation period lasts around 100 days (90–111 days) and the reproductive season is year-round. In some places, however, it has been reported that cubs are born mainly during the rainy season (Rabinowitz & Nottingham 1986, Crawshaw 1987), and in forested flooded savannas of the Llanos mainly during the dry season (Hoogesteijn & Mondolfi 1992). Litter size is one to four cubs, with two cubs being the most common (Jędrzejewski et al. 2017a). Females give birth in a protected place like a cave, burrow, under a fallen tree, or in dense vegetation. Cubs stay with the mother until they are approximately 1.5 to 2 years old and reach sexual maturity at about 20 months for females (Viau et al. 2020) and about 4 years for males (Mondolfi & Hoogesteijn 1986). The lifespan of wild jaguars is difficult to estimate, but there are records of jaguars of over 15 years old (A. Paviolo et al., unpubl. data). In captivity, they can live up to 22 years (Seymour 1989, Nowak 1991). The main causes of human-induced jaguar mortality are hunting and retaliatory killing, but recently road kills have often been reported as well (Crawshaw Jr. 2002, Carvalho & Morato 2013, Jędrzejewski et al. 2017b). Of the natural causes, there are records of males killing other males and of infanticide (Soares et al. 2006, Azevedo et al. 2010, Tortato et al. 2016). There is limited information on population structure. In a study in Los Llanos adult males constituted 21%, reproductively active females 26%, nonreproductive females 11%, and cubs 42% (Jędrzejewski et al. 2017a). Jaguar reproductive behaviour, breeding parameters and demographic patterns require further studies.

Habitat and space use, activity patterns, social behaviour and density

Jaguars inhabit a variety of habitats, including tropical humid and dry forests, subtropical forests, mangroves, forested or partially open marshlands, mountain forests (Sanderson et al. 2002). They inhabit savannahs and other partially open habitats as well, as long as water and sufficient prey are available. Jaguars are usually found from sea level to about 2,000 m, however there are records between 2,000–2,800 m from the USA, Mexico, Honduras, Bolivia and Argentina (Griffith et al. 2021, Polisar 2021). Temperature appears to be a limiting factor for the jaguar since they are not found in areas where mean annual temperature is less than 10°C (Jędrzejewski et al. 2017c, 2018), although there is a record of jaguar in snow in Arizona in 1926 (Brown & Lopez 2001), and a recent 2012 Arizona camera-trap photo (L. Hayes, pers. comm.). Jaguars are very good swimmers and are well-adapted to live even in partially flooded areas, like the "várzea" flooded forests in Amazon basin, where they hunt in water and rest on trees (Ramalho 2012, Ramalho et al. 2021). In several areas within their distribution, jaguars are strongly associated with water. They are very good swimmers, and they even have been reported to hunt caimans *Caiman* sp. and capybaras *Hydrochaeris hydrochaeris* in and under the water (Nowak 1991). They can cross large rivers (like the Orinoco or Amazon river) and are even found on coastal islands near the mainland, which is demonstrative of them being able to traverse marine habitats.

Jaguar social system is based on territoriality. Most adult jaguars of both sexes maintain individual home ranges, but non-resident roving males have also been recorded (Cavalcanti & Gese 2009, Morato et al. 2016, McBride & Thompson 2018, 2019). The purpose and the use of a home range in jaguar males and females are different. Apart of hunting for themselves, jaguar females maintain home ranges to provide food for their offspring, while males try to get access to as many females as possible (Sunquist & Sunquist 2002). Thus, male and female home ranges always overlap widely, but extensive overlapping of home ranges between individuals of the same sex has also been recorded. For example, in the Brazilian Pantanal, an overlap between home ranges of adjacent females was up to 50% and that of adjacent males was up to 91% (Azevedo & Murray 2007, Cavalcanti & Gese 2009, Erikson et al. 2021). At special circumstances jaguars may show high tolerance to other conspecifics, for example at a large prey carcass or at sites with prey concentration (Fig. 1; Hoogesteijn et al. 2014, Tortato et al. 2017). Also, coalitions of males with a likely goal to enlarge home range and take over more females, similar as in lions, have been reported (Concone & Azevedo 2012, Jędrzejewski et al. 2022). Infanticide is likely common in jaguars, although it is difficult to record (Soares et al. 2006, Tortato et al. 2016). Movements of adult jaguars inside their home ranges are related to hunting, territory defense, and mating (Fig. 2). In the case of males, their movement patterns are also related to defending their females from other males and in the case of females to taking care of their cubs (Scognamillo et al. 2002, Azevedo & Murray 2007, Cavalcanti & Gese 2009). Jaguars equipped with GPS telemetry collars in various habitats in Brazil, Argentina and Paraguay moved on average between 10 and 17 km/day in different study areas; in Amazon flooded forest they moved less, only about 4 km/day, on average (Morato et al. 2016, McBride & Thompson 2018, 2019). Males usually move longer and more directionally than females; as found in the same studies, it took on average between 3 to 7 days for females and 4 to 9 days for males to cross their entire home ranges. The species can be found active throughout the day; however, it appears to be primarily nocturnal and crepuscular (Cavalcanti & Gese 2009, Foster et al. 2010, Harmsen et al. 2011). On the Llanos, breeding females that looked after their young were active the longest, about 13 hours a day, while adult males and non-breeding females were active only about 10–11 hours a day (Jędrzejewski et al. 2021). Jaguar home range size is extremely variable, but it is dependent on habitat productivity factors and with a clear difference between males and females (Fig. 3). At a geographic scale, jaguar home ranges are largest in dry, low productivity habitats and decrease in size in more productive and more humid habitats (see also Thompson et al. 2021). As primary productivity is strongly correlated with abundance and productivity of herbivore populations (Jędrzejewski & Jędrzejewska 1996, Melis et al. 2009, Pettorelli et al. 2011, Polisar et al. 2003), this relationship can be interpreted as jaguar dependence on prey availability. This relationship is found for both males and females, but female home ranges are

Fig. 2. Camera trap record of jaguars showing a couple interaction that may lead to mating. Previous observation has characterised the receptiveness of the female as a pre-copulatory behaviour (Jorge-Neto et al. 2018; Photo: W. Jędrzejewski).

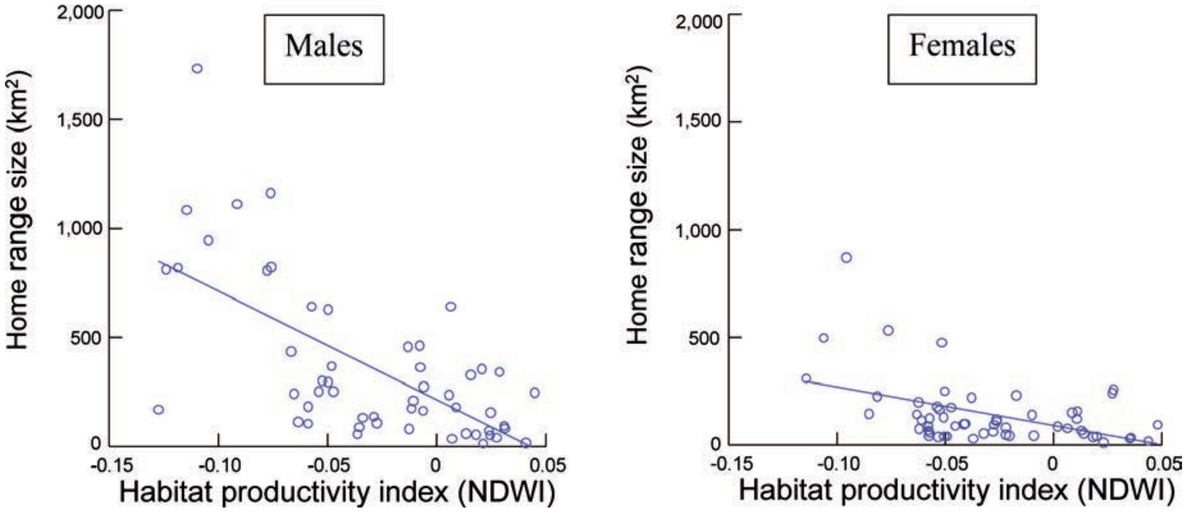

Fig. 3. Relationship between jaguar home range size and NDWI index. Jaguar home range sizes were calculated as minimum convex polygons (MCP 100%) based on radiotelemetry GPS data for 117 individual jaguars across jaguar range, published by Morato et al. 2018. NDWI (normalised difference water index, MODIS:MCD43A4_NDWI. https://lpdaac.usgs.gov/) is derived from satellite imagines and it reflects water content in vegetation and soil. It highly correlates with habitat primary productivity and humidity (McFeeters 1996, Gu et al. 2007).

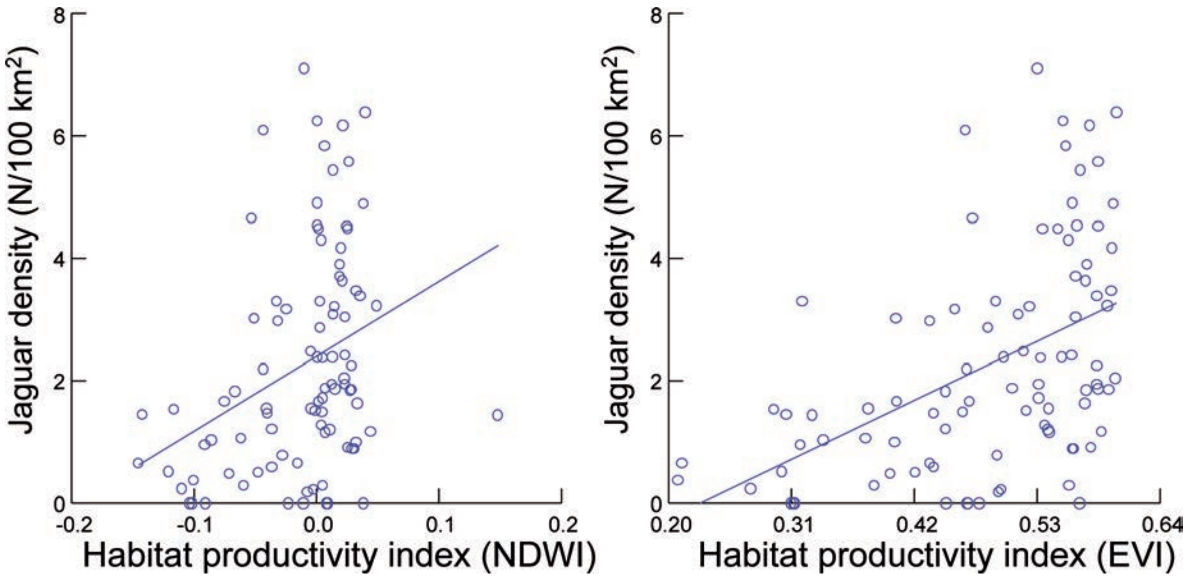

Fig. 4. Relationship between jaguar population density and indices of habitat primary productivity: NDWI and EVI. Jaguar population density data come from 117 camera trapping studies and were recalculated to the level of spatial capture-recapture models (Jędrzejewski et al. 2018). NDWI (normalised difference water index) as in Fig. 3. EVI (enhanced vegetation index, MODIS:MCD43A4_EVI, https://lpdaac.usgs.gov/) is derived from satellite imagines and it reflects amount of fresh vegetation in a habitat and is used as a measure of habitat primary productivity (Xiao et al. 2005, Jiang et al. 2008).

always smaller than those of males (Fig. 3). For example, in productive and humid habitats of the Pantanal of Brazil, mean jaguar female home range size was only 52 km², and in the flooded Amazon tropical forest it was 68 km² (Morato et al. 2016). In less productive habitats, such as Atlantic Forest and dry parts of Chaco in Paraguay, jaguar females maintained larger home ranges: 268 km² and 551 km², respectively (Morato et al. 2016, McBride & Thompson 2018, 2019). Male home ranges are usually larger as they may overlap with several female territories (e.g. Cavalcanti & Gese 2009, Morato et al. 2016, Erikson et al. 2022). In Pantanal, mean home range size of male jaguars was 150 km² and in the flooded Amazon Forest 212 km², while in less productive Atlantic Forest it was 463 km², in dry Chaco 924 km², and in Cerrado 1,216 km² (Morato et al. 2016; McBride & Thompson 2018, 2019). A similar pattern was found in several other home range studies of the jaguar (Crawshaw & Quigley 1991, Scognamillo et al. 2002, Azevedo & Murray 2007, Cavalcanti & Gese 2009, Cullen et al. 2005, de la Torre et al. 2017).

Jaguar population density is an important metric for estimating population numbers and reliable density estimates are important for well-informed jaguar conservation. As each jaguar can be individually identified by its coat pattern, jaguar photos obtained with camera traps are commonly used for estimating population densities with a help of spatial capture-recapture models (Borchers & Efford 2008; Royle et al. 2014). Data obtained from numerous camera trapping studies (see reviews in Maffei et al. 2011, Tobler & Powell 2013, Jędrzejewski et al. 2018) indicate that across its range, jaguar densities are highly variable. Because population density is determined by the number of individual home ranges in a given area, the spatial variation in both parameters, jaguar density and home range size, are driven by similar factors (Figs 3, 4). The highest jaguar densities are found in humid and more productive areas and the lowest densities in dry, low productivity habitats (Jędrzejewski et al. 2018). For example, high population densities (> 4 jaguars/100 km²) were found in tropical rain forests at the foothills of the Andes in Peru, in the flooded "varzea" forests at the central Amazon river, in the Pantanal in Brazil, and in Los Llanos in Venezuela (Soisalo & Cavalcanti 2006, Ramalho 2012, Tobler et al. 2013, Jędrzejewski et al. 2017a, Erikson et al. 2022), whereas very low jaguar densities (< 1 jaguar/100 km²) were documented in dry habitats in northern Mexico, in Uruguaí in northern Argentina, in the Cerrado and Caatinga biomes in Brazil (Coronel Arellano et al. 2008, Sollmann et al. 2011, de Paula et al. 2012, Paviolo et al. 2016).

Prey preferences and feeding ecology

Jaguar have a very eclectic diet which has allowed them to inhabit a diversity of ecosystems (Hayward et al. 2016). In the remote and nearly pristine upper Amazon rain forest in Peru, Emmons (1987) found jaguars to be taking most prey in proportion to their abundance, with the exception of collared peccaries *Pecari tajacu*, which were taken in higher proportions, suggesting preference for this larger-bodied prey item. In the heavily forested Cockscomb Basin in Belize, Weckel et al. (2006) found that jaguars took many prey items in proportion to availability, although collared peccaries were killed in greater proportion than available, and tapirs *Tapirus bairdi* and white-lipped peccaries *Tayassu pecari* less than expected. The proportion of white-lipped peccaries in jaguar diet in the Cockscomb increased following a complete hunting ban, but the relative occurrence of armadillos, a small bodied prey item, stayed relatively constant after the ban (51% after 20 years of formal protection vs. 54% before (Foster et al. 2010).

Carrillo et al. (2009) reported white-lipped peccaries and marine turtles being preferred prey in Corcovado National Park in Costa Rica, and Arroyo-Arce et al. (2014) found jaguar distributions tied to nesting green sea turtles *Chelonia mydas* in Tortugüero National Park in the same country. These records suggest that prey body size and the ease of capture are factors contributing to prey selection. In general, when a larger-bodied prey is encountered and can be taken without risk, jaguars will show some selection for them. In the heterogeneous savanna-forest mosaics of the Llanos of Venezuela, jaguars selected for capybara, caiman and collared peccaries, taking white-lipped peccaries in proportion to availability, and ignoring small prey items that constituted the majority of jaguar diet in the Cockscomb of Belize (Polisar et al. 2003, Scognamillo et al. 2003). Similar patterns were encountered in the southern Pantanal of Brazil (Azevedo & Murray, 2007, Perilli et al. 2016). However, in the northern Pantanal diet was dominated by fish and aquatic reptiles (Erikson et al. 2022). Azevedo & Murray (2007) found that jaguars did not hunt randomly but consumed more large and medium-sized prey species than could be expected from proportions of each species in the available prey community. Cavalcanti & Gese (2010) estimated kill rate of 10 jaguars equipped with GPS radio collars in an area of Pantanal, where jaguars and cattle intermingled. Each jaguar, on average, killed one big or medium sized prey every 4.3 days, which is equivalent to 85 kills per year and cattle (mostly calves), caimans, and peccaries accounted for the majority of prey, but the proportion changed during the dry and rainy seasons. Jaguar females with cubs kill prey at higher rate than other jaguars, occasionally up to one prey per day (Cavalcanti & Gese 2010, Jędrzejewski et al. 2014).

Infectious and non-infectious diseases

Infectious diseases may pose a threat for the wildlife species when it contributes directly or indirectly to the risk of population extinction (Woodroffe 1999). The increasing contact between wildlife and domestic animals has been considered the main route of infectious diseases transmission (Furtado & Filoni 2008). Considering the continuous expansion of agricultural activities in jaguar range (Romero-Muñoz et al. 2020), exposure to disease carried by domestic animals is likely to increase. For example, in a beef production area in the south-western region of Brazil, 60% of jaguars monitored were exposed to canine morbillivirus (CMV), a disease that had an outbreak and caused high mortality in the lion population of the Serengeti plains (Nava et al. 2009). Evidence of exposure to felid herpesvirus (FHV-1), carnivore protoparvovirus (CPPV-1) and rabies has been also reported (Furtado et al. 2013 and 2017) but none of the jaguars sampled showed any signs of infection (Furtado & Filoni 2008, Nava et al. 2009). Bacteria, fungus and parasites (endo and ecto) have been also reported for jaguars (Labruna et al. 2005, Filoni et al. 2006, Furtado et al. 2007, Onuma et al. 2014).

Non-infectious diseases such as neoplasias and degenerative spinal disorders have been reported for captive jaguars (Hope & Deem 2006). Dental disease is one of the most common causes of morbidity in captive animals and is the only cause of non-infectious disease reported for free-ranging jaguars (Rossi Júnior 2007). The expansion of agriculture and mining activities may also expose the jaguar to toxicants. In the Brazilian Pantanal, gold mining activities released mercury (Hg) into the environment causing the contamination of jaguars (May-Júnior et al. 2017). As Hg accumulates in tissues, chronical exposure may result in toxic effects such as neural, lung, and kidney disorders (May-Júnior et al. 2017). There are no studies yet about pesticides affecting the jaguar health. However, considering the effects of several pesticides on human health, jaguars are likely to experience similar issues if exposed to them. Thus, Hg and pesticides should be considered a threat to the jaguar. The gaps in information about domestic animal to jaguar transmission of disease and the effects of contaminants of jaguars highlight the need for well-designed and ambitious studies and monitoring programmes assessing the impacts of biological and non-biological agents.

Zoos, captive breeding, artificial reproductive techniques, and reintroduction

Zoos and captive breeding programs have played a major role in the recovery of several species (Conde et al. 2011). To assist in captive population management zoos have created a registry of the individuals known as studbook. This registry system monitors births, deaths, parentage, individuals acquired from the wild, their location, and transferences. Ultimately, this system is used to optimise breeding efforts by ensuring that paired individuals are not related (CCF 2017). The first regional studbook for the jaguar was approved by the American Zoo Association AZA in 1993 and has been periodically updated. In the AZA's affiliated zoos the annual percentage of births varies from 5.3 to 12.5%, indicating a low rate of reproduction. The recently published AZA's jaguar studbook highlights the need of new founders to maintain the desired level of genetic diversity (AZA 2019). Reproductive artificial techniques have the potential to contribute to the captive breeding programme (Morato et al. 2001) and even the recovery of an endangered population such as the Atlantic Forest (Galetti et al. 2013, Paviolo et al. 2016). Despite the advances in the semen collection technique (Araujo et al. 2018), ovarian stimulation (Jorge-Neto et al. 2018), artificial insemination (Cincinnati Zoo 2019), and in vitro fertilisation (Morato et al. 2002), reproductive techniques have had limited success in the production of offspring likely due to the lack of basic knowledge on reproductive biology (Songsasen 2015).

Zoo and rescued animals may also contribute with reintroduction programs. For example, in Argentina, where the species has experienced a 95% reduction on its distribution range (Di Bitetti et al. 2016), captive and rescued jaguars from Brazil, Paraguay and Argentina are forming the founding population for the reintroduction programme of the Iberá Natural Reserve (CLT 2019). In Brazil, two rescued jaguar cubs were successfully reintroduced in the Pantanal after the adoption of the IUCN soft release protocol (Gasparini-Morato et al. 2021).

Final considerations

Considering the large, estimated population of jaguar in the Amazon and Pantanal it is unlikely that the species will go extinct in the short term. However, rapid agricultural expansion to meet the global demand for beef and soy is driving habitat loss and direct killing of jaguars in both regions (Romero-Muñoz et al. 2020, Menezes et al. 2021, Tortato et al. 2022) generating concern over the current scenario. The large area of protected areas and indigenous lands in the Amazon are under increasing threats from illegal activities, resulting in considerable uncertainty about the conservation of Amazonian forests and the jaguar. Moreover, despite global recognition, the positive conservation outcomes in the Pantanal (Tortato et al. 2017), and the new techniques developed for the reduction of jaguar/cattle conflict resolution problems (Castaño-Uribe et al. 2016), they are limited in scope when considering the large area where the jaguar has been and is being extirpated, the threat from hunting throughout its distribution, and the relatively small extent of protected areas in the region. Considering that jaguar populations outside the Amazon have decreased by 80%, and many of those populations are small, isolated, have insufficient protection, and are located in areas of high human population density (de la Torre et al. 2017), the long-term outlook for the conservation of the jaguar is uncertain.

In recent years, we have advanced our knowledge of jaguar ecology to better understand how the jaguar copes with a continuously changing landscapes (local and range-wide), which can help to address threats and plan long-term conservation. Continuing habitat loss and direct killing of jaguars are driving a continuous range wide population decline. Consequently, conservation efforts need to be improved and broadened, whereby we call for a transformative change, as defined by Visseren-Hamakers & Kok (2022), as "a fundamental, society-wide reorganisation across technological, economic and social factors and structures, including paradigms, goals and values."

Considering that such as transformation may be challenging to implement due to political aspects, Visseren-Hamakers et al. (2021) proposed five governance approaches that are important for effective jaguar conservation: 1) be integrative, ensuring solutions that impact other locations and sectors; 2) be inclusive, by empowering and emancipating diverse groups of interest; 3) be adaptive, by continuously monitoring conservation plans and correcting management paths and actions as needed; 4) be transdisciplinary, recognising diverse knowledge systems and supporting their inclusion in conservation plans; and 5) be anticipatory, recognising the uncertainty of the future, including the development of new technologies and infrastructure implementation, and be prepared for adjustments and reorganisation of conservation plans.

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Distribution and status of the jaguar in the Guiana shield

With large tracts of intact forest, very low human population density, and limited road networks, the Guiana Shield supports jaguar *Panthera onca* populations across 99% of its historical range. Jaguars inhabit a diversity of forested habitats, from mangroves to mountain forest, with population density estimates ranging from 1.6 to 6.4 individuals/km². Protected areas cover 30% of the Guiana Shield and potential prey species are broadly distributed across the jaguar's current range and do not constitute a limiting factor to its distribution. Habitat destruction, fragmentation, and degradation mainly linked to mining, unsustainable logging, land conversion for intensive agriculture and cattle pastures, retaliatory killing for depredation, and targeted hunting to supply an illegal trade in jaguar parts represent the primary threats to jaguar populations. Capacity for, and ability to, manage wildlife and wild lands must be improved to ensure that the current optimistic outlook for jaguar populations in the Guiana Shield does not diverge significantly with impending economic development.

The Guiana Shield is the smaller, northern subunit of the Amazon Platform, covering six countries. At ca. 2,288,000 km², it stretches west from south-eastern Colombia across Venezuela, Guyana, Suriname, and French Guiana to its eastern margin along the Atlantic coast in the state of Amapá in northern Brazil (Hammond 2005). Mean elevation across the Guiana Shield is ca. 270 m, ranging from coastal areas at or just below sea level to the highest point at 2,995 m.

The region is considered, along with the western Amazon, one of the most well-preserved stretches of jaguar habitat across the species' range. Limitations on economic and infrastructure development have undoubtedly benefitted the preservation of jaguar habitat, but has also restricted potential for scientific research. Nevertheless, scientific studies combined with opportunistic observations have confirmed jaguar presence across most of the Guiana Shield. Here, we update information on the distribution of jaguar populations across the five main countries of the Guiana Shield (the area in Colombia is discussed in Chapter 4), highlighting current knowledge on population density, habitat use, and prey species. Current and growing threats faced by jaguars are described along with conservation actions that could be implemented to address them.

Methods

Each co-author completed a standardised questionnaire developed by the IUCN SSC Cat Specialist Group to collate knowledge on jaguars in their respective countries. Data on jaguars were compiled by the co-authors from published data (i.e. Zeller 2007) and unpublished data from either their own studies or their collaborators. Each individual jaguar record and associated geographic coordinates was categorised as C1 "hard fact", C2 "confirmed observations" (e.g. tracks verified by an expert), or C3 "unconfirmed observations" (e.g. any kind of direct visual observation) following the Status and Conservation of the Alpine Lynx (SCALP) protocol (Molinari-Jobin et al. 2012).

For camera-trap studies (data classified C1), each record was reported as either the central point of the study site or the coordinates of each camera station where at least one jaguar was documented by camera-traps. We deleted spatially duplicated records (multiple records from the same site) to reduce the data disparity between countries and autocorrelation problems in the distribution analysis. For the subsequent analysis we used jaguar records from 2000–2020. We also used data on jaguar absence (localities where jaguars were not found) collected by field interviews or randomly selected from the areas of known jaguar absence (Jędrzejewski et al. 2017a, 2023).

Records of jaguar presence and absence were used to estimate current jaguar range and prepare distribution maps. The current distribution of jaguar populations was estimated based on the combined species distribution modeling and kriging interpolation between jaguar presence and absence records collected across the Guiana Shield (see Jędrzejewski et al. 2023 for methods). We classified jaguar status in four categories: Extinct, Possibly Extinct, Possibly Extant, and Extant, following the IUCN guidelines for mapping species distribution (IUCN Red List Technical Working Group, 2019).

A general description of each country is provided to explain variation in the distribution of jaguar records. The three Guianas are described as a unit because of their shared features. Local population density estimates were based on camera-trap studies, with differences in analyses noted, where available. Additionally, we estimated the jaguar population size in each country by multiplying potential jaguar population densities by the probabilities of jaguar occurrence. The potential jaguar densities were predicted by the regression model based on 110 jaguar density estimates obtained by camera-trapping studies across jaguar range and a set of predictive variables that included primary productivity indices and mean annual temperature (Jędrzejewski et al. 2018). The probabilities of jaguar occurrence were predicted by the updated jaguar distribution model, based on the jaguar records and absence data and predictive variables that included both environmental and anthropogenic factors (Jędrzejewski et al. 2023). The combination of both models ensures that resulting jaguar densities are likely better adjusted to the actual habitat conditions and human impacts. Based on the adjusted jaguar population densities we estimated the total jaguar numbers for each country within the Guiana Shield. To evaluate the uncertainty of our estimates we calculated the 95% lower and upper credible limits, applying for each country the percentage credible intervals calculated for the same type of estimates with Markov Chain Monte Carlo iterations by Jędrzejewski et al. (2018).

In preparing the maps, we used country and administrative borders (after Porto Tapiquén, 2020) to help locate data and results; however, they do not include any disputed boundaries and do not pretend to represent any political opinions.

Region-wide distribution

We gathered 1,143 jaguar records from across the Guiana shield (Table 1, Fig. 1). The majority of these data (94%) were collected since 2000, with Venezuela contributing 83% of the pre-2000 data. Of the records collected since 2000, 55% are classified C1 (mostly derived from camera-traps), 22% as C2 (mainly derived from interviews), and 23% as C3 (largely unverified direct observation and livestock attack testimonies; Table 1).

Historically, jaguars occurred in almost all territory of the Guiana Shield (Fig. 1). Our modeling showed that the current estimated distribution of jaguar populations covers ca. 97.5% (1,511,000 km²) of the historical distribution for the species in the Guiana Shield, with 94% of the historical range having jaguar status classified as "Extant" (Table 2). Models showed a high probability of occurrence throughout the region (Fig. 2A) and jaguar current status mostly classified as 'Extant' (Fig. 2B). Low probabilities of jaguar occurrence and 'Extinct', 'Possibly Extinct', or 'Possibly Extant' categories are associated with more populated northern parts of the region or other areas around the largest cities (Table 2, Fig. 2) and with the Gran Sabana (large highland savanna area with numerous tepuis, table-top mountains, covering south-eastern Venezuela, northern Brazil and western Guiana) and Mount Roraima region, whose high elevation habitats limit jaguar occurrence.

This extensive distribution is not surprising considering the region's relatively limited road networks, low human population density concentrated along the Atlantic coast and, the presence of large expanses of intact forests to which the cover of protected areas and indigenous territories contributes (Jędrzejewski et al. 2018; Table 3, Fig. 3).

Table 1. Number of contemporary (≥2000), C1 ("confirmed"), C2 ("Probable") and C3 ("Possible") jaguar records compiled (sensu Molinari-Jobin et al. 2012). A jaguar record is defined as a unique GPS location where at least one jaguar has been observed during the two periods of time.

Country	C1	C2	C3	Total/country
Venezuela	114	24	133	331
Guyana	291	90	28	409
Suriname	63	55	0	127
French Guiana	64	68	87	222
Brazil	54	0	0	54
Total	**586**	**237**	**248**	**1143**

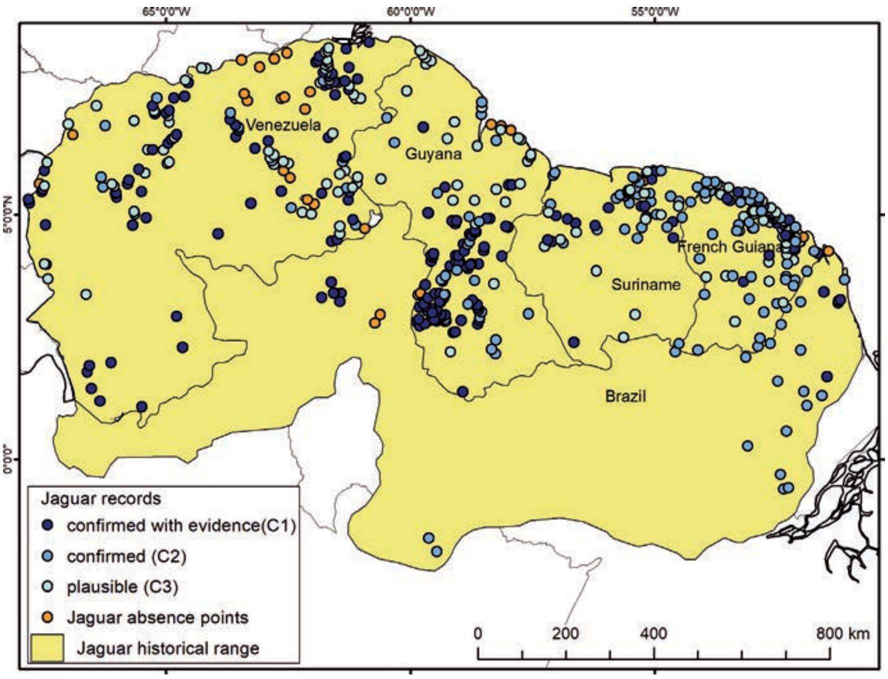

Fig. 1. Jaguar records and absence points used in the analysis of the current jaguar status against the historical range of the species in the Guiana Shield. Jaguar records are classified into three reliability categories: C1 – confirmed with hard evidence, C2 – confirmed by an expert but without hard evidence, C3 – plausible but without hard evidence or confirmation by an expert (Molinari-Jobin et al. 2012). Jaguar historical range after Sanderson et al. 2002, modified by Jędrzejewski et al. 2017a.

Venezuela

The Venezuelan portion of the Guiana Shield (450,000 km², Fig. 1, Table 2) stretches from the eastern bank of the Orinoco basin to the source of Orinoco River, in the Amazonas and Bolivar states (Fig. 1). Its total population is 2.2 million inhabitants with an average density 4.8 people/km² (http://sedac.ciesin.columbia.edu/data). The northern part of this area is the most impacted by urbanisation, hosting four large cities. The Guri Dam reservoir covers 4,250 km². Agriculture and cattle ranching are most intensive in the northern part, but small farms and ranches are spread throughout the region, even deep into the Amazon basin. The driest parts of Gran Sabana and the highest elevations of tepuis possibly did not host jaguar populations (Sanderson et al. 2002, Jędrzejewski et al. 2017a). Protected areas cover 49% of the jaguar range (207,800 km²) in the Venezuelan Guiana Shield (Table 3, Fig. 3). 28% of the data from the Guiana Shield (331/1143 records) come from Venezuela (Table 1), nearly equally divided between C1 and C3 classes, with many coming from direct interviews or testimonies with farmers and hunters. 40.8% of the records (135/331) were hunted animals (based on interviews, Jędrzejewski et al. 2017b) and only 5,4% stemmed from camera-trapping (18/331) due to the remote and inaccessible nature of many areas. We estimated jaguar population size at 7,800, with an average density of 1.9 individuals/100 km² (Table 4). Studies in the upper Caura River estimated population density with camera traps at 2.3 individuals/100 km² using spatial capture-recapture models (Perera-Romero et al. 2013).

The three Guianas

The three Guianas, including French Guiana, Suriname and Guyana, are ranked among the least populated countries in the world with 3.5, 3.6, and 4 inhabitants/km², respectively (ONU 2019). They share common unequal distribution of its inhabitants, with the vast majority of the population (ca. 90%) living in the capitals and cities along the countries' coastal plain. The extensive interior is inhabited by only about 10% of the human population, mainly representatives of Indigenous and Maroon communities. Those three countries' common characteristics may explain why the estimated current jaguar range is almost equal to its historic range (99.5% to 100%; Table 2, Fig.1).

The coastal distribution of this low human population explains the region's high percent forest cover – 85% of Guyana's (Roopsind et al. 2019), and 93% of Suriname's and French Guiana's total land area (Gond et al. 2011).

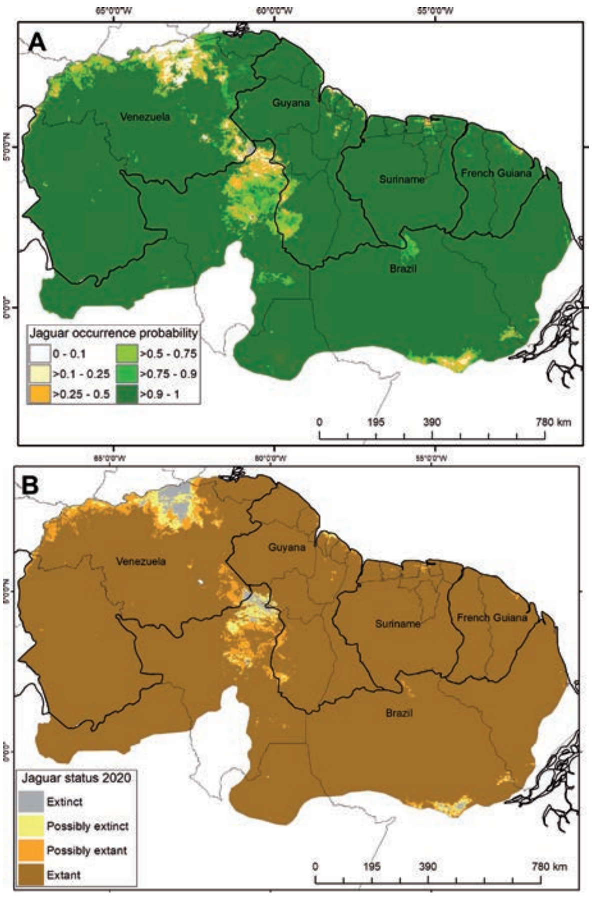

Fig. 2. A. Probability of jaguar occurrence (indicating also habitat suitability for jaguars) estimated with the logistic regression model of jaguar presence and absence; B. Jaguar status in Guiana Shield classified into four IUCN categories: Extinct, Possibly Extinct, Possibly Extant and Extant; assessment resulting from the combination of logistic regression and kriging interpolation models. Combined Extant and Possibly Extant categories indicate the current (2020) jaguar range. For methodological details see Jędrzejewski et al. (2023).

The coastal capitals of all three countries are linked by a single paved road running from east to west. Brokopondo reservoir in Suriname is also linked to the capital by a paved road. Towns, villages, and mining concessions in the southern two-thirds of Suriname and French Guiana can only be reached by plane or by water, whereas in Guyana unpaved roads in varying condition give access to villages and mining and logging concessions in the interior.

In Guyana, jaguars have been documented throughout the country, likely inhabiting all vegetation types with the exception of highly degraded urban and agricultural areas along the coastal plain and the highest elevation tepuis along the country's western border. Most jaguar research in Guyana has taken place in the country's southern half, especially in the Rupununi Region (Figs 1, 3). More than two-thirds (71%) of the jaguar records from Guyana come from camera-trap studies (C1), with the remaining coming from interviews (22%) and opportunistic observations (7%; Table 1). A recent study using >350 camera locations set across nine sites of various habitat (from savanna to forest) and land tenure (village, state, protected area) found that jaguar density was highly correlated with forest cover, estimating densities ranging from 1.96 to 5.58 individuals/100 km² (Hallett 2017). Four other camera-trapping studies from Guyana estimated densities varying between 1.06 to 4.48 individuals/100 km², both studies using spatial capture-recapture analysis (Paemelaere & Payán 2012, Paemelaere & Payán 2013). Camera trap surveys from working landscapes indicate that jaguar occupancy and relative abundance in concessions that practice reduced-impact logging RIL and restrict access to other activities (hunting, mining) are higher (Paemelaere & Payán 2013, Roopsind et al. 2017, Hallett 2017) than those that allow unrestricted access and multiple use (Pierre et al. 2016, Liddell, unpubl. data). We estimated the total jaguar population in Guyana at 4,100 (95% CI: 3,000 to 5,100) individuals, with 10% and 11% of the population in protected areas and Indigenous territories, respectively (Table 4).

In Suriname jaguars occur across the entire country (Kasanpawiro & Ouboter 2013), even at the outskirts of the capital and on top of the only tepui in the country (Ouboter 2005). About 50% of jaguar records came from camera trapping studies (C1), with the other half coming from interviews or expert observations (Table 1). Knowledge of habitat preferences and population density is limited to north and central Suriname, mainly due to a low number of researchers and general lack of access to most of the country, especially in the south and west (Fig.1). Investigations carried out in coastal swamps estimated a density of 0.81 individuals/100 km² (Mangalsing 2017). A nine-year study in the Brownsberg Nature Park estimated jaguar densities between 0.51 and 4.21 individuals/100 km² (Kadosoe 2020), both studies using spatial capture-recapture analyses. A camera-trap study at Rosebel mining concession (hunting is prohibited, but logging is allowed) documented 1.38 captures of jaguars per 100 trap nights (P. Ouboter & V. Kadosoe, unpubl. data). The savannas of Coesewijne Nature Reserve and a non-forested portion of the Rosebel area (mining concession, no hunting allowed) showed 2.06 (Ouboter et al. 2011) and 0.36 (P. Ouboter & V. Kadosoe, unpubl. data) captures per 100 trap nights, respectively. Although actual population densities are unknown, differences in capture rate are likely correlated with broad differences in jaguar abundance with tropical rainforests supporting more individuals than savannas and intact areas supporting more than areas subject to resource exploitation.

Table 2. Area of the jaguar historic range (after Sanderson et al. 2002) and estimated area of current jaguar status in the Guiana Shield (in thousand km²).

Country	Total area inside GS	Historic jag. range	Area with current jaguar status				Current (2020) jag. range	Percentage of historical range
			Extinct	Poss. Extinct	Poss. Extant	Extant		
French Guiana	84	83	0	0	0	83	83	100.0
Suriname	164	162	0	0	1	161	162	100.0
Guyana	215	211	0	1	5	205	210	99.5
Venezuela (GS)	450	443	9	13	25	396	421	95.0
Total Guiana Shield	**1,567**	**1,549**	**13**	**25**	**51**	**1,460**	**1,511**	**97.5**

Based on our modeling, we estimated the total population of jaguars in Suriname at 2,900 (95% CI: 2,100 to 3,700) jaguars, with 16% of that population inside the protected areas (Table 4).

In French Guiana, jaguars have been recorded across most of the country. Most of the data on jaguar presence comes from northern French Guiana where access forest habitat is relatively easy (Fig.1). Data were fairly equally divided between C1 data (ca. 29% from camera-traps and physical capture), C2 (31% from interviews), and C3 (40%; majority from online naturalist database Faune-guyane.fr; Table 1). Four camera-trap studies (one from the Nouragues Natural Reserve in the interior and three others along the coast) used non-spatial capture-recapture modeling to estimate jaguar densities ranging from 2.9 to 5.1 individuals/100 km² considering the half MMDM and from 1.4 to 2.1 individuals/100 km² considering the full MMDM (De Thoisy 2016). A more recent camera-trap study from a well-preserved 320 km² stretch of coastal forest in the Centre Spatial Guyanais produced a spatially-explicit density estimate of 3.22 ± 0.87 individuals/100 km² (Petit et al. 2018). We estimated the total population of jaguars in French Guiana at 1,400 (95% CI: 900 to 1,800) jaguars, with 43% inside protected areas and 4% inside indigenous territories (Table 4). Preliminary results from a study of nine GPS-collared jaguars revealed the importance of forest cover in aiding jaguar movement, as individuals routinely avoided open habitat (savanna) along the coast (R. Berzins, pers. obs.).

Brazil

In Brazil, the Guiana Shield encompasses parts of the Amapá, Roraima, Northern Pará, and Amazonas states. A large proportion of the Brazilian Guiana Shield is protected by 20 conservation units and 16 indigenous territories (Fig. 3). Jaguars can be found across the region with 79% of the jaguar range included in protected areas (44%) and indigenous territories (35%; Table 3). Research in this region has been hampered by the difficulty of access, contributing only 5% of records from across the Guiana Shield (Table 1, Fig. 1). Recently, a monitoring programme established by the Instituto Chico Mendes de Conservação da Biodiversidade and partners captured jaguars on camera-traps at Cabo Orange and Tumucumaque National Parks, Maracá and Lago Piratuba Biological Reserves, Raposa do Sol Indigenous Land, and Maracá-Jipióca Ecological Station. The latter reported a density of 1.6 individuals/100 km² (Endo et al. pers. comm). Here, we estimated the total population of jaguars in the Brazilian part of Guiana Shield at 11,400 (95% CI: 8,800 to 14,000) jaguars (Table 4).

Habitat

The Guiana shield is naturally covered by ca. 1.342 million km² of continuous, intact tropical forest (Hammons 2005). This area represents one of the largest expanses of intact tropical forest in the world and has been identified as being among the most important to prioritise in 'proactive' approaches to conservation (Brooks et al. 2006). Guiana Shield forests are diverse in their composition (Gond et al. 2011, Guitet et al. 2015, De Dijn 2018) and these patterns in floristic diversity are known to influence communities of medium to large-bodied vertebrates (Richard-Hansen et al. 2015). Guyana, Suriname and French Guiana are mainly composed of tropical forest categorised into about twenty different habitat types varying from mangrove and swamp forests along the coast, to terra firme, basimontane and montane cloud forest in the highlands, to grassland, white-sand- and rock savannas (Guitet et al. 2015, De Dijn 2018, ter Steege et al. 2000). Each of these habitats, with the possible exception of the highest extents of the tepuis, are inhabited by jaguars. More open habitats, like the Neotropical grasslands and Cerrado savanna that are scattered across the central Guiana Shield form large landscape units at the borders of Suriname and Brazil (Sipalawini savanna), as well as Guyana, Brazil, and Venezuela (Grand Sabana, Sierra de Imataca, and the Rupunui-Rio Branco savannas). The floor of Takutu Graben also consists of a large savanna-wetland complex. Recent studies indicate that jaguars use these open savanna grassland and savanna wetland habitats but show lower rates of occurrence (Ouboter & Kadosoe 2016) and population density (Hallett 2017), with individuals selecting forest fragments and gallery forest over open grasslands (R. Berzins, pers. obs.) and shifting towards more nocturnal behaviour in open habitat (Hallett 2017). Large portions of this habitat in Brazil and Venezuela have been converted to industrial agriculture and cattle ranching, reducing habitat suitability, introducing conflict with livestock, and resulting in the jaguar's status classified as "Possibly Extant" in some areas (Fig. 2B).

Diet and prey availability

As an opportunistic, generalist predator, jaguars are not associated with a specific resource or highly preferred prey species (Hayward et al. 2016). While diet studies may indicate slight local preferences for one or two prey species (Polisar et al. 2003, Weckel et al. 2006b, Ralmaho & Magnusson 2008, Ramalho 2012), these preferences are likely tied to specific environmental conditions and the availability and accessibility to potential prey species. Rather, jaguar distribution is determined by the availability of suitable habitats with sufficient potential prey and limited anthropogenic landscape change (Paviolo et al. 2018). Jaguar diets are diverse, with 111 species identified as potential prey across their range (Hayward et al. 2016), ranging from cattle (>200 kg) to rodents (<50 g; Harmsen et al. 2011). Many potential prey species from the Amazon Basin occur at similar abundances in the Guiana shield (Forget & Hammond 2005) and have been documented by inventory, camera-traps, or surveys of the

Table 3. Area of protected areas PAs and Indigenous territories ITs within each country and inside the current (2020) estimated jaguar range in the Guiana Shield (all areas are given in thousand km²).

Country	Total cover of PA	Total cover of IT	Jag. range 2020	PA inside jag. range	IT inside jag. range	% jag. range inside PA	% jag. range inside IT
French Guiana	36.5	8.1	83	36.3	8.0	44	10
Suriname	24.7	0.0	162	21.1	0.0	13	0
Guyana	17.8	24.2	210	17.8	23.7	8	11
Venezuela	210.3	0.0	421	207.8	0.0	49	0
Brazil	283.0	231.2	635	282.5	222.6	44	35
Total	**572.2**	**263.5**	**1,511**	**565**	**254**	**37**	**17**

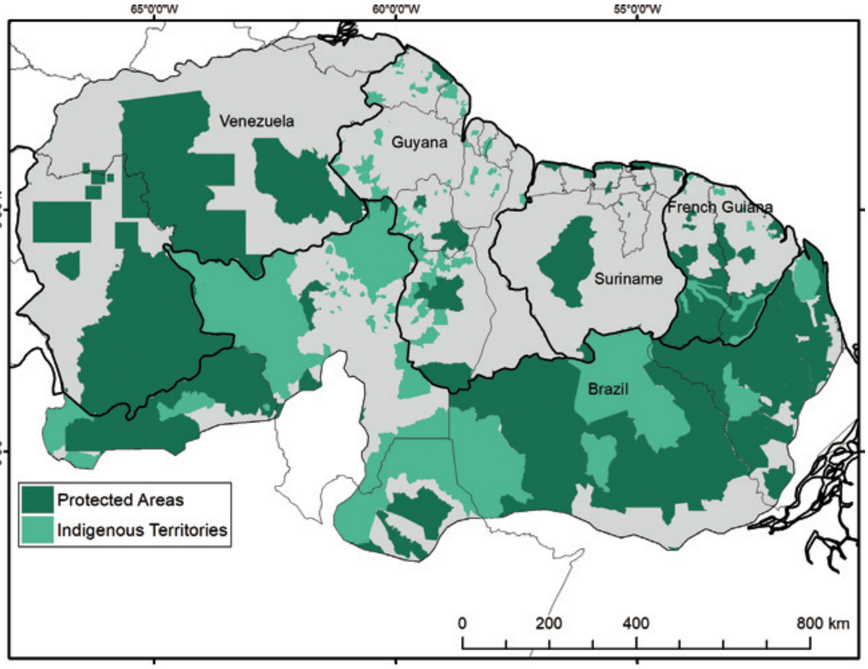

Fig. 3. Protected areas and indigenous territories of the Guiana Shield. Protected areas included National Parks, Nature Parks, Biological Reserves, Biosphere Reserves, National Natural Reserves, National Monuments and Ramsar sites.

hunting practices in studies across the Guiana Shield (Lim et al. 2005, Peres et al. 2007, Pickles et al. 2011, Fragoso et al. 2016, Ouboter & Kadosoe 2016, Richard-Hansen & Berzins 2016, Hallett et al. 2019, Richard-Hansen et al. 2019, Pierre et al. 2020). To our knowledge, only one jaguar diet study (in French Guiana and is still at a preliminary stage), has been conducted in the Guiana Shield (Berzins et al. 2019). Of 32 scats representing ca. 20 individuals, researchers identified ca. 30 vertebrate species using metabarcoding. Species in the jaguar diet included nine-banded armadillo *Dasypus novemcinctus*, white lipped peccary *Tayassu pecari*, coati *Nasua nasua*, red-footed tortoise *Chelonoidis carbonarius*, tamandua *Tamandua teradactyla*, collared peccary *Pecari tajacu*, iguana *Iguana iguana*, and capybara *Hydrochoerus hydrochaeris* (Berzins et al. 2019). In Guyana, direct observation, carcasses, and scat have also identified spectacled caiman *Caiman crocodilus* (M. Hallett, pers. obs.), giant river turtles *Podocnemis expansa* (A. Holland, pers. comm.), yellow-footed tortoise *Chelonoidis denticulatus* (M. Davis, pers. comm.), white-tailed deer *Odocoileus virginianus* (A. Mendes, pers comm), juvenile lowland tapir *Tapirus terrestris* (M. Hallett, pers. obs.) as potential prey. Along the coast of the three Guianas, marine turtles, most notably green *Chelonia mydas* and leatherback *Dermochelys coriacea* sea turtles, are periodically consumed along nesting beaches (R. Berzins, pers. obs., P. Ouboter & V. Kadosoe, pers. obs., R. De Freitas, pers. comm.).

Dogs *Canis lupus familiaris* are frequently preyed upon by jaguars on the outskirts of cities, villages, and peri-urban human settlements (Berzins & Petit 2018, Kasanpawiro & Ouboter 2013; L. Cromwell, pers. obs.), where jaguars also attack poultry, sheep *Ovis aries*, goats *Capea aegagrus hircus*, and both juvenile and adult cattle *Bos taurus* and horses *Equus ferus caballus*. A study in Venezuela quantified depredation rates on cattle (79% of all livestock killed), horses (12%), pigs *Sus scofra domesticus* (11%), and donkeys/mules *Equus asinus* (12%; Jędrzejewski et al. 2017) and a preliminary study of 102 households from six indigenous villages in Guyana's interior estimated annual cattle depredation at 5–25% of total stock (Hallett 2015, unpubl. data). Depredation on large domestic animals affects both household and commercial scale farms in Suriname (P. Ouboter, pers. comm.) and in Guyana (E. Paemelaere, pers. obs.). Depredation of dogs and livestock has also been reported at Lago Piratuba Biological Reserve and Cabo Orange National Park in Brazil (R. G. Morato, pers. comm.). Depredation events cannot be explained with a single driving factor accordingly with the depredatory jaguars' profiles observed by the authors and their preliminary studies.

Threats

Our distribution modeling, combined with density estimates from previous studies, provide an optimistic outlook for the status of jaguars in the Guiana Shield. Much of the jaguar's range currently remains largely intact; however, these conditions are rapidly changing in some areas.

While deforestation continues to be a primary driver of jaguar habitat loss, the Guiana Shield supports the top three countries (French Guiana, Suriname, Guyana) in terms of highest percent forest cover and lowest deforestation rates in the world. While the core remains strong, increasing deforestation around the southern and eastern edges of the Guiana Shield are a growing concern. In French Guiana, agriculture is the leading driver of deforestation, while illegal logging and human settlements are the main causes of deforestation in Amapá (Rahm et al. 2017). In Brazil, deforestation in Roraima state increased by 216% in 2019 and cattle ranching increased by 85% in the Pará State between 2000 and 2017. In Venezuela, the combined effect of deforestation, notably for cattle ranching, and retaliatory killing due to conflicts have driven a number of local extinctions of jaguar populations (Jędrzejewski et al. 2017a,b).

Mining continues to be a primary driver of deforestation across the Guiana Shield, with 85% of forest loss in Guyana and 55% in Suriname attributed to mining (Rahm et al. 2017, Guyana Forestry Commission 2014, 2018). Gold mining, specifically, continues to be a major contributor to the GDP of Guiana Shield countries. Currently, 14% of Guyana's total land area is leased to mining concessions (ca. 3,000 km^2), 9.6% in timber concessions (ca. 2,000 km^2), and 12.8% (2,700 km^2) falls under concessions that are leased for both mining and timber harvest (ESRI 2016). In the Venezuelan Guiana Shield, destruction and degradation of jaguar habitat linked to gold mining has increased rapidly over the last 3 years, with 112,000 km^2 recently designated as the "Orinoco Mining Belt" for the legal mining of gold, coltan, diamonds, and other minerals (Scherer 2018). Illegal mining also affects protected areas, as observed in the Brownsberg Nature Park in Suriname, the Iwokrama International Centre and Kaieteur National Park in Guyana, the Amazonian National Park in French Guiana, as well as Canaima, Caura, Yacapana National Parks in Venezuela (RAISIG 2019).

Importantly, mining does not only cause forest and soil loss, but the use of toxins (i.e. mercury) and erosion can also cause large-scale water contamination (Ouboter et al. 2012, Legg et al. 2015). Extractive industries also create a network of roads through otherwise forested interiors to transport materials that increase access and hunting pressure on jaguars and their prey (Wilkie et al. 2011, Hallett et al. 2019).

Considering that 46% of jaguar population remain outside of protected areas in the Guiana Shield (Table 4), this makes understanding the threats that jaguars face within state, private, and indigenous lands critical to the conservation of Guiana Shield jaguars in the future.

Illegal hunting of jaguars (specialised hunters are called "mata tigre" in Venezuela) have also been linked to a trade in jaguar parts for medicine or ornamental purposes, with confirmed cases in Suriname (Bale 2018, Lemieux & Bruschi 2019, Romo 2020) and Venezuela (Sánchez-Mercado et al. 2016). Additionally, a recent boom in logging and mining activities by Chinese-owned companies has become a significant concern in Suriname, driving hunting and trapping of jaguars using baited snares (P. Ouboter, pers. comm.), to supply jaguar carcasses, meat, pelts, and parts sold at high prices to the Chinese community who values these products for their perceived medicinal value in Suriname and abroad. Additionally, jaguars are opportunistically killed by commercial and subsistence hunters, who encounter jaguars while hunting game species, and take advantage of the black market for selling jaguar parts (Jędrzejewski et al. 2017b). The growing black market for jaguar parts in the Guiana Shield, most often associated with Chinese investment and demand, is of concern for the conservation of jaguar populations in the region and are part of an emerging range-wide conservation issue for the jaguar (Arias 2021).

Direct persecution and retaliatory killing have been identified as a primary threat to jaguars across the Guiana Shield, driven by a wide variety of factors. Persecution is often associated with a generally low tolerance for the presence of a large predator, notably among livestock owners or rural communities who kill jaguars in retaliation for depredation on livestock, dogs, or just out of fear (Jędrzejewski et al. 2011, 2017b, Marchini & Macdonald 2012, Pierre et al. 2016). Retaliatory killing of jaguars is frequent and widespread in each of the Guiana Shield countries wherever livestock is present. Depredation behaviour is also directly linked to habitat loss and fragmentation caused by land conversion to agriculture and pasture, which reduce natural prey and introduce domestic animals into the landscape (Medan et al. 2011, De Souza et al. 2018).

Despite the commonness of jaguar-human conflict, weak institutions and a lack of resources limit the effective management of jaguars and other wildlife by all Guiana Shield countries, including adequate law enforcement.

Conservation

With jaguars remaining in 97.5% of their historic range within the Guiana Shield, the current outlook for the species in the region is optimistic; however, ensuring that the region remains a critical refuge for jaguar populations will require forethought and planning, as the Guianas are expected to undergo a significant economic development in the next few decades as a consequence of human population increasing and dependence of countries on the exploitation of natural resources (wood, mineral, gas and oil) submitted to the law of the market and supported by the leaders of the countries.

Economic development (increase in GDP, decrease in unemployment) is the primary objective of government's officials, whose limited terms of office do not allow the luxury of planning for the long-term effects of current actions. At the same time, public awareness of environmental issues is growing and citizen movements against unsustainable government policies and corporate actions are becoming increasingly frequent and heard.

Bottom-up approaches to economic development that provide people and communities with a voice in policy and action provide a means for reconciling citizens' expectations and government objectives (as involvement of indigenous community in protected areas management in Guyana or gold mining project halted after 2 years of citizen struggle in French Guiana).

Environmental movements, along with international programs and agreements, can affect policy and activities in the private sector as well. In the forestry sector in Guyana, most forestry operations have already adopted reduced-impact logging techniques, which local and global studies have shown to maintain an almost full complement of tropical forest biodiversity, including healthy jaguar populations (Bicknell et al. 2015, 2017, Hallett 2017, Roopsind et al. 2017, Tobler et al. 2018). In French Guiana, sustainable management of exploited forest has also been implemented through the Pan European Forest Council (PEFC) label since 2012. Restricting access to timber concessions to other activities, such as hunting and mining, remains the key factor to maintaining a healthy prey base, reducing conflict, and as a result maintaining jaguar populations in these selectively logged forest (Polisar et al. 2016, Roopsind et al. 2017).

Conservationists and conservation organisations can also be proactive in encouraging decision makers to incorporate wildlife protection into land use planning by designing and maintaining ecological corridors composed of suitable habitat for jaguars and sufficient prey. This, in turn, would ensure functional connectivity, benefiting many species of fauna and flora, while mitigating negative impacts of infrastructure development. Such principles could serve as a based and promoted through guidelines of a regional jaguar action plan.

Additionally, human-wildlife coexistence specialists are needed to implement interven-

Table 4. Jaguar population estimates for each country and percentages of the jaguar population inside protected areas, indigenous territories, and in not protected territories. Credibility intervals CRI and general methodological approach to estimate jaguar population numbers after Jędrzejewski et al 2018.

Country	Jag. population 2020 estimate (95% CRI) in thousands	Mean jag. density (per 100 km²)	% of jag. pop. inside PAs	% of jag. pop. inside indigenous territories	% of jag. pop. outside PAs
French Guiana	1.4 (0.9–1.8)	1.6	43	4	54
Suriname	2.9 (2.1–3.7)	1.8	16	0	84
Guyana	4.1 (3.0–5.1)	1.9	10	11	79
Venezuela	7.8 (5.9–9.6)	1.9	45	0	55
Brazil	11.4 (8.8–14.0)	1.8	47	35	18
Total	**27.6 (20.7–34.2)**	**1.8**	**38**	**16**	**46**

tions that help to mitigate conflict between jaguars and ranchers, miners, loggers, and communities in rural areas. There is an urgent need to work with landowners to develop effective strategies to improve livestock management and promote human-jaguar coexistence (e.g. Quigley et al. 2015). Support for this process may require incentives to reduce fear, financial loss, and social/cultural barriers to participation.

Lastly, we must gain a better understanding of the drivers of the trafficking of jaguars and their parts along all links of the value chain from hunter to market to consumer. Disrupting felid trafficking networks will require additional support, training, and access to technology for border patrol, customs, and wildlife officers so that jaguar parts may be correctly identified and those involved held responsible.

The Guiana Shield has the major advantage of having a large amount of protected areas (572,200 km^2) supplemented by extensive Indigenous territories (263,500 km^2) that are sufficient to maintain viable jaguar populations (Tables 3, 4, Fig. 3; Woodroffe & Ginsberg 2000).

Nevertheless, all Guiana Shield protected areas are under threat, mostly by illegal gold mining. Improving capacity to enforce compliance with laws restricting mining within protected areas, increasing sustainable development opportunities (i.e. tourism), building capacity in resource management (i.e. education), and integrating traditional knowledge and input of the communities living within or near protected areas will be essential for the effective management of protected areas.

Conclusion

Jaguar habitat, populations, and prey in the Guiana Shield have remained well protected by its relative inaccessibility. However, that can also contribute to lack of data, particularly in northern Brazil which is under prospected. This issue needs to be overcome by implementing more scientific research in those remote areas. Less developed infrastructure has undoubtedly served as a buffer against the most destructive impacts of activities such as hunting, mining, and logging, and proved an asset to jaguar conservation, but conversion of forest to industrial agriculture and cattle ranching notably in Venezuela and Brazil is a growing concern that to deal with. Access must be taken into account in the future as anticipated economic development begins to improve infrastructure and facilitates access to the region's abundant and intact natural resources. The Guianas, with its low overall human population density, limited infrastructure, and large tracts of intact forest largely held within protected areas and the titled land of indigenous communities is in a unique position for a well-organised bottom-up approach to conservation that could be supported by local environmental institutions, NGOs, and government agencies, which help to preserve traditional and sustainable use of natural habitat and thwart the destructive plans of natural resource extraction companies. Conflict mitigation, notably regarding depredation, must be an ongoing process. Solutions and alternatives must be disseminated and anticipated through more education and training to change the often negative perception of the feline and promote coexistence of the two species.

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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

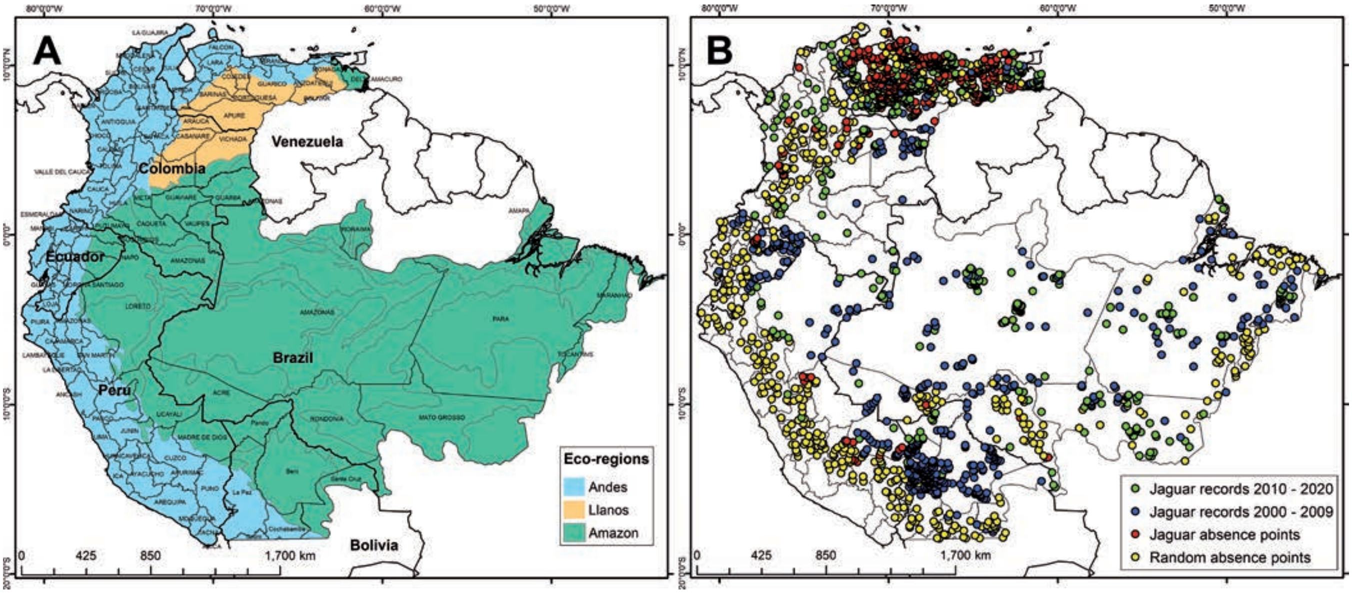

Fig. 1. A: North-western South America and its main eco-regions (after Griffith et al 1998); B: Jaguar records (from 2000–2009 and 2010–2020) and jaguar absence points used for the analysis of jaguar distribution inside the study area.

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 km^2, 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 km^2 and has about 29 million inhabitants with an average population density of 62 people/km^2. 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 km^2) 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 km^2 (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-

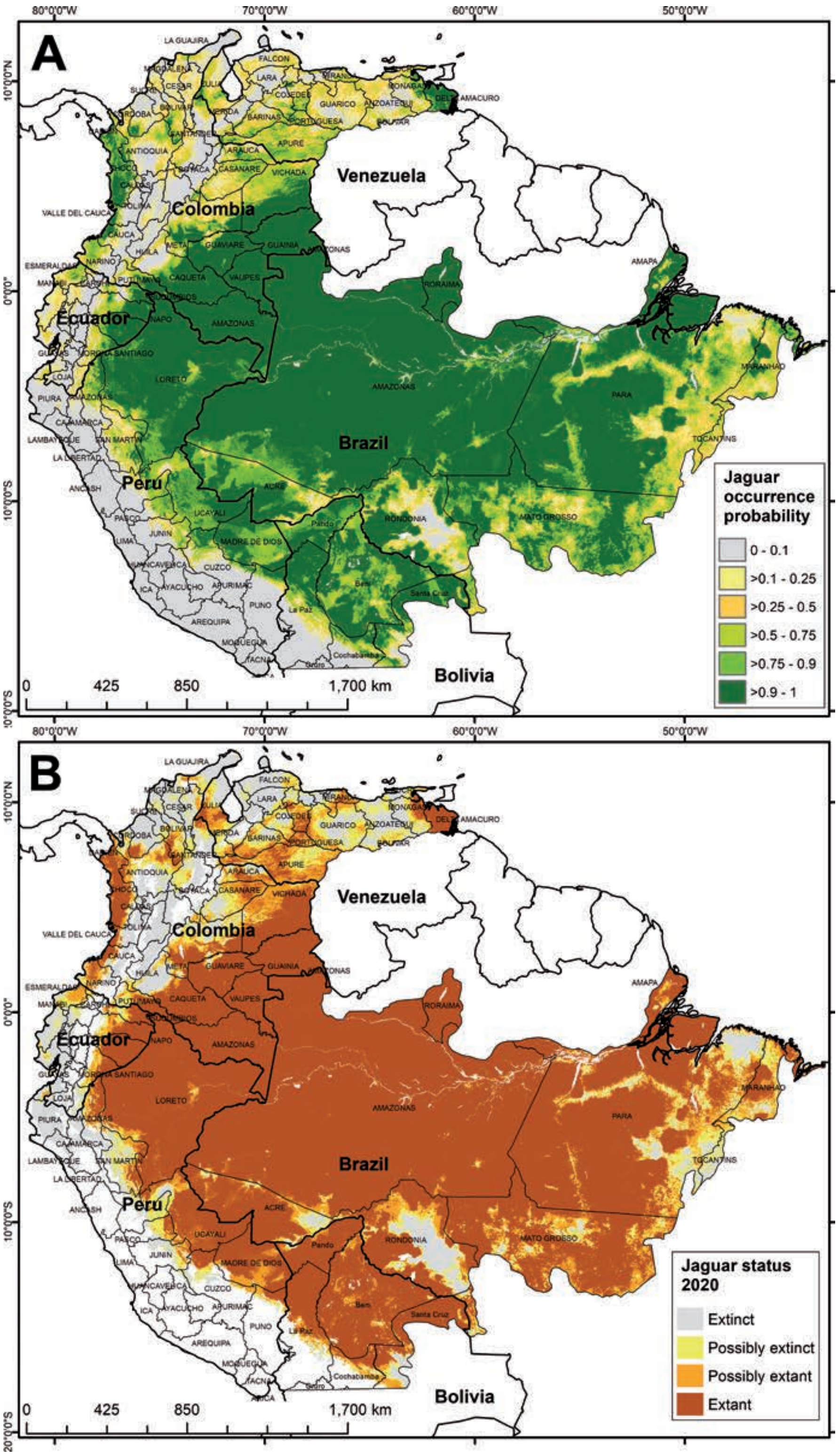

Fig. 2. A: Probability of jaguar occurrence (indicating also habitat suitability for jaguars) estimated with the logistic regression model of jaguar presence and absence. B: Jaguar status in north-west SA classified into four IUCN categories: Extinct, Possibly Extinct, Possibly Extant and Extant; assessment 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 km^2) 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	% unpro-tected 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 km^2.

We estimate the current jaguar range in Peru at 617,000 km^2 (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/km^2, 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/km^2), 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 km^2 and has a population of 7 million people, with an average population density of 12.8 people/km^2 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 km^2 (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 km^2 (89% of the current jaguar range) while those with the 'Possibly Extant' status occupy 47,000 km^2 (11%; Table 1, Fig. 2).

Brazilian Amazon

The Brazilian portion of NW South America (Brazilian Amazon, Fig. 1) covers 3,440,000 km^2 and has a population of 22.3 million people (6.5 people/km^2); however, most of its area has very low human population with densities between 0 and 2 people/km^2. 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 km^2 (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 km^2 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 km^2 and mean male home ranges at 100 and 167 km^2, 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 km^2, 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).

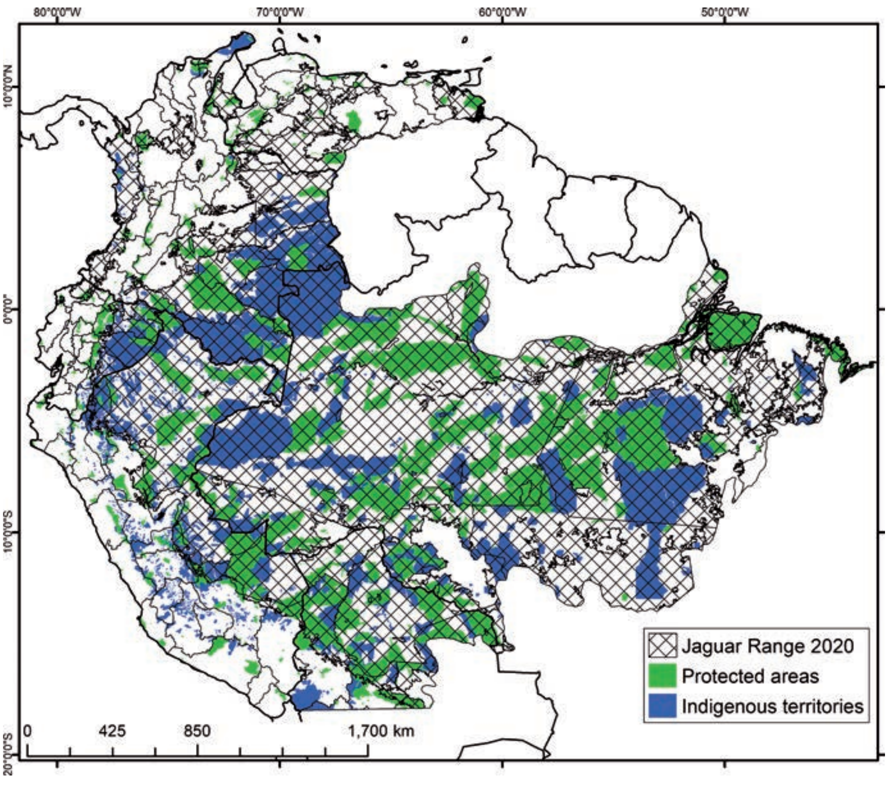

Fig. 3. Protected areas and indigenous territories within NW South America compared with the current (2020) jaguar range. Sources of data on protected areas and indigenous territories: World map of protected areas, http://www.protectedplanet.net/, Amazonia Socioambiental RAISG 2019, https://www.amazoniasocioambiental.org/es/mapas/#!/areas, 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 km²)	% 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.

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Jaguar status, distribution, and conservation in south-eastern South America

The jaguar *Panthera onca* has experienced a significant reduction in its global distribution, particularly in south-eastern South America. This chapter conducts an extensive assessment of the jaguar's distribution, population status, and threats in this region, encompassing Argentina, Paraguay, Uruguay, southern and eastern Bolivia, and south-eastern Brazil. Spanning 8.3 million km², this area contains diverse ecosystems, including tropical forests, grasslands, and wetlands, making it of global conservation significance. To assess jaguar distribution and population size, we employed a comprehensive dataset, expert opinions, and ecological models, categorising jaguar population status into four classes: Extinct, Possibly Extinct, Possibly Extant, and Extant. We estimated that jaguars are extant in 20% of their historical range, with potential existence in an additional 14%, primarily located in fragmented habitat patches. The Pantanal, Northern Chaco, and Chiquitano together emerge as a population stronghold, while the Atlantic Forest, Caatinga, and Eastern Cerrado exhibit lower jaguar occurrence. Country-level assessments indicate that the jaguar is extinct in Uruguay and has decreased extensively in distribution in Argentina and Paraguay. Bolivia retains substantial jaguar populations, particularly in the Chaco, Chiquitano, and Pantanal regions. South-eastern Brazil, despite extensive historic range loss, harbours a significant jaguar population, especially in the Pantanal and Cerrado. Our study underscores the importance of evaluating under-researched regions like the Bolivian Andes, Chiquitano Forest, Humid Chaco, Caatinga, and the Cerrado. Additionally, it highlights the need for conservation efforts in the Pantanal, northern Chaco, and the Chiquitano for the jaguar's conservation. Moreover, our findings emphasise the urgency to restore populations and connectivity in the Atlantic Forest, Caatinga, and southern Chaco. Conservation priorities are habitat preservation, the maintenance of prey availability and landscape connectivity, and the reduction of hunting to secure jaguar populations in south-eastern South America.

Although the jaguar's global distribution has been reduced by about 50% (de la Torre et al. 2018, Quigley et al. 2017, Sanderson et al. 2002), this reduction has been considerably greater at the northern and southern extremes of its distribution where most of its populations are highly threatened (de la Torre et al. 2018, Sanderson et al. 2002). In this chapter we evaluate the distribution, population status, and threats to jaguar populations in south-eastern South America, including Argentina, Paraguay, Uruguay, and south-eastern Bolivia and south-eastern Brazil delimited by ecoregional limits and the jaguar's historic distribution (see methods). This focal area covers about half of South America (8.3 million km²) and 7.2 million km² of the southern historical distribution of the jaguar.

The climate and topography of our focal region is highly variable, including extremes for the distribution of the jaguar in terms of altitude, temperature, and precipitation. The interactions of climate and topography result in a high diversity of ecosystems with large variations in productivity and vegetational structure. These include humid tropical and subtropical forest (Atlantic Forest, Yungas), dryland forest, scrubland, and savanna systems (Chiquitanía, Dry Chaco, Cerrado, Caatinga), grasslands (Pampas) and large wetlands (Pantanal, Humid Chaco). Our focal region not only harbours a great diversity of ecosystems, but also includes global biodiversity hotspots (Atlantic Forest, Cerrado, Tropical Andes) and other ecoregions of high conservation value (Gran Chaco and Chiquitano), and is consequently of broader global conservation relevance (Kareiva & Marvier 2003, Myers et al. 2000, Redford et al. 1990).

Our focal region has witnessed an increase in the human footprint over the last several decades (Venter et al. 2016), a range of habitat conversion, as well as of socio-economic activities. Regions such as the Atlantic Forest and the Pampas have undergone centuries of habitat transformation and support most of the human population of Argentina, Brazil, Paraguay, and Uruguay. For example, the Brazilian Atlantic Forest has been reduced by 88%, with most remnants being degraded (Ribeiro et al. 2011). Conversely, regions such as the Caatinga and Pantanal have a long history of relatively low-intensity habitat conversion and low human population density, while the Gran Chaco, Cerrado, and Chiquitano have undergone a more recent, but extensive and intensive habitat conversion (Beuchle et al. 2015, Da Ponte et al. 2021, Hansen et al. 2013, Pinto-Ledezma & Rivero Mamani 2014, Ribeiro et al. 2011, Vallejos et al. 2015, Viglizzo 1997), This pattern is illustrated in the Gran Chaco where annual deforestation rates accelerated to about 4% starting during the 2000s (Da Ponte et al. 2022, Vallejos et al. 2015).

Using a large dataset on occurrence and various analyses presented in other chapters of this Special Issue (Jędrzejewski et al. 2023a, 2023b, Morato et al. 2023, Payán et al. 2023, Polisar et al. 2023), in combination with regional expert opinion and the literature, we updated the state of knowledge on jaguar distribution, population status, and threats in south-eastern South America while accounting for the high variability of ecological and anthropogenic determinants of habitat suitability across this region.

Methods

We estimated the current distribution of jaguars based on the analysis performed for the whole of South America by Jędrzejewski et al. (2023a). Our focal region (Fig. 1) was delimited by the estimated historic distribution of the jaguar (Sanderson et al. 2002) and the ecoregional limits used in the analysis (see below). For our focal region we compiled jaguar presence and absence data between 2000 and 2020, including data from published sources and monitoring projects (Fig. 1). To facilitate this process the coauthors completed a standardised questionnaire developed by the IUCN SSC Cat Specialist Group (Supplementary Online Material SOM Questionnaire).

Most data came from camera trapping, telemetry, record of tracks, and field interviews. To avoid bias from spatial autocorrelation, we reduced clustered data points to a maximum of one record per 100 km² (De Angelo et al. 2011, Dormann et al. 2007). We used 585 jaguar presence records from 2000–2009 and 415 records from 2010–2020. We also compiled 30 jaguar non-detection points collected from within the jaguar's current distribution and randomly selected 1641 points within the historic distribution of the jaguar where individuals have not been recently recorded (Fig. 1).

To estimate ecoregion-specific occurrence probability for jaguars and understand the factors that determine its distribution we used logistic regression models with a set of 21 predictive variables (see Jędrzejewski et al. 2023a). We then combined the results of these models with a kriging interpolation to estimate the current jaguar status and distribution (Jędrzejewski et al. 2017, 2023a). We defined ecoregions by combining the Level I and Level II ecoregions of Griffith et al. (1998) to broadly represent the ecological characteristics of geographic regions within the historic and current distribution of the jaguar. While this categorisation loses intra-ecoregional variation (e.g. Gran Chaco includes Dry Chaco, Humid Chaco, and temperate Espinal Forest, while south-western Cerrado also encompasses Chiquitano Forest; Olson et al. 2001), it permits a more tractable geographic assessment of jaguar status in our focal area.

Following the IUCN guidelines for mapping species distribution (IUCN Red List Technical Working Group 2021), we classified jaguar status in four categories based on our estimated occurrence probability: Extinct (0.0–0.25), Possibly Extinct (>0.25–0.49), Possibly Extant (>0.49–0.75), and Extant (>0.75–1.0). 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' to 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'. Additionally, we estimated the jaguar population size by country and ecoregion for the focal region by multiplying the potential jaguar population densities and their 95% credibility intervals (Jędrzejewski et al. 2018) by the probabilities of jaguar occurrence inside the current (2020) jaguar range within our focal region, following the methodological approach of Jędrzejewski et al. (2018).

Results

Range-wide distribution

The historical range of the jaguar in south-eastern South America covered 7.2 million km² that was 86% of the focal region, with the remainder corresponding to the portions of the Andes and Patagonia ecoregions (Sanderson et al. 2002, Fig. 1, Table 1). A large portion of the jaguar's range was converted to unsuitable habitat through increases in agriculture, infrastructure, and exploitation of jaguar and their prey as the human population grew (Quigley et al. 2017). We estimated that jaguars are extant in 799,000 km² (11% of the historical range) and possibly extant in an additional 633,000 km² (9% of the historical range), for a total of 1,432,000 km² for the current (2020) jaguar range in our focal region (Fig. 2, Table 1). Most of the remaining jaguar distribution in the focal region is fragmented in relatively small habitat patches that are often surrounded by unsuitable habitat for jaguars (Fig. 2). The exception is a large patch of relatively continuous habitat located in the northern Chaco in Bolivia and Paraguay, the Chiquitano, and the Pantanal where jaguars are contiguously present throughout most of these ecoregions (Fig. 2).

At the ecoregional level the Pantanal retained the highest estimated proportion of jaguar occurrence compared to the historical extent (90%), whereas in the Pampas ecoregion the jaguar has been extirpated from

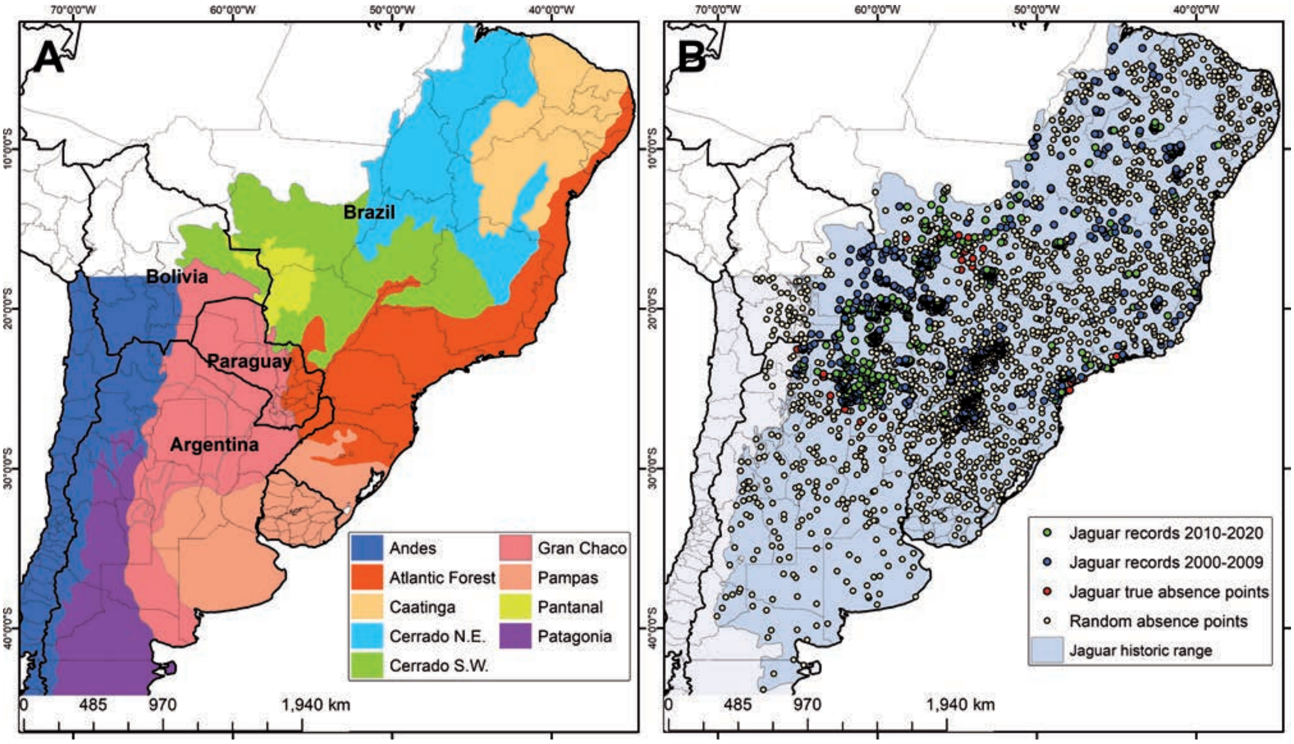

Fig. 1. Figure 1. A) Ecoregions within the analysis focal area in south-eastern South America and B) the jaguar;s historic range (after Sanderson 2002; darker grey) and the distribution of data points within the focal area used in the analysis.

Table 1. Area of the jaguar historic range (after Sanderson et al. 2002), area of the estimated 2020 jaguar distribution by country (Jędrzejewski et al. 2023a, Chapter 6 this volume), extrapolated country-level population and density and their 95% credibility intervals CRI in south-eastern South America. The estimated 2020 distribution is the sum of the estimated Extant and Possibly Extant categories.

Country	Area with current jaguar status (x 1000 km²)							2020 range as % of historic range	2020 Jaguar population estimate (95% CCI)	Mean jaguar population density (95% CRI) (jaguars/ 100 km²)
	Study focal area	Historic jaguar range	Extinct	Possibly Extinct	Possibly Extant	Extant	2020 Jaguar distribution			
Argentina	2,780	1,900	1,689	80	89	42	131	6.9	464 (158–813)	0.35 (0.12–0.62)
SE Bolivia	550	340	50	31	46	213	259	76.2	3,875 (3,095–4,661)	1.50 (1.20–1.80)
Paraguay	407	399	105	63	57	174	231	57.9	2,181 (0,972–3,427)	0.94 (0.42–1.48)
SE Brazil	4,421	4,380	2,700	869	441	370	811	18.5	8,809 (6,783–10,764)	1.09 (0.84–1.33)
Uruguay	176	176	176	0	0	0	0	0.0	0.0	0.00
Total	**8,334**	**7,195**	**4,720**	**1,043**	**633**	**799**	**1,432**	**19.9**	**15,329 (11,008–19,665)**	**1.07 (0.77–1.37)**

all of its original distribution (Table 2). The other ecoregions have all witnessed large-scale reductions in the distribution of the jaguar with only 7.8–35.7% of the original distribution being estimated to be occupied or potentially occupied (Table 2). Of these ecoregions, the Atlantic Forest, Caatinga, and Eastern Cerrado had the greatest estimated reductions, with only 7.8–19.0% of the historical distribution estimated to be occupied by jaguars (Table 2).

Country-level jaguar status

Uruguay

The jaguar was extirpated from Uruguay in the beginning of the 20th century (Pereira-Garbero & Sappa 2016). The historical jaguar range covered all the country where the species inhabited grasslands and riparian forests. The extinction of the species was driven by persecution related to the expansion of ranching activities and for the commercialisation of its skins, as well as the reduction of main prey species (Pereira-Garbero & Sappa 2016).

Argentina

The historical distribution of the jaguar in Argentina covered approximately 1.9 million km² (Table 1), including most of the northern and central regions of the country, north of the province of Río Negro (Di Bitetti et al. 2016, Perovic & Herrán 1998). Historically, the species' distribution included the Gran Chaco, Andean forests (which corresponds to Yungas Forest within our focal region), Atlantic Forest, Pampas grasslands, and northern Patagonia (Table 2). According to our analysis, the species is estimated to be Extinct in 1.69 million km² (89% of the historical range of the country; Table 1), and is Possibly Extinct in an additional 80,000 km² (4.2% of the historical range; Table 1). The disappearance of the species occurred from south to north during the last 150 years, becoming extinct in northern Patagonia and the Pampas region, then in most of the Gran Chaco region (Di Bitetti et al. 2016, Perovic & Herrán 1998; Table 2). The rapid contraction of the species' range coincided with economic and demographic growth, driven by the colonisation of much of the territory (Di Bitetti et al. 2016, Romero 1978).

We estimated the jaguar to be Extant across 42,000 km² (2.2% of the historical range) of Argentina and Possibly Extant across 89,000 km² (4.7% of the historical range; Table 1). However, a previous analysis estimated that the jaguar occurs in only 85,000 km² (Paviolo et al. 2019). Within Argentina the remaining jaguar population is divided into three subpopulations in the Atlantic Forest of the Misiones province, the Andean Forest of Salta and Jujuy, and the northern Gran Chaco (Paviolo et al. 2019). Additionally, restoration efforts are underway to restore jaguars in the Ibera marshland in the eastern Chaco region (Donadio et al. 2022). There is genetic evidence that the Atlantic Forest population is isolated from other populations in Argentina (De Angelo et al. 2011, Robino 2022), and it is likely that the Yungas and Chaco populations have recently become isolated from each other but not yet at the genetic level (Robino 2022) The three populations are, however, connected to varying degrees with other populations in neighboring countries, the Andean Forest population with Bolivia, the Gran Chaco population with Bolivia and Paraguay, and the Atlantic Forest population with Brazil (Paviolo et al. 2019).

Based upon previous modeling (Jędrzejewski et al. 2018) and that of this study, we estimated mean jaguar density of 0.35/100 km² and the total jaguar population within Argentina at 464 individuals (95% credibility interval of 158–813; Table 1). However, systematic camera-trap surveys in Argentina estimated a population between 200 and 300 animals (Paviolo et al. 2019). All the subpopulations are highly threatened, with the largest population in the Andean Forest with previous estimates of between 100 and 200 individuals (Di Bitetti et al. 2016, Paviolo et al. 2019, Perovic et al. 2015) which is consistent with our estimate of 33–171 individuals (Table 2).

For the Atlantic Forest of Argentina, we estimated between 34 and 172 individuals (Table 2) which is similar to recent estimates of between 72 and 123 obtained with camera trap surveys (A. Paviolo et al., unpubl. data). However, our estimate of 90–464 individuals in the Gran Chaco is much greater than field-based estimates of <20 jaguars (Paviolo et al. 2019, Quiroga et al. 2014). This discrepancy is likely the result of the very low human tol-

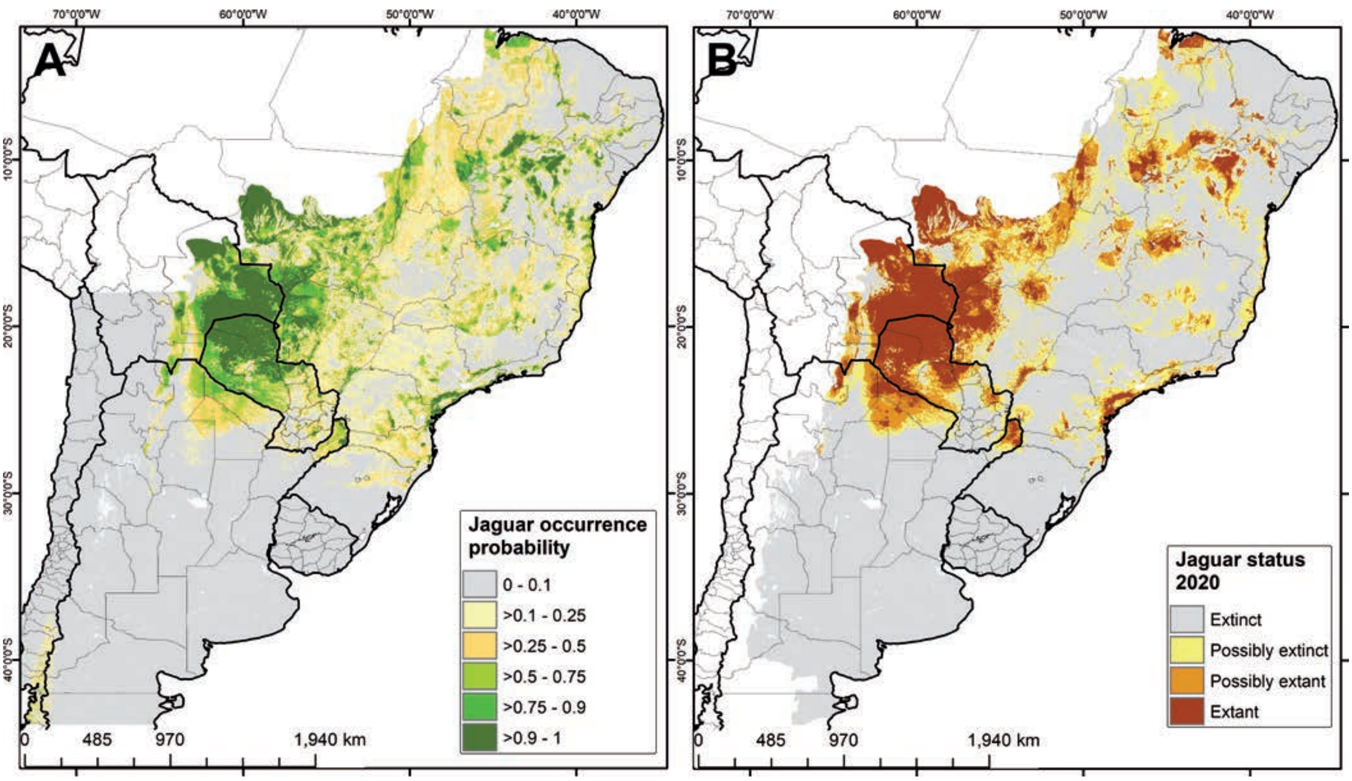

Fig. 2. A) Estimated probability of jaguar occurrence resulting from the logistic regression model of jaguar presence and absence and B) the estimated current status classified into four categories within the study's focal area based upon the jaguar occurrence probability estimated with the combined logistic regression and kriging interpolation models; Extinct (0.0–0.25), Possibly Extinct (>0.25–0.49), Possibly Extant (>0.49–0.75), and Extant (>0.75–1.0). 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. For methodological details see Jędrzejewski et al. (2023a).

erance of the species in the region and the consequent high anthropogenic mortality that suppresses the population below potential levels (Fig. 3; Quiroga et al. 2014, Thompson et al. 2020).

Paraguay

The historical distribution of the jaguar covered nearly all of Paraguay including areas of the Atlantic Forest, Gran Chaco, Cerrado, and Pantanal (Fig. 1, Table 2). However, agricultural expansion and infrastructure development have greatly reduced the availability of jaguar habitat (Da Ponte et al. 2017, 2021, Hansen et al. 2013, Venter et al. 2016). We estimated that the jaguar is Extinct or Possibly Extinct in 43% of its original distribution within the country (Table 1). The most impacted ecoregion is the Atlantic Forest where most of the area has become unsuitable (Fig. 2, Table 2) with the remaining populations located in two small and isolated areas (De Angelo et al. 2013, López Duré 2021, McBride & Thompson 2019).

We estimated the jaguar to be Possibly Extant in 14% of the country and Extant in 43% of the historical range (Table 1). Jaguars remain in large portions of the Gran Chaco (Table 2), but since 2000 the Chaco forests have undergone rapid and extensive conversion for cattle pasture and row crops (Baumann et al. 2017, 2022, Romero-Muñoz et al. 2019, Vallejos et al. 2015). This activity not only is affecting the habitat availability for the species, but also resulting in high levels of persecution in response to real or perceived livestock predation (McBride and Thompson 2018, Romero-Muñoz et al. 2019).

According to the jaguar density estimates of 0.94/100 km^2 from Jędrzejewski et al. (2018), and our analysis, we estimated the total jaguar population within Paraguay at 2,181 individuals (95% credibility interval 972–3427, Table 1). Most of the estimated population was distributed in the Gran Chaco region and it is believed that in the Atlantic Forest of eastern Paraguay <20 individuals remain (Paviolo et al 2016), although our estimate of 87 jaguars is considerably larger (Table 2).

South-eastern Bolivia

In our focal area in south-eastern Bolivia (hereafter SE Bolivia; 550,000 km^2) jaguars were historically distributed over 340,000 km^2 (Table 1), including in the Gran Chaco, the Chiquitano, Andean Forest, and the Pantanal. We estimated that in our focal region within Bolivia the jaguar disappeared from 15% of its historic range and is Possibly Extinct in an additional 9% (Table 2). The most negatively affected regions have been parts of the Andean Forest, the Gran Chaco, and the western Chiquitano in the department of Santa Cruz that have been modified by agricultural development (Maffei et al. 2016).

We estimated jaguars to be extant in 63% and possibly extant in 14% of the historical distribution in SE Bolivia (Table 1). The species remains in large areas of continuous habitat in the Chaco, Chiquitano, and Pantanal that are connected with contiguous blocks of suitable habitat in Brazil and Paraguay (Fig. 2). However, the Chiquitano forest has recently experience rampant deforestation which may affect the jaguar population, and important connectivity areas between the Chaco and the Amazon (Thompson et al. 2021). Furthermore, the situation in the Andean Forest is more precarious due to increasing habitat fragmentation (Table 2).

Table 2. Area of the jaguar historic range (after Sanderson et al. 2002) and area of current estimated jaguar distribution by country and ecoregion (Jędrzejewski et al. 2023a, Chapter 6 this volume) in south-eastern South America. The estimated 2020 jaguar distribution calculated as the sum of extant and possibly extant categories.

Ecoregion	x 1000 km²							Current range as % of historic range
	Country	Historic range	Extinct	Possibly Extinct	Possibly Extant	Extant	Current 2020 jaguar range	
Andes	Argentina	76	53	9	9	6	15	20.0
	Bolivia	55	16	13	17	9	27	48.6
	Total	131	68	21	26	15	42	**31.9**
Atlantic Forest	Argentina	31	7	7	9	8	16	53.7
	Brazil	1,127	871	186	45	25	70	6.2
	Paraguay	89	50	27	10	2	12	12.9
	Total	1,246	928	221	63	34	98	**7.8**
Caatinga	Brazil	779	567	104	60	49	109	**14.0**
Cerrado East	Brazil	1,143	603	324	151	66	217	**19.0**
Cerrado West	Bolivia	123	10	5	12	95	108	87.7
	Brazil	960	445	239	148	128	276	28.7
	Paraguay	7	0	1	2	3	6	82.2
	Total	1,090	455	245	163	226	389	**35.7**
Pantanal	Bolivia	23	0	1	2	20	22	96.4
	Brazil	149	5	12	33	99	132	88.9
	Paraguay	2	0	0	0	1	2	99.9
	Total	173	5	13	36	121	156	**90.0**
Gran Chaco	Argentina	895	733	62	72	28	100	11.1
	Bolivia	138	24	12	14	88	102	73.9
	Brazil	7	2	1	2	2	5	61.2
	Paraguay	299	54	34	44	167	211	70.6
	Uruguay	0	0	0	0	0	0	0.0
	Total	1,340	813	110	132	286	417	**31.1**
Pampas	Argentina	478	478	0	0	0	0	0.0
	Brazil	168	168	0	0	0	0	0.0
	Uruguay	174	174	0	0	0	0	0.0
	Total	819	819	0	0	0	0	**0.0**
Patagonia	Argentina	381	381	0	0	0	0	**0.0**
Total		**7,104**	**4,639**	**1,037**	**631**	**797**	**1,428**	**20.1**

Combining 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 the Bolivian portion of our study region at 3,875 individuals (95% credibility interval of 3,095 to 4,661; Table 1) which equated to a mean density of 1.5 jaguars/100 km² (95% credibility interval: 1.20–1.80). Most of these individuals are estimated to occur in the Gran Chaco and Chiquitano (Table 2).

South-eastern Brazil

Our focal region within Brazil (here after SE Brazil) covered 4.42 million km², of which 4.38 million km² was historic jaguar range. We estimated that of this historic distribution the jaguar is Extant or Possibly Extant in 18% of its area, while Extinct in 62% and Possibly Extinct in 20% (Table 1). The Brazilian portion of our focal region had the highest country-level estimate of the number of jaguars (8,809; 95% credibility interval: 6,783–10,764), which translated to a mean density of 1.09 jaguar/100 km² (Table 1).

Within SE Brazil the historic jaguar distribution included seven of the nine ecoregions in our study area. We estimated the jaguar to be extinct or possibly extinct in 100% of the historic range in the Pampas, 86% in the Caatinga, 85% in the Atlantic Forest, 81% in eastern Cerrado, and 71% in the western Cerrado. The ecoregions with the lowest estimated area where the jaguar is extinct or possible extinct was the

Fig. 3. The remains of a GPS collared male jaguar in the Paraguayan Dry Chaco killed in retaliation for cattle depredation (Photo: R. T. Mcbride, Jr.).

Gran Chaco (43%) and the Pantanal (11%; Table 1).

As in Argentina and Uruguay, in Brazil the jaguar has been extirpated from grassland systems (Pampas ecoregion), while also being highly negatively impacted in the easternmost ecoregions of the Atlantic Forest, eastern Cerrado, and Caatinga. The Atlantic Forest has undergone centuries of widespread land conversion resulting in extensive forest loss and fragmentation that has driven the large-scale reduction in the occurrence of the jaguar (Paviolo et al. 2016, Ribeiro et al. 2011). This process of habitat loss has resulted in a highly fragmented jaguar population that now occurs in multiple sub-populations throughout the Brazilian Atlantic Forest (Paviolo et al. 2016), resulting in reduced genetic diversity among these populations (Haag et al. 2010, Srbek-Araujo et al. 2018).

The most studied jaguar population in Brazil is in the Atlantic Forest and consequently have permitted a more detailed understanding of the regional status of the jaguar (Azevedo et al. 2016, Paviolo et al. 2016). Previous extrapolations of jaguar densities generated an estimated population of 281 jaguars in the Brazilian Atlantic Forest (Azevedo et al. 2016), which was very similar to our estimate of 271 jaguars (Table 1).

The Caatinga also has a long history of extensive land conversion and degradation whereby the jaguar population in this region is fragmented (Azevedo et al. 2016). The jaguar population in the Caatinga has previously been estimated to be 262 individuals, however it was based on a conservative constant density of 0.3 individuals/100 km^2 (Azevedo et al. 2016). Our population estimate for the Caatinga (1,017 jaguars; 95% credibility interval 783–1,243) is based on varying densities from our modeling, however, is about four times larger than those based upon a uniform density of 0.3 individuals/100 km^2.

For the Brazilian Pantanal we estimated a population of 2,177 jaguars (95% credibility interval: 1,676–2,660) which indicates that the Brazilian Pantanal remains a population stronghold for the jaguar. However, we point out that despite the common recognition of the importance of the Pantanal for jaguar conservation, relatively few studies have estimated densities in the region, generating varied estimates ranging from 3.6 to 12.4 jaguars/100 km^2 (Cavalcanti et al. 2012, Devlin et al. 2023, Eriksson et al. 2022, Soisalo & Cavalcanti 2006). Consequently, there is a conspicuous need for an ecoregion-wide assessment of jaguar densities given the relatively small proportion of protected area in the ecoregion, habitat conversion and other anthropogenic threats, and the persecution of jaguars (Azevedo et al. 2016, Cavalcanti et al. 2010, 2012, Thompson et al. 2021, Tomas et al. 2019).

The Cerrado potentially supports a large number of jaguars as it is the second largest biome in Brazil, however, large-scale land conversion in the region for agricultural production has greatly reduced the distribution of the jaguar. This is exacerbated by only 2% of the ecoregion being protected (de la Torre et al. 2018, Moraes Jr. 2012). Our estimated population of 4,863 individuals for the entire Brazilian Cerrado, equates to a mean density of 1.01 individuals/100 km^2. This is higher than a previous estimate of 0.67 individuals/100 km^2 for the entire region (Moraes Jr. 2012) and of 0.29 individuals/100 km^2 from Emas National Park (Sollmann et al. 2011), but is similar or lower than density estimates from other dryland systems in southern South America (Noss et al. 2012, Silveira et al. 2010, Sollmann et al. 2013, Thompson et al. 2022).

Conclusions

Our analysis indicates that optimistically jaguars remain Extant in about 20% of its historic distribution within our focal region in southern South America. However, at the same time, the high uncertainty of the occurrence of the jaguar in 23% of its original distribution (Possibly Extant or Possibly Extinct) points to a need for an improved quantification of the distribution and abundance of jaguar across this region. Although the status and ecology of jaguars in some ecoregions, such as the Atlantic Forest, have been well studied (Fusco-Costa et al. 2023, McBride & Thompson 2019, Paviolo et al. 2016), and others such as the Dry Chaco are gaining attention, others have received relatively little attention despite their importance for jaguar conservation.

The Bolivian Andes, Chiquitano forest, and the Humid Chaco cover relatively large areas and with the potential to support significant jaguar populations, as well as playing important roles in maintaining continent-wide connectivity (Thompson et al. 2021). However, jaguars in these ecoregions have been little studied and is a research void that needs to be addressed (Maffei et al. 2016, Maillard et al. 2020, Meißner et al. 2023, Thompson et al. 2021). Similarly, the Cerrado, despite its large size, has had jaguar research mostly confined to protected areas even though the ecoregion is dominated by working landscapes, highlighting a need for a more representative focus on quantifying the abundance and occurrence of jaguars in the Cerrado. Perhaps of most concern is the lack of a quantitative assessment of the status of the jaguar in the Pantanal given the conventional view of the ecoregion as a population stronghold for the species. The Pantanal is subject to widespread agricultural and ranching activities, among other anthropogenic pressures (Cavalcanti et al. 2012), however, a rigorous ecoregional evaluation of the jaguar is conspicuously absent and necessary.

Some of our large-scale population and density estimates differ from other local studies, particularly in the Argentine Chaco, Paraguayan Atlantic Forest, and Caatinga which indicates the need for further research which takes into account both the impact of environmental and anthropogenic factors on the variability of jaguar densities (Azevedo et al. 2016, McBride & Thompson 2019, Morato et al. 2016, Romero-Muñoz et al. 2019, Thompson et al. 2020). Consequently, given the uncertainty in some of our estimates, we caution against interpreting our results as absolutes or at overly fine geographic scales, although the majority of our estimates are consistent with field-based observations. We believe that our estimates capture the general state of the distribution and population of jaguars within south-eastern South America, however, new abundance estimations from additional sites would be valuable in validating our estimates.

Based upon our analysis, jaguars likely remain in about 20% of their historic distribution in south-eastern South America (Extant or Possibly Extant), and potentially occur in an additional 14% of our focal region (possibly extinct). Consequently, at the regional level, conservation efforts must be directed towards maintaining the existing, relatively healthy, and connected populations in the Pantanal, northern Chaco, and the Chiquitano. Moreover, our findings emphasise the urgency to restore populations and connectivity in the Atlantic Forest, eastern Cerrado, Caatinga, and southern Chaco.

Concurrently, we demonstrated that there are large areas of potentially suitable, unoccupied habitat that can support jaguars in our focal region. Therefore, to ensure the conservation of existing populations, the recolonisation of jaguars into suitable unoccupied habitat, and the connectivity and genetic variability of jaguars throughout south-eastern South America and beyond, it is imperative that the country-specific management goals outlined in the national jaguar management plans for the countries in the focal region (Desbiez et al. 2013, Pinckert de Paz et al. 2020, Ramadori et al. 2016, Secretaría del Ambiente et al. 2016) are met to maintain sufficient habitat, prey availability, and landscape connectivity for jaguars, and to reduce their direct anthropogenic mortality (i.e. hunting, roadkill).

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Supporting Online Material SOM Questionnaire is available at www.catsg.org.

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Estimating species distribution changes due to human impacts: the 2020's status of the jaguar in South America

Monitoring species distribution over time and understanding factors and mechanisms that determine it is crucial for effective conservation planning. We estimated the current jaguar *Panthera onca* distribution in South America based on a large set of records (2,557) from 2000–2020 and a set of absence points (both field collected and randomly selected from known jaguar absence areas) using a combination of kriging interpolation and logistic regression models. The current jaguar range in South America is estimated at 7.9 million km² which is 14% less than the estimate for 2015 and 25% less than for 2000. The reduction of the jaguar's South American range has been continuous and relatively rapid. Our logistic regression models show that the decrease in jaguar distribution across South America was mainly driven by increasing deforestation, road density, pasture and farmland area, and human population density. During the last 20 years, negative changes in the jaguar habitat suitability (ranging from minor to major) occurred over various parts of the jaguar's range, including core areas in the Amazon basin, covering 9.3% of the area of the jaguar range. We also show that different ecological factors drive the distribution of jaguar populations in different eco-regions. Based on this work, we propose a stronger international collaboration in monitoring jaguar populations and conservation efforts and a new approach for estimating species distribution for IUCN Red List assessments.

The natural distribution of a species depends on its evolutionary adaptations to habitats and available resources, the current distribution of those habitats, and a set of limiting factors, for example, competition with other species (Krebs 2001). However, the distribution of many species today is progressively shaped by human activities (Ripple et al. 2014). Therefore, estimating the current distribution and understanding factors and mechanisms that determine it is crucial for effective conservation planning and actions, including the IUCN Red List assessments and subsequent action plans (IUCN 1994, Baillie et al. 2004).

There are two main approaches for determining species distributions: (1) mapping presence records and delimiting distribution patches in strict relation to the distribution of species records, for example, as a minimum convex or concave polygon encompassing all data points, often supplemented with expert opinions where data are not available (IUCN Red List Technical Working Group. 2019); and (2) modelling the occurrence and distribution of a species based on the association between known presence or presence/absence data and a set of predictive variables, generally referred to as species distribution modelling (Guisan & Thuiller 2005, Elith & Leathwick 2009, Phillips et al. 2017). The advantage of the first mapping approach is that it is simple and directly related to data points. The main shortcoming is that often data are limited and do not cover the entire area where a species may be present, leading to underestimation in some areas or uncertainty when supplemented by expert opinions. On the other hand, presence points can also be spatially mixed with absence, which are usually not evaluated, leading to an overestimation when using presence points only. An advantage of the habitat suitability or species distribution modelling (henceforth referred to as 'SDM') is that the models are capable of predicting the probability of species presence or absence in areas where data may be limited or completely lacking. Another important advantage of SDM is that it helps to identify factors determining species distributions and driving declines, critical information for planning conservation efforts. However, SDMs may also suffer from small datasets or inadequate predictive variables, leading to unsatisfactory predictions, such as presence predicted in areas where the species is absent or vice versa (Hirzel et at. 2006). Additionally, populations of animal species are often not homogenous, they may consist of genetically unique sub-populations that have adapted to specific local habitats and prey communities and may respond differently to environmental factors over space and time (Pilot et al. 2006, 2012, Jędrzejewski et al. 2012). Such differences must be accounted for to predict species distribution across large geographic regions accurately.

Here, we estimate the current distribution of the jaguar in South America. Earlier assessments of the jaguar's range in South America in 2000 and 2015, prepared for the IUCN Red List assessment, resulted in estimated total areas of 10.2 and 8.4 million km², respectively (Sanderson et al. 2002, Zeller 2007, Caso et al. 2008, Quigley et al. 2018). However, recent high deforestation rates driven by increasing demands for beef, soybeans and other commodities, extensive fires, mining expansion, human population growth, as well as political instability in several parts of South America may have changed the jaguar's status (Romero-Muñoz et al. 2020) requiring a re-assessment of the distribution of jaguar populations across South America. Additionally, those earlier estimates were largely based on expert opinions, especially for areas where data were limited, likely resulting in high prediction uncertainty.

In this paper, we compiled the most up-to-date dataset of jaguar presence and absence records from across South America, as well as new data on forest cover, human population density, road density, changes in agriculture areas, and other predictive variables

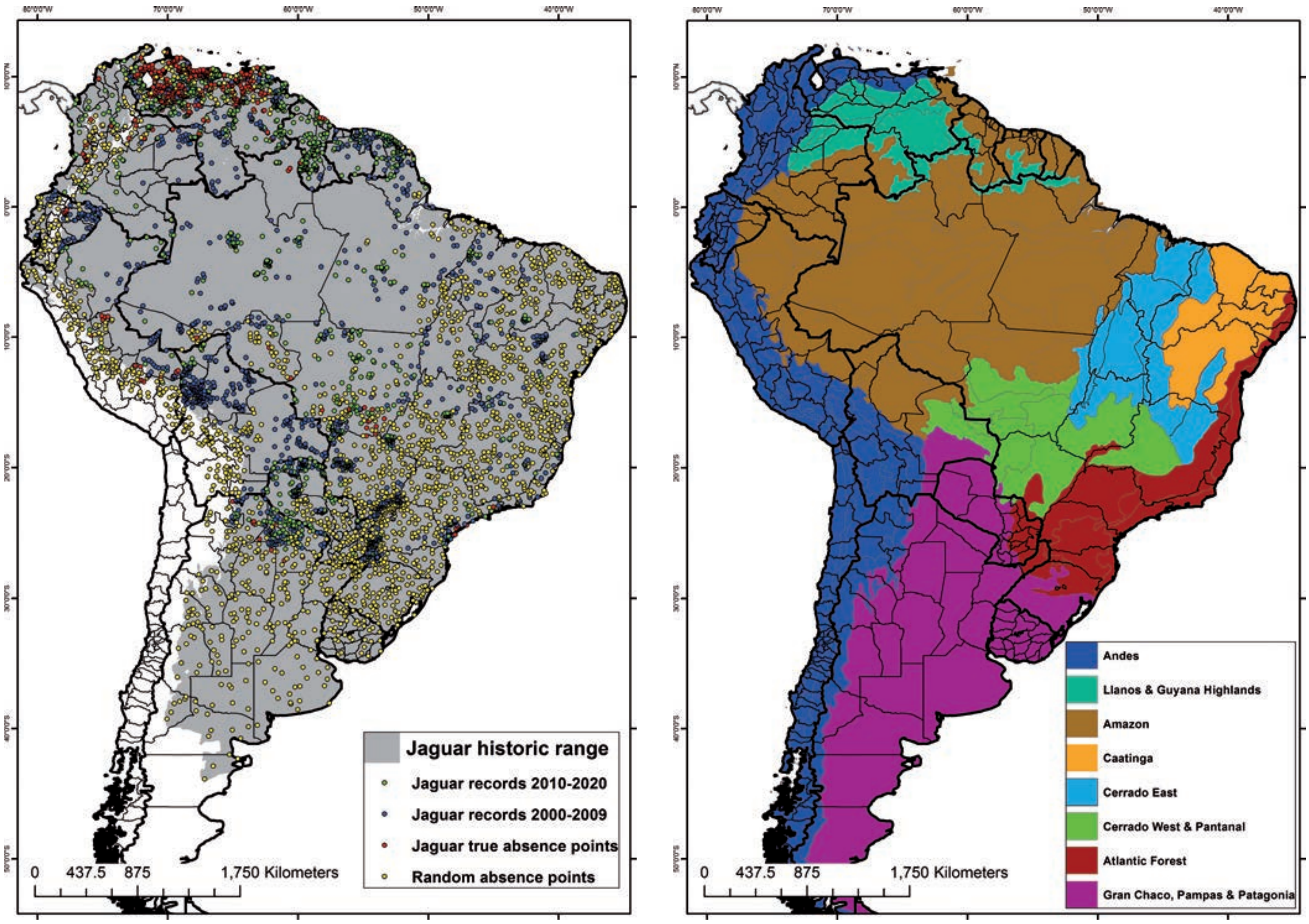

Fig. 1. Left: the historic jaguar range in South America (after Sanderson et al. 2002) and jaguar records (from 2000–2010 and from 2011–2020), jaguar true absence points, and randomly selected points from the known jaguar absence areas used to analyse current jaguar distribution. Right: the division of eco-regions of South America, used in our analysis (based on Griffith et al. 1998). We distinguished the following eco-regions: 1 – Andes, 2 – Los Llanos and Guiana Highlands; 3 – Amazon, 4 – Caatinga, 5 – Cerrado East, 6 – Cerrado West and Pantanal, 7 – Atlantic Forest, 8 – Gran Chaco, Patagonia, and Pampas. Country and administrative borders after Porto Tapiquen (2020).

known to affect jaguar distribution including any recent changes. We combined the records' mapping and SDM approaches to estimate the actual jaguar distribution better while still fulfilling the requirements of the IUCN Red List mapping standards (IUCN Red List Technical Working Group 2019). We also considered the recently discovered genetic differences between jaguar populations inhabiting different eco-regions (Roques et al. 2016, Lorenzana et al. 2020) and the fact that each of these populations may have different adaptations to ecological factors.

Finally, we compared our estimate of jaguar distribution in 2020 with earlier IUCN Red List assessments of jaguar populations for 2000 and 2015 (Sanderson et al. 2002, Zeller 2007, Caso et al. 2008, Quigley et al. 2018) to identify changes in the jaguar's range over the last twenty years, as well as to make inferences about the effect of different methodological approaches on estimates of species distribution.

Methods

We compiled a large set of records of jaguar presence and a smaller set of records of jaguar absence from each of the twelve countries of South America, including data from published sources and ongoing monitoring projects collected primarily with camera trapping, radiotracking, recording of tracks, and field interviews (see Supporting Online Material SOM Table T1 and Data Set D1 for the complete list of data records and their sources). Absence points came mostly from interviews and a smaller number of long-term camera trapping studies. As the presence of jaguars is fairly easily recorded by hunters, ranchers, or researchers through distinctive tracks, attacks on livestock, prey remains, roaring, and also direct observations, we assumed that a declared absence of jaguar records in the interviews is a reliable indicator of a true jaguar absence in an area (Zeller et al. 2011). The reliability of presence/absence data obtained with interviews was earlier verified by comparisons with data obtained independently by other methods and by spatial autocorrelation tests (Jędrzejewski et al. 2017a). To ensure equal numbers of jaguar presence and absence points for the subsequent logistic regression analysis (see below), we randomly selected the balance of the absence points from the areas within the historic jaguar range where jaguars were identified as locally extinct by the IUCN 2000 (Sanderson et al. 2002, Caso et al. 2008) or 2015 assessments (Quigley et al. 2018) and where no new jaguar records were collected (see SOM Text T1 for more information).

To estimate the current distribution of jaguar populations and identify factors driving changes over the last 20 years, we combined kriging interpolation technique (corresponding to the records' mapping/IUCN approach) with logistic regression (species distribution modelling SDM approach), following the procedure in Jędrzejewski et al. (2017a). We applied kriging interpolation to our dataset

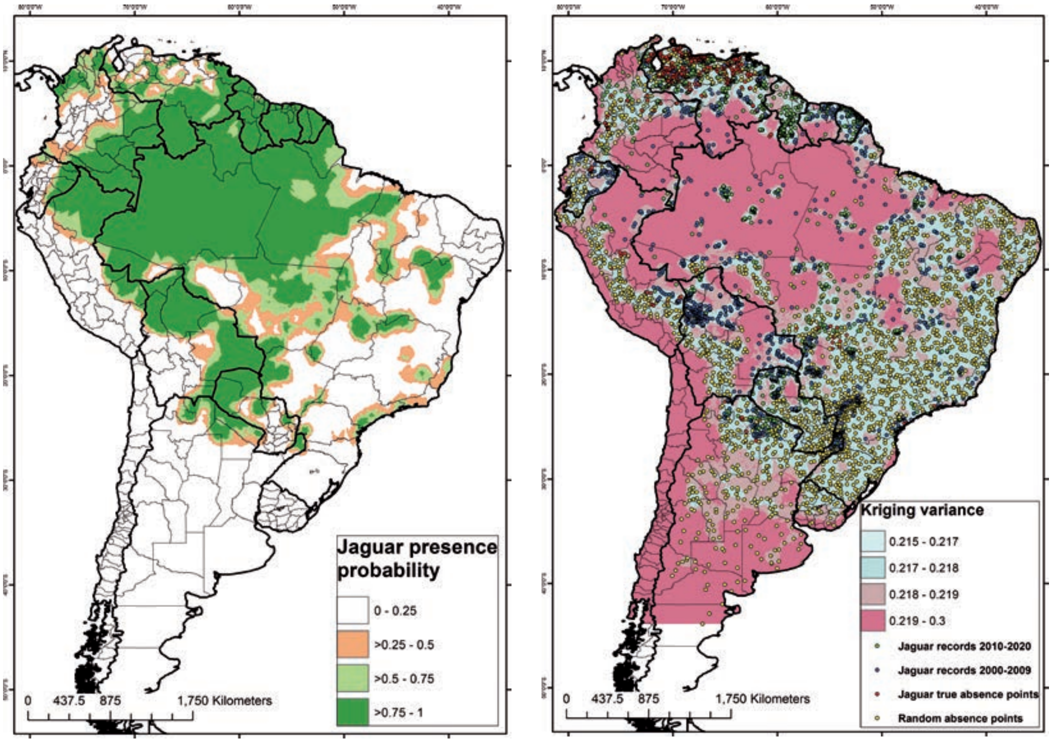

Fig. 2. Jaguar presence probability based on kriging interpolation of jaguar presence-absence (left) and kriging variance (right). High kriging variance (> 0.218, pink) corresponds to the areas with low data point density and indicates low confidence in kriging prediction.

of jaguar presence-absence. We calculated a spatial prediction of the probability of jaguar presence (values from 0 to 1) by interpolating all jaguar presence (value 1) and absence (value 0) records using the kriging interpolation function within ArcGIS 10.3 (see further information in SOM Text T1).

In the case of logistic regression, we fitted a general model to presence-absence data for the whole of South America but also produced individual models for each of the eight eco-regions of South America (Fig. 1). In the case of the latter, the data has been divided into eight appropriate subsets to take into account possible different responses to environmental variability resulting from documented or potentially possible genetic differences between jaguar populations. We distinguished eco-regions following the classification proposed by Griffith et al. (1998), adjusted to the genetic variation between jaguar populations of the Amazon, Pantanal, western and eastern Cerrado, Caatinga, and Atlantic Forest identified by Roques et al. (2016) and Lorenzana et al. (2020). We also distinguished the ecologically unique Gran Chaco and Andes regions, which were not included in genetic studies. Additionally, jaguars from the Llanos region have shown morphological (and thus possibly genetic) dissimilarity from jaguars in adjacent areas (Hoogesteijn & Mondolfi 1996). Finally, eco-region divisions were adjusted to the distribution of our data points to ensure that we could fit models with sufficient data). For this reason, we combined Gran Chaco with

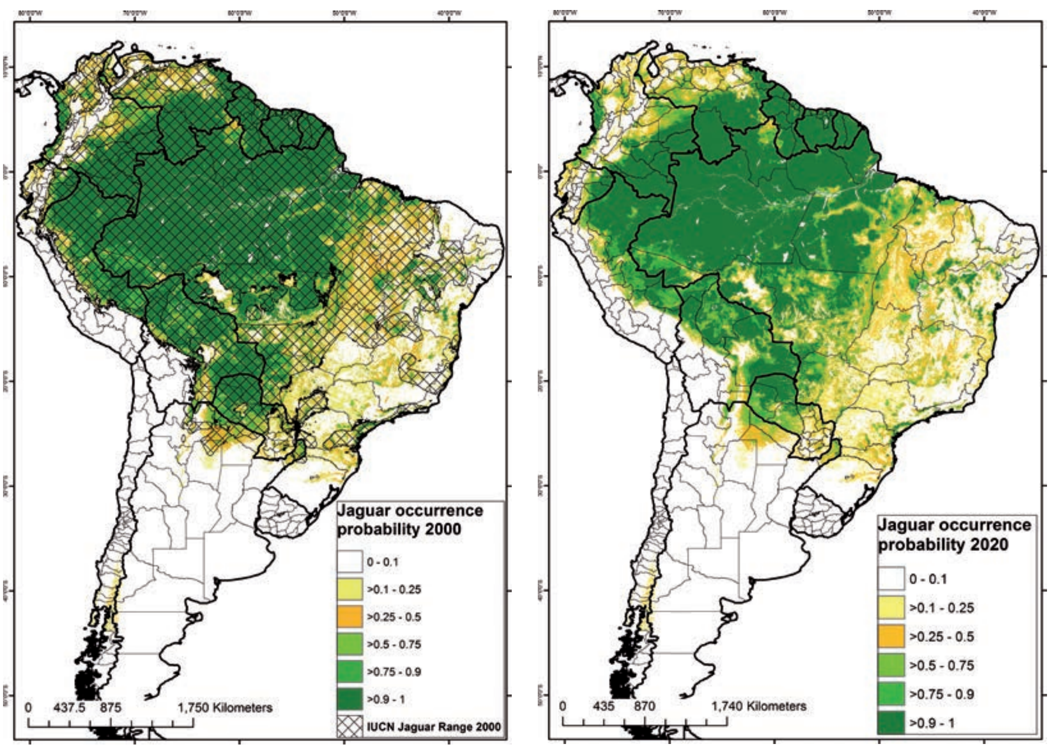

Fig. 3. Probabilities of jaguar occurrence in 2000 (left) and 2020 (right), resulting from the composition of predictions of logistic regression models fit separately to data in each of eight Eco-regions (as in Fig. 1 and Table 1). Both predictions are based on a total set of 21 predictive variables (SOM Table T2); however, for the 2000 and 2020 predictions we used different (respective) data for four variables: human population density, pastures, croplands, and forest cover. Prediction for 2000 is compared with the IUCN estimate of jaguar range in 2000 (Caso et al. 2008).

Patagonia and Pampas, western Cerrado with Pantanal, and Los Llanos with adjacent Guiana Highlands (Fig. 1).

Variables used to fit the logistic regression models included % forest cover, annual precipitation, mean annual temperature, mean and standard deviation of vegetation indices obtained from satellite images related to vegetation abundance and primary productivity (NPP, GPP, NDVI, EVI) as well as with water content in leaves and the ground (NDWI), human population density, human footprint index, indicators of protected areas and indigenous territories, proportions of croplands and pastures in an area, and road density index (SOM Table T2, SOM Fig. F1, SOM Dataset D2). We used climatic and vegetation productivity indices (mean values) because they are related to the density and productivity of herbivores, the jaguar food base, and thus indirectly, they affect jaguar populations (Polisar et al. 2003, Karanth et al. 2004, Melis et al. 2009, Pettorelli et al. 2011). Standard deviations of vegetation indices are measures of the seasonality of vegetation development and also may be related to densities of herbivores and carnivores. We converted the logit values from the best regional models to the probability of jaguar occurrence and made spatial predictions at the same resolution (1 km^2) for each eco-region. We then combined the regional maps into a single map for South America. Predictions for 2000 and 2020 were based on the relevant data for each period for four variables: forest cover, croplands, pastures, and human population density; for the other independent variables we used the same data for both predictions (see further information in SOM Text T1).

All model fitting was conducted using SYSTAT 13.2 (Systat Software, Inc. 2017, San Jose, CA, USA).

To estimate the current (2020) jaguar distribution in the areas with a high density of data points and low kriging variance (high certainty of kriging prediction), we averaged probability values obtained with both models (kriging interpolation and logistic regression with data for 2020) for each 1 km^2 raster cell. We did so because each type of model carries partly different information. Combining them allowed us to evaluate conservation status better (see below) and to reduce the probability of wrong classification of any area as presence or absence. We produced a confusion matrix and calculated the proportion of correctly classified presence and absence points ("sensitivity" and "specificity", respectively) to verify if this combined method fits better to data points than single models. However, we could not use interpolation results and calculate average probabilities for areas with low confidence in kriging prediction (low density of data points and high kriging variance). Instead, we chose to use probabilities from predictions based on the logistic regression models alone for these areas. We used the same classification criteria as for the areas with averaged probabilities. We then classified the estimated probability values into four classes that refer to the categories of distribution mapping standards for the IUCN Red List (Technical Working Group, 2019): (1) Extinct (mean probability values between 0 and 0.25), (2) Possibly Extinct (>0.25–0.49), Possibly Extant (>0.49–0.75), and Extant (>0.75–1). See further information in SOM Text T1.

We assumed that the combined areas classified as "Extant" and "Possibly Extant" represent South America's current 2020 jaguar distribution. Therefore, we compared this area with the estimates developed for the IUCN 2000 and 2015 Red List assessments (Sanderson et al. 2002, Zeller 2007, Caso et al. 2008, Quigley et al. 2018). However, as those assessments were partly incomplete due to the lack of data from some areas (e.g. from Mato Grosso state in Brazil), we filled these knowledge gaps by inputting the results for 2020, assuming that areas inhabited by jaguars in 2020 likely also hosted jaguar populations in 2000 and 2015.

In preparing the maps, we used country and administrative borders (after Porto Tapiquén, 2020) to help locate data and results; however, they do not include any disputed boundaries and do not pretend to represent any political opinions.

Results

The total number of collected jaguar records from South America, after reducing densely distributed points to only one per 100 km^2, was 2,557. This included 1,305 records from 2000–2010 and 1,252 from 2011–2020. We also collected 426 verified jaguar absence points from South America (SOM Table T1), and we selected 2,136 random points from the area of known jaguar absences (Fig. 1, SOM Dataset D1).

Spatial kriging interpolation of jaguar records (value 1) and all absence points (value 0) produced an estimation of the distribution of jaguar populations, with probability of presence (Fig. 2). However, an analysis of kriging variance indicated which areas have higher or lower certainty of this prediction (Fig. 2). Areas with a kriging variance <0.218 corresponded to a relatively high density of data points (mean 15.0/10,000 km^2, SD = 13.2) and predictions from these areas were used for further analyses. On the other hand, areas with the kriging variance > 0.218 (prevailing in our study area; Fig. 2) had a lower density of data points (mean 2.2/10,000 km^2, SD = 1.1). For these areas, we excluded predictions based on kriging interpolation from the subsequent analysis of the jaguar range.

The highest performing logistic regression model of jaguar occurrence based on the entire dataset included 12 variables (Table 1). Five of them (mean annual temperature, water index, forest cover, protected areas, and indigenous territories) had a positive effect on jaguar occurrence across the continent. In contrast, six (human population density, road density, croplands, pastures, and standard deviations of NDVI and NPP) had negative effects. This model also included the division of eco-regions as a categorical variable (Table 1 and SOM Table T3). Mean annual temperature, protected areas, human population density, croplands, road density, and forest cover had the strongest impact on jaguar probability of occurrence, as indicated by Z values (SOM Table T3). This general model had good predictive power ($p < 0.001$, AUC = 0.911, Nagelkerke's R^2 = 0.62, sensitivity = 0.83, specificity = 0.85) and performed well in cross-validation (mean AUC value for the smaller subsamples = 0.902, range 0.897 to 0.909). However, individual models for eight eco-regions had high predictive performance (AUC from 0.89 to 0.97) except for the eastern Cerrado (AUC = 0.84). These models included various sets of predictive variables. Protected areas, human population density, and pastures were included in seven models, temperature and road density in six, and croplands and NPP_SD in five models (Table 1 and SOM Table T3). Interestingly, temperature, which had a positive effect in the general model, had a negative effect in Caatinga and Cerrado (very dry and hot areas). Similarly, pastures had a negative effect in the general model but positively affected jaguar occurrence in the Andes and Caatinga. We used the mosaic composition of these individual models for each eco-region to predict jaguar occurrence probability across South America in 2000 and 2020 (Fig. 3, SOM Dataset D3). The overall prediction for 2020 (Fig. 3 right) improved predictive performance (sen-

Table 1. The best logistic regression models of jaguar occurrence for the whole of South America (based on the whole data set) and for each Eco-region (based on the split data), selected with the Akaike Information Criterion (AIC), as well as information on predictive performance of all models used to estimate the current (2020) jaguar distribution in South America. See SOM Table T2 for information on predictive variables and SOM Table T3 for detailed parameters of each model. Sign in front of a variable indicates if its impact on jaguar occurrence was positive or negative.

Eco-region	Variables	N presence points	N absence points	Sensi-tivity	Speci-ficity	AUC	Nagle-kerke's R^2
All South America (general model)	+TEMP, -NDVI_SD, -NPP_SD, +NDWImean, +CANOPY, -HPDEN_LN, -ROAD_DENSITY, -CROPLAND, -PASTURE, +INDTER, +PROT_AR, ECOREG (8 cat)	2,478	2,492	0.83	0.85	0.911	0.624
Andes	+PRECIP, +TEMP, -NPP_SD, +EVImean, +EVI_SD, +CANOPY, -HPDEN_LN, -ROAD_DENSITY, -HFOOTP2004,+PASTURE, +PROT_AR	241	596	0.64	0.91	0.891	0.532
Los Llanos & Guiana Highlands	+PRECIP, +TEMP, +EVImean, -HPDEN_LN, -ROAD_DENSITY, -HFOOTP2004, -PASTURE, -CROPLAND	374	185	0.89	0.69	0.893	0.560
Amazon	+TEMP, +GPP_SD, -NPP_SD, -HPDEN_LN, -ROAD_DENSITY, -PASTURE, -CROPLAND, +INDTER, +PROT_AR	947	158	0.96	0.58	0.925	0.575
Caatinga	-TEMP, +GPP_SD, -NDVI_SD, -HPDEN_LN, -ROAD_DENSITY, +PASTURE, +PROT_AR	60	179	0.83	0.96	0.968	0.786
Cerrado East	-EVI_SD, -HPDEN_LN, -PASTURE, +PROT_AR	85	227	0.51	0.95	0.838	0.415
Cerrado West & Pantanal	+PRECIP, -TEMP, +NPP_SD, -NDVI_SD, +NDWImean, +CANOPY, -ROAD_DENSITY, -PASTURE, -CROPLAND, +PROT_AR	267	262	0.82	0.86	0.912	0.625
Atlantic Forest	-GPP_SD, +NPP_SD, +CANOPY, -HPDEN_LN, -ROAD_DENSITY, -PASTURE, -CROPLAND, +PROT_AR	219	489	0.73	0.95	0.892	0.590
Gran Chaco, Pampas, Patagonia	+TEMP, -GPP_SD, +NPP_SD, +EVI_SD, -NDWI_SD, -HPDEN_LN, -CROPLAND, +PROT_AR	316	409	0.92	0.90	0.968	0.806
Mozaic composition of logistic regression models for each eco-region	According to the models for each region	2,509	2,505	0.83	0.88	0.932	-
Final classification: combined kriging interpolation and mosaic composition of logistic regression models	-	2,501	2,304	0.91	0.92	0.969	-

Variables' abbreviations: TEMP – mean annual temperature, PRECIP – annual precipitation, CANOPY – forest cover, HPDEN_LN - human population density, ROAD_DENSITY – index approximating road density, CROPLAND – proportion of croplands in 1 km^2 area, PASTURE – proportion of pastures in 1 km^2 area, PROT_AR – protected areas, INDTER - Indigenous territories, HFOOTP2004 - Human footprint index 2004, NDVI_SD - Standard deviation of normalised difference vegetation index, EVImean – enhanced vegetation index (mean value), EVI_SD - Standard deviation of enhanced vegetation index, NDWImean - Mean annual value of normalised difference water index, NDWI_SD - Standard deviation of normalised difference water index, NPP_SD - Standard deviation of net primary productivity, GPP_SD - Standard deviation of gross primary productivity ECOREG (8 cat) - respective ecoregion number.

sitivity 0.83, specificity 0.88) compared to the general model. It reveals that the most optimal habitats for the jaguar are generally in the great Amazon Basin, up to the Orinoco River in the north, and south to the Pantanal - Gran Chaco region. However, it also identifies the destruction of large portions of jaguar habitat even inside the core of the jaguar's current distribution and a high degree of fragmentation on the edges of its range, especially in eastern Brazil, Argentina, Colombia, and Venezuela (Fig. 3 right). Predictions for 2000 and 2020 (based on different data for four variables: human population density, pastures, croplands, and forest cover; see SOM Table T2) were only slightly different (Fig. 3). A comparison of our model prediction for 2000 with the IUCN estimate of jaguar range in 2000 (Caso et al. 2008) indicates that already by 2000 several areas inside the predicted jaguar range were of low suitability for jaguars (e.g in Brazil, Colombia, and Venezuela, Fig. 3 left). However, our models identified some areas as highly suitable in 2000 that were not included in the IUCN 2000 jaguar estimate, e.g. central parts of Mato Grosso in Brazil (Fig. 3 left). We subtracted both predictions (2020 and 2000) to estimate changes in jaguar occurrence probability across the continent during the last 20 years (Fig. 4). About 9% of the total area inside the 2000 jaguar range has experienced major or minor negative change, about 3% slight positive change, while 87.6% showed no change (Table 2, Fig. 4). The highest proportion of areas with a negative change was in Ecuador (25.8%). At the same time, all other countries, except Suriname, Guyana, and French Guiana, experienced a deterioration of jaguar habitats over some parts (7%–13%) of the jaguar range inside their territories (Table 2). These changes in the jaguar occurrence probability were driven by an increase in human population density, increase in areas of croplands and pastures, decrease in forest cover, or the combined effects of these factors.

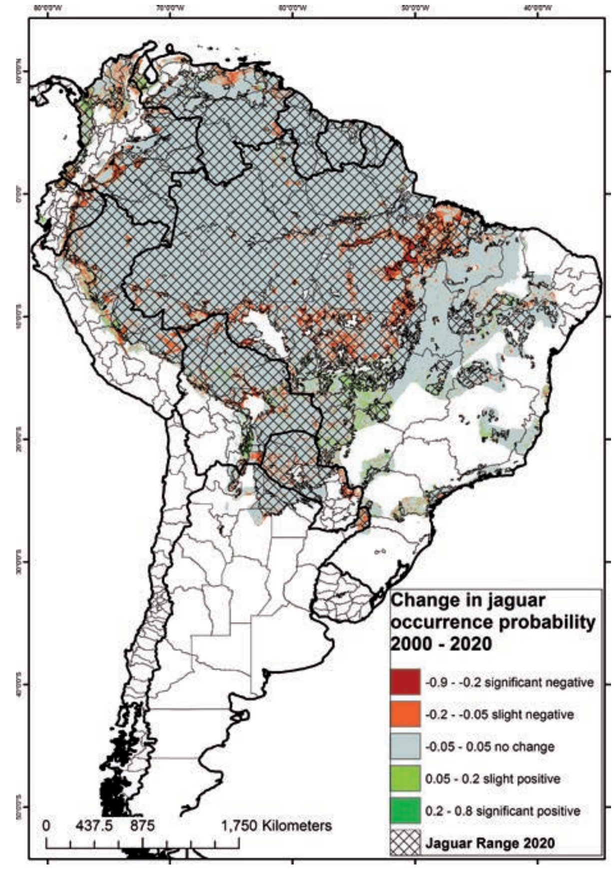

Fig. 4. Changes in the probability of jaguar occurrence during the last 20 years due to human impacts (red - negative change, green - positive change), inside the IUCN 2000 jaguar range (Caso et al. 2008), compared to the current (2020) jaguar range (this work). Probability changes were calculated as difference between predictions of our logistic regression models for 2020 and 2000, based on respective data for four predictive variables: human population density, cropland, pasture, and forest cover.

We combined the results of kriging interpolation with the composed prediction of logistic regression models for eight eco-regions (see Methods) to estimate the current (2020) jaguar status across South America (Fig. 5, SOM Dataset D4). This estimate combines a good fit to the data points (sensitivity 0.91, specificity 0.92, AUC 0.969; Table 1, Fig. 5, right) with the information on habitat suitability. It is in line with the independent estimates obtained by national censuses at the country levels (SOM Fig. F1). Following our reclassification of occurrence probabilities to the jaguar status categories, jaguars are Extinct or Possibly Extinct from 47% of their historic range in South America. They

Table. 2. Percentage of area with changes in jaguar occurrence probability during the last 20 years due to human impacts (approximated by changes in human population density, area of croplands and pastures, and forest cover). The changes are calculated within the IUCN 2000 jaguar range (Caso et al. 2008) extended by the areas detected as occupied by jaguars in the 2020 estimate (compare Figs 4 and 5).

Country	Area of the 2000 Jaguar range (thousands km²)	% of the 2000 jaguar range with a probability change				
		Signif. neg. change (-0.9 – -0.2)	Slight neg. change (-0.2 – -0.05)	No change (-0.05 – 0.05)	Slight pos. change (0.05 – 0.2)	Signif. pos. change (0.2 – 0.8)
Argentina	187	1.1	9.8	87.7	1.2	0.1
Bolivia	766	1.7	8.8	85.1	3.9	0.5
Brazil	6,215	2.0	6.9	88.0	2.9	0.2
Colombia	897	1.5	10.5	83.7	3.9	0.4
Ecuador	117	5.2	20.6	67.6	5.7	0.9
French Guiana	84	0.2	1.8	98.1	0.0	0.0
Guyana	211	0.0	0.3	99.6	0.1	0.0
Paraguay	270	3.4	9.8	86.1	0.6	0.0
Peru	758	1.2	9.2	86.1	2.9	0.6
Suriname	145	0.1	0.8	99.1	0.0	0.0
Venezuela	809	0.5	6.7	90.5	2.1	0.2
Total	**10,459**	**1.7**	**7.6**	**87.6**	**2.9**	**0.2**

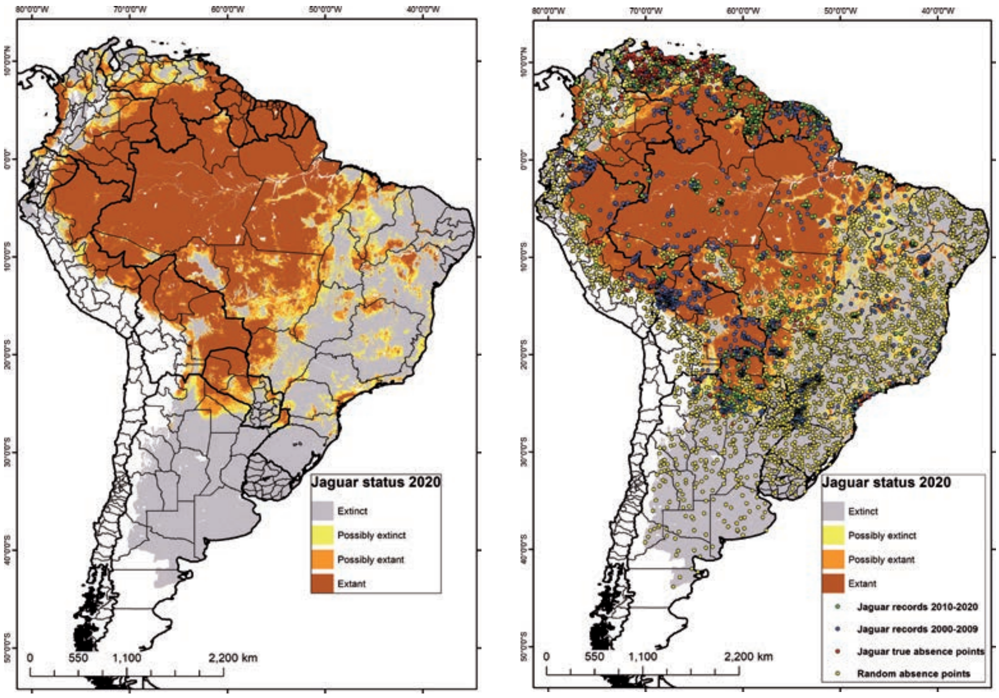

Fig. 5. Left: Current (2020) jaguar status in South America within its historic range based on probabilities of occurrence obtained with two methods combined: kriging interpolation of jaguar presence-absence points and logistic regression models (see Methods). The category Extinct corresponds to the averaged probability values from 0 to to 0.25, Possibly Extinct >0.25–0.49, Possibly Extant >0.49–0.75, and Extant >0.75–1. Right: A comparison of the estimated jaguar status with the distribution of data points.

are Extant or Possibly Extant in 53% of the historic range (Table 3, Fig. 5). We assume that these two latter categories combined represent the current jaguar range, with a total area of about 7.9 million km² (Table 3, Fig. 5). The largest areas still occupied by jaguars are in Brazil (4.5 million km², which constitutes about 57% of all jaguar range), followed by Bolivia, Colombia, Peru, and Venezuela, respectively. Countries with the largest overall areas of extinction are Brazil and Argentina, but those with the highest proportion of the extinction area are Uruguay, Argentina, Ecuador, Brazil, Paraguay, Colombia, and Venezuela. The lowest proportion of the extinction area occurred in the Guiana Shield: in Suriname, French Guiana, and Guyana (Table 3).

A comparison of the results obtained by the combined method (Fig. 5) with the results obtained by only one model, i.e. the kriging-interpolation (records' mapping/ IUCN ap proach; Fig. 2) or the logistic regression (species distribution modelling; Fig. 3), proved that the combined approach gives better results (Table 1). When compared to the national censuses (SOM Fig. F1), the kriging interpolation cut-off some parts and overestimated other parts of the jaguar range in Peru, Bolivia, and Brazil, while logistic regression overestimated the jaguar distribution in parts of Peru and Brazil (compare Figs 2, 3, 5, and SOM Fig. F1).

Our estimate of the current (2020) jaguar range (combined categories "Extant" and "Possibly Extant") is substantially different from IUCN estimates of jaguar ranges for 2000 and 2015 (Table 4, Fig. 6). Our results show that several very large areas classified previously as being inhabited by jaguars are now classified as extinct or possibly extinct (Fig. 6). However, some areas were not included in the earlier estimates, which our models show are occupied by jaguars (Fig. 6). In total, our prediction of the area of current jaguar distribution

Table. 3. Total historic area of jaguar occurrence (after Sanderson et al. 2002) and percentage of area where jaguars are Extinct, Possibly Extinct, Possibly Extant, and Extant for each country of South America, based on the combined methods of kriging interpolation and logistic regression models of jaguar presence– absence (see Methods and Fig. 5).

Country	Total historic range (1000s km²)	% Extinct area	% Possibly Extinct area	% Possibly Extant area	% Extant area	Extinct and Possibly Extinct		Extant and Possibly Extant	
						total area (1000s km²)	%	total area (1000s km²)	%
Argentina	1,870	88.7	4.3	4.7	2.3	1,740	93.0	130	7.0
Bolivia	784	8.3	5.5	12.0	74.2	108	13.8	676	86.2
Brazil	8,337	33.6	12.7	8.8	44.9	3,867	46.3	4,470	53.7
Colombia	1,026	24.5	12.1	11.5	51.9	376	36.6	650	63.4
Ecuador	187	37.5	16.9	12.2	33.4	102	54.5	85	45.5
French Guiana	83	0.0	0.0	0.4	99.6	0	0.0	83	100.0
Guyana	211	0.1	0.3	2.3	97.3	1	0.5	209	99.5
Paraguay	396	26.1	15.5	14.6	43.8	165	41.7	231	58.3
Peru	784	13.6	7.7	8.9	69.8	167	21.3	617	78.7
Suriname	143	0.0	0.0	0.6	99.4	0	0.0	143	100.0
Uruguay	174	100.0	0.0	0.0	0.0	174	100.0	0	0.0
Venezuela	893	17.0	16.6	14.5	51.9	299	33.5	594	66.5
Total	**14,888**	**36.2**	**10.8**	**8.9**	**44.1**	**7,000**	**47.0**	**7,888**	**53.0**

is 14% (1.2 million square kilometres) smaller than the IUCN's 2015 estimate and 25% (2.6 million square kilometres) smaller than the IUCN's 2000 estimate. Compared with the estimates for 2000, the most significant difference in the jaguar range occurred in Brazil, Colombia, Venezuela, and Peru. A remarkable difference between the 2015 and 2020 estimates was documented for Colombia (26%) and somewhat smaller for Peru and Brazil (17% and 14%, respectively, Table 4).

Discussion

Our study shows that combining kriging interpolation and logistic regression models can improve estimates of species distribution at broad scales. The combination of these methodologies and a large dataset of jaguar records have produced the most detailed map of jaguar distribution across South America. This approach to species distribution modelling shows a high degree of compatibility with the assessments conducted at the national level in some South American countries. Compared to the IUCN's 2015 and 2000 assessments (Sanderson et al. 2002, Zeller 2007, Caso et al. 2008, Quigley et al. 2018), our estimate of the jaguar range in South America differs by 14% and 25%, respectively. These differences partly result from methodological dissimilarities and different approaches of the previous studies; however, they also indicate that the jaguar range is decreasing consistently and relatively rapidly. This conclusion was also confirmed by our analysis of changes in jaguar habitat suitability during the same period.

We demonstrated that major and minor negative changes in habitat suitability occurred over several parts of the jaguar's range, including in the Amazon basin. Our models show that the deterioration of jaguar habitats is driven mainly by deforestation combined with the development of agriculture and cattle ranching, an increase in road density, and factors related to increasing human population densities (e.g. hunting, Woodroffe 2000). Similar results, especially the high importance of forest cover for jaguar distribution, have also been indicated by earlier studies (De Angelo et al. 2011, 2013, Olsoy et al. 2016, Paviolo et al. 2016, Jędrzejewski et al. 2017a, 2018, Thompson & Velilla 2017). The negative impact of croplands and pastures in our models confirms that expansion of agriculture and cattle ranching are among the main drivers of jaguar declines. Furthermore, the development of cattle ranching is often related to deforestation and retaliatory killing of jaguars, with the combined effects resulting in rapid extirpation of jaguar populations (Jędrzejewski et al. 2017b, Romero-Muñoz et al. 2019, 2020). In our models, the development of road infrastructure had a particularly strong negative impact on jaguar distribution and areas with high road density in parts of Colombia, Brazil, and Argentina showed the highest rates of fragmentation and jaguar population decline, as also indicated by others (Payán et al. 2016, Rich et al. 2017, Espinosa et al. 2018, Thompson et al. 2020).

Conversely, habitat productivity, approximated by vegetation and water abundance indices derived from satellite images, showed a positive effect on jaguar distribution in the models. Higher primary productivity is linked to increases in prey availability and translates to higher jaguar population density, higher reproductive rate, and resiliency to the impact of human activities (Jędrzejewski et al. 2017a, 2018, Santos et al. 2019). Our models also stress the importance of protected areas and indigenous territories for jaguar conservation, agreeing with earlier studies that showed that these protective measures are

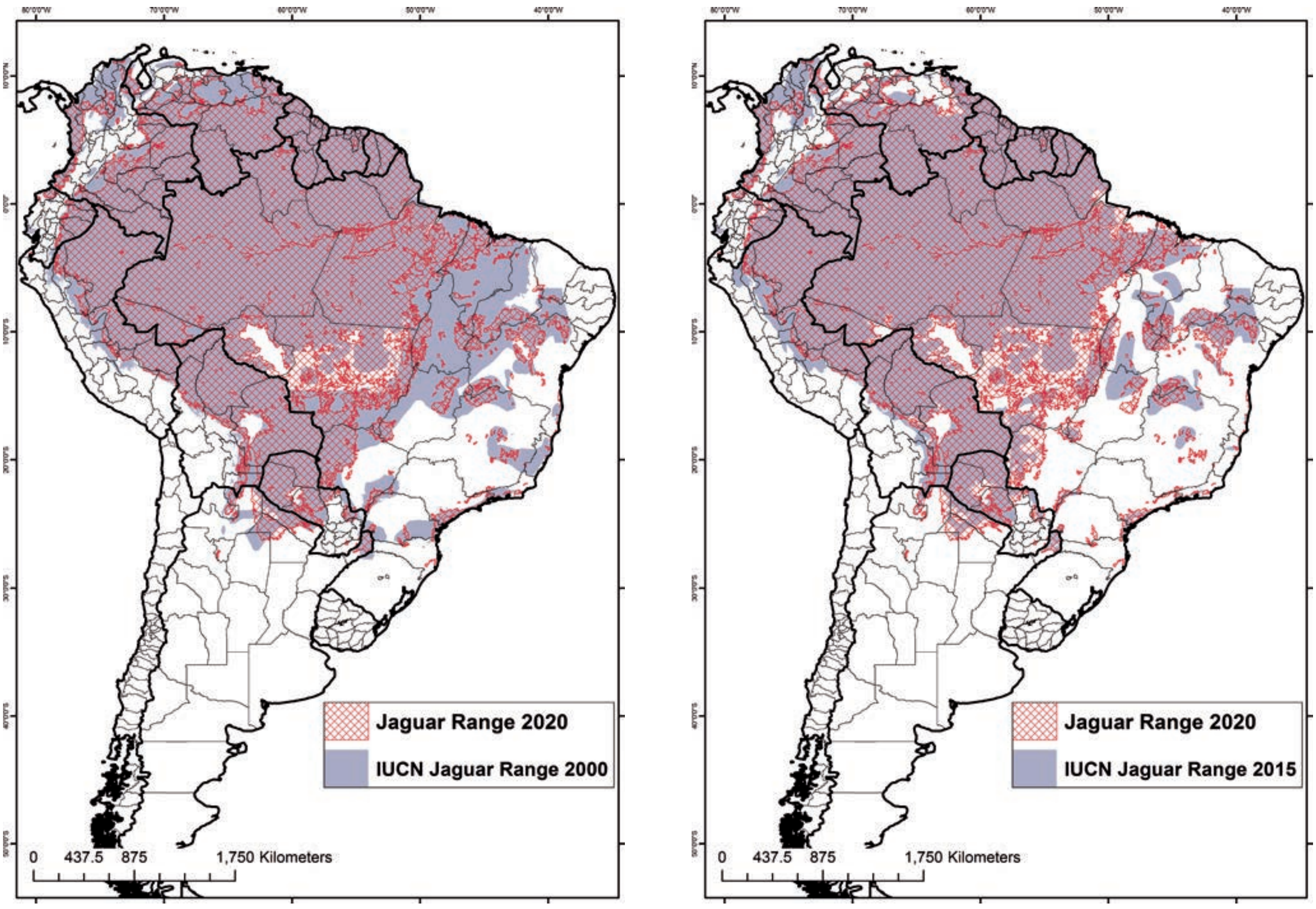

Fig. 6. Comparison of the current jaguar range estimated for 2020 with estimates of jaguar distribution for 2000 (Sanderson et al. 2002, Zeller 2007, Caso et al. 2008, left panel) and 2015 (Quigley et al. 2018, right panel).

Table. 4. Comparison of the area of the current (2020) jaguar range estimate (combined classes "Extant" and "Possibly Extant"; Figs 5, 6) with the jaguar ranges from 2000 and 2015. Jaguar ranges for 2000 and 2015 are based on IUCN Red List assessments (Caso et al. 2008, Quigley et al. 2018) extended by additional areas found to be inhabited by jaguars in 2020.

Country	Jaguar range 2000 (1000s km²)	Jaguar range 2015 (1000s km²)	Jaguar range 2020 (1000s km²)	2020–2000 area difference (1000s km²)	% area change 2020–2000	2015–2020 area difference (1000s km²)	% area change 2020–2015
Argentina	187	134	130	-57	-30	-4	-3
Bolivia	766	755	676	-90	-12	-79	-10
Brazil	6,215	5,192	4,470	-1,745	-28	-722	-14
Colombia	897	882	650	-247	-28	-232	-26
Ecuador	117	93	85	-32	-27	-8	-9
French Guiana	84	83	83	-1	-1	0	0
Guyana	211	210	209	-2	-1	-1	-1
Paraguay	270	260	231	-39	-14	-29	-11
Peru	758	739	617	-141	-19	-122	-17
Suriname	145	145	143	-2	-1	-2	-1
Uruguay	0	0	0	0	0	0	0
Venezuela	809	642	594	-215	-27	-48	-7
Total	**10,459**	**9,135**	**7,888**	**-2,571**	**-25**	**-1,247**	**-14**

critical for jaguar and carnivore conservation in general (Weber & Rabinowitz 1996, Rodrigues et al. 2004). Protected areas have been shown to maintain more stable prey populations (Beaudrot et al. 2016) and host lower rates of deforestation and retaliatory killing of jaguars (Jędrzejewski et al. 2017b) when compared to areas under other land tenures.

Our study also shows that a different set of ecological factors drives the distribution of jaguar populations in each eco-region. This may result from genetically based adaptations to the environmental conditions of each eco-region, as well as from the variation in the effect of ecological forces at broad scales. For example, jaguar populations inhabiting distinct eco-regions of South America are genetically and morphologically different (Hoogesteijn & Mondolfi 1996, Roques et al. 2016, Lorenzana et al. 2020). These genetic differences likely indicate distinct adaptations for hunting different prey species inhabiting unique habitats, and this may lead to variation in responses to vegetation and water indices in the models. Similar genetic divisions corresponding to the distribution of different biomes and prey communities were identified across populations of European wolves, which also showed different responses to ecological factors (by selecting different prey species) in each biome (Pilot et al. 2006, 2012, Jędrzejewski et al. 2012). However, ecological factors may also affect species differently at continental, regional, or local scales, as was the case of temperature in our models. At the continental scale, temperature had a strong positive effect on jaguar occurrence. In contrast, it has a negative effect in the continent's hottest and driest habitats, such as Caatinga and Cerrado (as earlier shown by Morato et al. 2014, Portugal et al. 2019), possibly indicating some optimum temperature range for the jaguar. Similarly, a moderate proportion of pastures in the Caatinga and Andes eco-regions positively affected jaguar occurrence (e.g. by increasing a limited prey base), while pastures in other eco-regions had a strong negative effect.

Through this study, we propose a new approach to estimating species distribution across broad scales, combining the interpolation of presence and absence points with species distribution modelling. This combined method capitalizes on the advantages of both records' mapping and SDM methodologies, and the resulting distribution better fits the actual data points and national estimates than any single model alone. Despite the generally high number of data points we collected, the kriging interpolation technique (records' mapping/IUCN approach) produced a prediction of low certainty for large areas, while logistic regression (SDM approach) overestimated jaguar distribution, indicating jaguar presence outside the actual jaguar range. Comparing our predictions for 2000 and 2020 with the IUCN estimates of jaguar distribution in 2000 and 2015 showed several important differences, which the shrinking of the jaguar range cannot entirely explain. Our analysis suggests that IUCN assessments overestimated the jaguar range in parts of Venezuela, Colombia, and Brazil, as was also suggested by other studies. For example, large areas of Venezuela north of the Orinoco where jaguar extirpations are known to have occurred between 1970 and 2000 (Jędrzejewski et al. 2017a) were still included in the IUCN's 2000 jaguar range estimate. Likely, those shortcomings were related to insufficient data coverage, which is understandable considering that all these assessments are being made across broad scales for a naturally rare, elusive, and wide-ranging species. However, another likely source of incompatibilities between ours and the IUCN's estimates stems from the methodological differences, especially from the wide use of expert opinions in the earlier estimates (Sanderson et al. 2002, Zeller 2007). In our method, we tried to reduce significantly the role of expert opinions, which in our opinion, carries a high risk of incorrect estimates if not supported by field collected data.

Using such a combined approach and not only the IUCN records' mapping (IUCN Red List Technical Working Group 2019) is especially important when data do not cover the entire potential range of a species or when the actual distribution is a mosaic composed of intermixed presence and absence patches, but the availability of absence data is more limited. Apart from the problems of insufficient data coverage, there are also some important logical differences to consider when compared to the IUCN methodology, given that spatial patterns of species presence/absence do not always result from a gradual extinction process. For example, individuals may recolonise some areas or disperse into unsuitable areas, where the species generally does not occur. None of the IUCN categories meets these conditions. For these reasons, we propose that the interpretation and definition of these categories should be broadened from the original IUCN mapping standards to include: (1) Extinct = low-quality habitat/adverse conditions and no jaguar records; (2) Possibly/functionally Extinct = low or medium quality habitat and no or few jaguar records; (3) Possibly Extant (possibly present) = good habitat and few records, or numerous records in a poor/adverse habitat; (4) Extant = good habitat and numerous jaguar records.

The final precision of any estimate of species distribution will depend on the amount and quality of data available. In this work, we combined data (in total 2,257 sparsely distributed records) from 2000–2020 to produce an extensive jaguar database which also covered areas where data was previously unavailable. Although we believe that in most cases, older (early 2000) data still represent the current jaguar distribution, this remains a source of uncertainty in our data because jaguar presence at a local scale can change quickly in the face of intense pressure from human activities driven by policy changes, infrastructure development, and economic downturns (Romero-Muñoz et al. 2020). Therefore, it is critical to ensure that data are collected more regularly across a greater proportion of the jaguar's range, ideally using a standardised methodology to increase the precision of future estimates. Collecting data on the species presence and absence is also equally important. Absence data improve the precision of SDM model predictions and, when combined with information on the timing of extirpations and land use changes, it can be used to estimate local extinction rates and model the extinction process (Jędrzejewski et al. 2017a).

We conclude that conservation policies should consider the main positive and negative drivers of jaguar distribution changes identified by this study. These policies should focus on the increase in the area and number of protected areas, supporting indigenous territories and sustainable alternative livelihoods, stopping deforestation, mitigating man-jaguar conflicts, and mitigating negative effects of roads and other infrastructure development, as well as identifying and protecting ecological corridors. We also propose that an international collaboration focused on continuous and coordinated jaguar monitoring covering extensive areas and using standardised techniques and methodology is crucial for the accuracy of future assessments of jaguar distribution and its trends and should remain a cornerstone of the conservation of jaguar populations.

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Supporting Online Material SOM Text T1, Figures F1–F2, Tables T1–T3 and Datasets D1–D5 are available at www.catsg.org.

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Landscape connectivity analysis and proposition of the main corridor network for the jaguar in South America

Large parts of the formerly continuous jaguar *Panthera onca* range have been lost or fragmented. We performed an analysis with Linkage Mapper to evaluate connectivity between all 92 patches of the 2020 jaguar range in South America. We used two Linkage Mapper tools: (1) the Linkage Paths to calculate the cost-distance values and to select least-cost paths as potential corridors for jaguar movements and (2) the Barrier Mapper to identify barriers along the potential corridors. We derived land-scape resistance values necessary for this analysis from the probabilities of jaguar occurrence estimated with species distribution models. Our analysis indicates that connectivity for jaguars is still good within the central Amazonian and Guiana Shield portions of the jaguar's range. However, outside of this central core, connectivity between the fragmented jaguar populations is generally poor, e.g. in the Andes, Llanos, Atlantic Forest, Caatinga, and Cerrado. Barrier sections cover 21% of the area of potential corridors, and high resistance values were found on 30% of the corridor area. This situation is worsened by high road density around most barrier sections of the potential corridors. The Chocó region of north-western Colombia is likely isolated from the rest of the jaguar range in South America, which means that jaguar populations of Central America have no or minimal connections with the Amazonian populations. Similarly, the connectivity between fragmented jaguar populations in eastern South America (Caatinga, Cerrado, and Atlantic Forest eco-regions) is disrupted at several potential corridors, although some corridors of this region may still retain some potential to facilitate jaguar movement. Only 9% of the area of potential corridors are located within protected areas. Our results can guide planning for jaguar conservation action on a large spatial scale and help focus on sites where such efforts can be most effective and are most needed.

Habitat fragmentation is one of the main drivers of species extinctions on a global scale. Fragmented, small, and isolated populations are vulnerable to demographic and mortality factors and the effects of genetic drift (Sinclair et al. 2006, Crooks et al. 2017). In addition, roads and traffic create additional barriers to animal movement and cause increased animal mortality (Benítez-López et al, 2010, Van Der Ree et al. 2011, Cullen et al. 2016).

Ecological corridors are an important conservation tool that helps mitigate the negative effects of fragmentation on animal populations. These are special areas intended to maintain or restore ecological connectivity, i.e. movement of species and their populations, individuals, and genes (Hilty et al. 2011). The identification of corridors helps in conservation planning, especially in identifying conflicts with existing or planned infrastructure and planning mitigation measures e.g. animal passes (Forman et al. 2003, Glista et al. 2009, González-Gallina 2018), and also helps in directing the efforts of reforestation to restore connectivity (McRae et al. 2012).

The configuration of ecological corridors on the landscape is planned based on a detailed analysis of existing connectivity. Such an analysis usually involves three important steps: (1) determining the core areas, i.e. the areas to be linked; (2) preparation of the resistance map (raster) assessing the potential for movement of individuals through the landscape; and (3) determining the most optimal course of the corridors which ensure the highest probability of animal movements. If the goal is to plan corridors for a threatened species, the selection of core areas should take into account the distribution of all relevant populations of that species, and in particular of those at risk of isolation. Preparing an appropriate resistance raster is a crucial task for proper connectivity analysis. Landscape resistance values can be derived from habitat suitability or species distribution models based on data such as species individual records or movements recorded by GPS telemetry (ref. Keeley et al. 2016, Carroll et al. 2020). It is also essential to consider area protection status in planning ecological corridors. Efforts should be made to ensure that the largest possible part of the corridors is covered by legal area protection or included in spatial management plans (Hilty et al. 2011, Belote et al.2016).

Fragmentation of jaguar populations across Central and South America has been increasing recently (Martinez Pardo et al. 2022, Jędrzejewski et al. 2017, 2018, 2023a), mainly driven by deforestation and habitat alteration aimed at increasing areas of cattle production, agricultural plantations, and human settlements (Petracca et al. 2014, Olsoy et al. 2016, Menezes et al. 2021). The development of infrastructure, especially road networks, also leads to fragmentation and a corresponding decline in the number of jaguars (Colchero et al. 2011, Espinosa et al. 2018). Understanding the importance of maintaining ecological connectivity for the persistence of jaguar populations has spawned several initiatives to plan ecological corridors in different parts of the jaguar's range (e.g. Morato et al. 2014, Silveira et al. 2014, Stoner et al. 2015, Martinez Pardo et al. 2017, Thompson and Velilla 2017). Rabinowitz and Zeller (2010) analysed connectivity and proposed the first range-wide network of ecological corridors to connect all jaguar conservation units.

In this paper, we present an analysis of the ecological connectivity for jaguars across South America as a follow-up to the updated analysis of jaguar distribution carried out as a

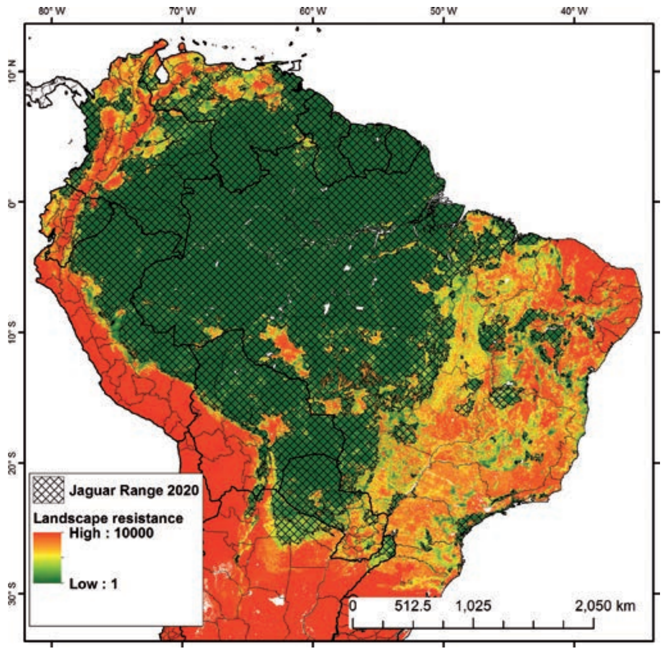

Fig. 1. Jaguar range 2020 in South America shown against the values of landscape resistance for jaguar movements. Jaguar range 2020 (SOM Dataset D1) consists of 92 separate polygons used as core areas in the connectivity analysis. Landscape resistance values (SOM Dataset D2) were calculated as the inverse of the probabilities of jaguar occurrence estimated with species distribution models (Jędrzejewski et al. 2023, see Methods) and they synthesise an impact of several factors important for jaguar populations, such as climate, environmental productivity, water abundance, forest cover, human population density, the share of pastures and agricultural crops, and road density.

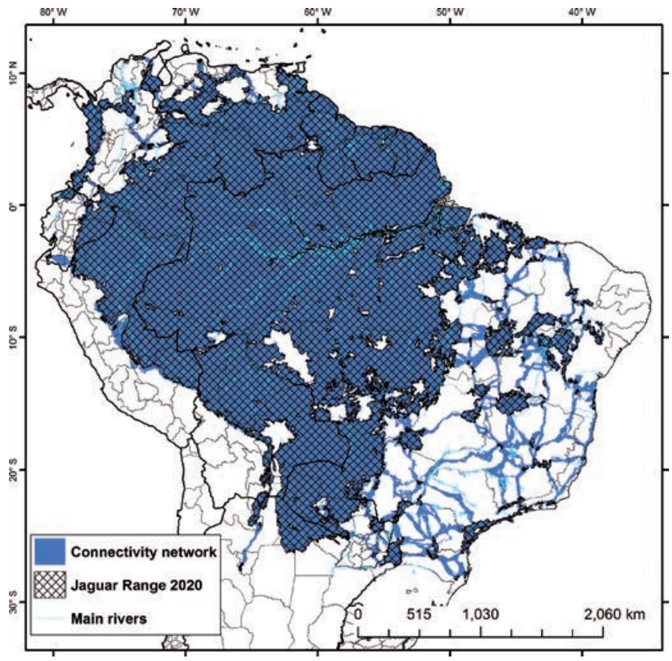

Fig. 2. Jaguar connectivity network selected with the Linkage Mapper as the areas with the lowest cost distance values (see Methods). This network includes: (1) the 92 pathes of the current (2020) jaguar range (SOM Dataset D1); and (2) the principal ecological corridors (SOM Dataset D3), connecting patches of the jaguar range. Banks of rivers and water reservoirs may provide additional linkages between fragmented jaguar populations, as indicated on this map. Numeration of the corridors is provided in the attribute table of the shape file in SOM Dataset D3. The network of the principal jaguar corridors proposed here can be farther developed at the regional or local levels.

part of the IUCN jaguar conservation strategy (Berzins et al. 2023, Jędrzejewski et al. 2023 a,b, Thompson et al. 2023). The main objectives of this analysis were: (1) to assess the overall degree of connectivity between jaguar populations in South America; (2) to determine which populations are most isolated; (3) to propose a network of ecological corridors for jaguars; (4) identify the most important barriers within this network; and (5) to estimate the role of existing protected areas and indigenous territories in maintaining connectivity throughout the jaguar range.

Methods

We estimated connectivity for jaguar populations in South America using two tools in Linkage Mapper v.3.0: Linkage Pathways and Barrier Mapper (McRae and Kavanagh 2011, McRae 2012, McRae et al. 2012). Linkage Pathways identifies least-cost linkages between core areas based on landscape resistance values and calculates the cost-weighted distance values. Barrier Mapper identifies critical barriers within the least-cost corridors.

As core areas, we used all 92 separate polygons representing the updated jaguar range in 2020 (Jędrzejewski et al. 2023a, Supplementary Online Material SOM Dataset D1). The landscape resistance values (SOM Dataset D2) were calculated as the inverse (subtracting from 1 and multiplying by 100) to the probability of jaguar occurrence estimated with the models presented in Jędrzejewski et al. 2023a. These models included several predictive variables reflecting the effect of natural and anthropogenic factors, such as precipitation, mean temperature, habitat productivity indices, water abundance, forest cover, human population density, the proportion of pastures and agriculture in the landscape, and road density. Models were run separately for each of the eight main ecoregions of South America to account for recently discovered genetic differences between jaguar populations (Roques et al. 2016, Lorenzana et al. 2020) and potential variation in responses to habitat features unique to each ecoregion. To increase the effect of barriers on the cost-distance values in the analysis in Linkage Mapper, we squared resistance values (McRae 2012a, Keeley et al. 2016) which resulted in the final cell values from 1 to 10,000.

We trimmed the mosaic normalised cost-distance ("corridor") map generated by Linkage Pathways to the values equal to or less than 50,000,000, and we presented the result as a map of potential connectivity network that included all patches of the jaguar range and connecting corridors. We supplemented this map with the network of main rivers (https://www.esri.com/arcgis-blog/products/product/mapping/esri-data-maps/) to indicate that water courses are important for jaguar movements and may provide additional movement opportunities (Silveira et al. 2014, Castilho et al. 2015, Azevedo et al. 2021, Eriksson et al. 2022). Corridors connecting individual fragments of the jaguar range were identified, separated from the entire connectivity network, and transformed into polygons, treating them as a network of principal ecological corridors (SOM Dataset D3).

To assess the quality (permeability) of corridors indicated by Linkage Pathways, we ran the Barrier Mapper and plotted the resulting barrier values along the corridors (SOM

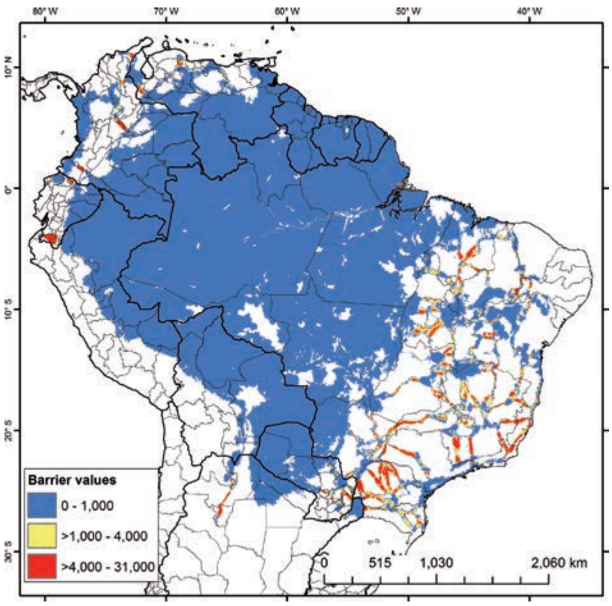

Fig. 3. Barriers for jaguar movements within the connectivity network, as indicated by the analysis with the Barrier Mapper tool in the Linkage Mapper (SOM Dataset 4).

Dataset D4). To the final map, we also added main and secondary roads (Meijer et al. 2018, https://www.globio.info/download-grip-dataset) to indicate which potential corridors between jaguar populations are most threatened by existing high-density infrastructure. To obtain another indicator of the quality of potential corridors, we transferred the values from the resistance raster to each corridor and presented the results on a separate map. To estimate the proportion of the connectivity network that is under legal protection, we laid maps of protected areas and indigenous territories over the obtained connectivity network and calculated the percentage of the overlapping area (http://www.protectedplanet.net, Amazonia Socioambiental RAISG 2019; https://www.amazoniasocioambiental.org/es/mapas/#!/areas).

Results

In general, the overlay of the 2020 jaguar range and the resistance map indicated that connectivity for jaguars is still good within the core of its range (central Amazonia & the Guiana Shield), while outside, it is relatively poor (Fig. 1, SOM Datasets D1 & D2). Also, the normalised cost-distance values calculated with Linkage Mapper within all persisting patches of jaguar distribution were low, indicating remaining good connectivity within the areas inhabited by jaguars.

Linkage Mapper selected the best possible connections (least-cost paths with the lowest cost-distance values) between and within the 92 patches of the jaguar range, producing a potential connectivity network. This network is complemented by the main rivers (Fig. 2). However, the analysis performed with Barrier Mapper revealed that outside the core jaguar's range, connectivity was disrupted along the least cost paths (principal corridors) at many points. In addition, most of the corridors had some sections with high barrier values (Fig. 3). Overall, 45% of the area of corridors indicated by Linkage Mapper had low barrier values (high permeability), 34% medium values, and 21% high barrier values (Fig. 3). The superimposition of the values obtained from the resistance raster in the corridor network showed, in general, a similar situation along the corridors outside the patches of jaguar range (Fig. 4), with 26% of the corridor area with low resistance values (high permeability), 43% medium, and 30% high values (low permeability). In contrast, within the jaguar's range patches, the connectivity was generally high, with 95% of the area with low resistance values, 4% medium, and 1% high values (Fig. 4).

Connectivity between jaguar range patches was further worsened by the high density of roads, especially in trans-Andean corridors (e.g. in Colombia) as well as in the Atlantic Forest and Cerrado (eastern Brazil, Fig. 5). Some areas within the core of the jaguar range also had high road density, e.g. in Mato Grosso in Brazil and in Paraguay (Fig. 5).

Frequent barrier sections along the potential corridors and high road density cut off several fragments of the jaguar range from the main central core. Among them was the Choco region in western Colombia and Ecuador and various patches of the jaguar range in eastern Brazil, Argentina, and Venezuela.

Protected areas and indigenous territories covered 49% (29% and 20%, respectively) of the total area inside the jaguar range patches (Fig. 6). However, only 9% of the area of the least-cost paths (principal corridors) was covered by protected areas or indigenous territories (8% and 1% respectively, Fig. 6).

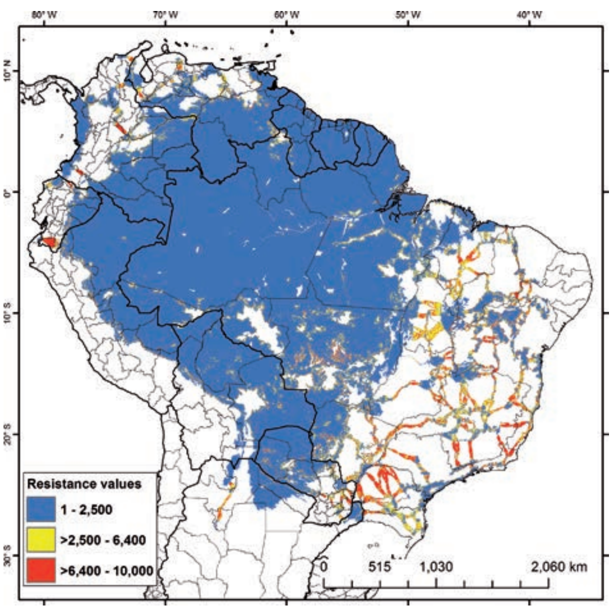

Fig. 4. Permeability within the jaguar connectivity network indicated by the direct superimposition of the resistance values (as in Fig. 1). Lower resistance values indicate higher permeability for jaguar movements.

Discussion

In this paper, we show the current connectivity status within and between jaguar populations in South America and propose a network of potential principal ecological corridors that may facilitate continued jaguar movement between existing patches. Our analyses demonstrate that the central core of the jaguar's range, located mainly in the Amazon basin and Guiana Shield, retains good connectivity. In contrast, the connectivity between the fragmented parts of the former jaguar range has largely been lost due to habitat transformations and transportation infrastructure development. Furthermore, most of the ecological corridors selected by Linkage Mapper as the best options (least-cost paths) are interrupted by frequent barriers that prevent or hinder jaguar movements and may lead to the isolation of some jaguar populations.

Our results indicate that among those likely to become isolated from the central core is the jaguar population of the Choco region in Colombia and Ecuador, which is an extension of jaguar populations in Central America. This means there is likely no longer any or very limited gene flow between the jaguar populations in the Amazon and Central America. Similarly, jaguar movement and genetic exchange may currently be disrupted in the east of the continent, within the Caatinga, Cerrado, and Atlantic Forest ecoregions. However, not all of the corridors identified by our analysis are of equally poor quality. Some corridors have relatively few barriers along their course, which may still offer favourable conditions for jaguar movement. Narrow bands of gallery and riverine forests, river valleys, and the banks of other bodies of water may offer additional linkages between fragmented populations (Silveira et al. 2014, Castilho et al. 2015), and it would be advisable to conduct a more detailed analysis of their potential to serve as additional corridors. Several local or regional connectivity analyses for various parts of the jaguar range have already been performed, e.g. for Argentina, Paraguay, Bolivia, and Brazil (Morato et al. 2014, Silveira et al. 2014, Castilho et al. 2015, Paviolo et al. 2016, Portugal et al 2019, Thompson & Velilla 2017, Diniz et al. 2018, Wallace et al. 2020), and their results can be combined or compared with ours for a better understanding of jaguar connectivity.

In our analysis, the landscape resistance values were derived from jaguar distribution models based on a large set of presence and absence points across South America and a broad set of predictive variables that included environmental and anthropogenic factors known to affect jaguars (Jędrzejewski et al. 2023a). Moreover, these models were conducted separately for eight main ecoregions of South America to account for the genetic differences between jaguar populations (Roques et al. 2016, Lorenzana et al. 2020) and possible adaptations to the unique ecological factors of each ecoregion. We believe this approach also increases the probability of correctly estimating the resistance values, resulting in improved connectivity assessment.

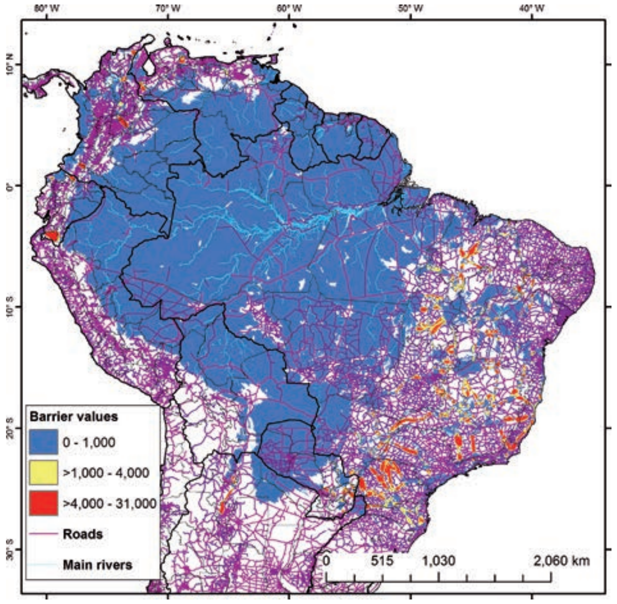

Fig. 5. South America's major and minor road network as an additional factor in the fragmentation of the jaguar population in addition to the barriers within the connectivity network identified by the Barrier Mapper analysis.

The loss and fragmentation of jaguar habitats are increasing (Menezes et al. 2021, Martinez et al. 2022), causing declines in jaguar population size and genetic diversity (Haag et al. 2010, Srbek-Araujo et al. 2018). Therefore, it is important to support conservation and management efforts that halt further fragmentation of jaguar habitat and increase connectivity between habitat areas that have already been fragmented. In addition, restoration of some habitat patches within corridors (e.g. reforestation) could reduce barriers and increase the permeability of some corridors (McRae et al. 2012, Banks-Leite et al. 2020, Hilty et al. 2020). This recommendation coincides with the Decade on Ecosystem Restoration proclaimed by UN Environmental Program to promote Global Ecosystem Restoration (UNEP 2021).

Additionally, nominating important corridor fragments for legal protection is important (Hilty et al. 2020), as only 9% of the corridor areas are currently legally protected. Another critical action is the construction of animal passes wherever conflict between potential jaguar movements and existing or planned highways or other heavy traffic roads exist, both inside the jaguar inhabited areas or between them (Forman et al. 2003, Glista et al. 2009, Jędrzejewski et al. 2009, Matthews et al. 2015, González-Gallina et al. 2018). The results of our work can guide the planning of any of these conservation actions at a large scale and help focus on sites where such actions can be most effective and are most needed.

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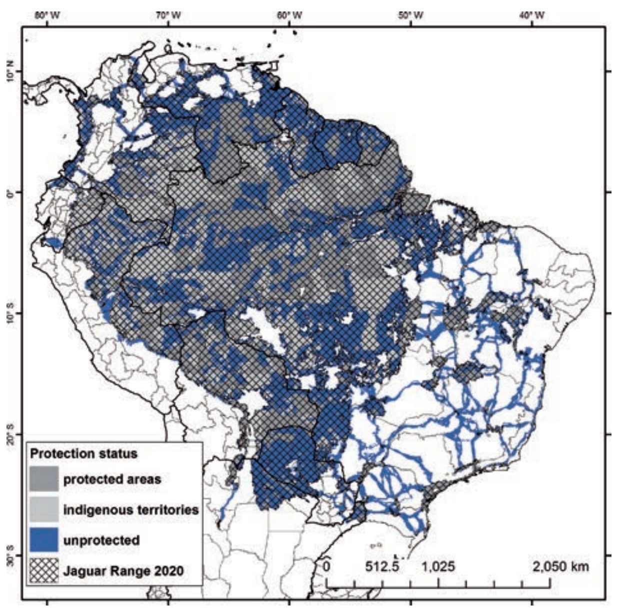

Fig. 6. Role of protected areas and indigenous territories in the protection status of the jaguar connectivity network.

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We dedicate this work to colleagues - scientists from Ukraine who had to abandon their research in order to fight for freedom and all human values that lie at the basis of noble scientific work.

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Legal status, utilisation, management and conservation of the jaguar in South America

The jaguar *Panthera onca* is widely distributed throughout South America with its stronghold in the Amazon. It is protected by law in all countries, but some countries have legal loopholes and all lack a strict enforcement of the laws in place. Jaguar killing is common, even in strictly protected areas, but detailed records are lacking. Jaguars have been historically hunted for their pelts, however, inclusion of the species in the CITES Appendix I proved effective to curtail the spotted cat trade in the 1960s and 70s. Over the last few decades, there exists little information on jaguar hunting for trade, but recently reports have surfaced showing increased illegal trafficking of body parts with evidence of domestic and Asiatic demand. Conservation of jaguars in South America has been relatively well-informed by research data. National parks and indigenous lands have been and still are the cornerstones for jaguar conservation throughout the continent, but are hampered, with a few exceptions, by underfunding, understaffing and a lack of governance and political will. Financing the operation of national parks and protected areas, while securing rights of indigenous lands should be a priority for funding agencies, especially in areas where most jaguar populations are restricted to protected areas like Argentina and south-eastern Brazil. In countries where jaguars are still widespread efforts should also be directed toward unprotected areas where threats like habitat loss and killing are higher. There the biggest management challenge is upscaling conflict prevention and mitigation measures. The Jaguar 2030 Roadmap marks a milestone for the species, aiming to join range governments, NGOs and private partners to advance conservation action for jaguars, but getting the initiative off the ground is the current challenge. It is noteworthy to highlight the importance and need for transboundary cooperation and action, especially among the trans-frontier population hotspots. The new, or emerging threats like jaguar part smuggling and man-made fires need extra attention and action to be curtailed. If jaguar conservation is to be effective despite increasing threats, it needs to be streamlined from high level agreements through scalable effects on the ground, combining protected areas, corridors, and local people buy-in.

The jaguar, the largest felid in the Americas, has been a cultural icon, ever-present in the imagery of lowland forest pre-Hispanic ethnic groups (Saunders 1998, Payán & Gomez Garcia-Reyes 2017). Jaguars have lost more than 50% of their historical distribution and continue to decline due to habitat loss, direct killing, and decline of prey (Rabinowitz & Zeller 2010, Quigley et al. 2017). In South America, the species' range covers 7.9 million km^2, extending from Colombia to northern Argentina, with its stronghold in the Amazon basin, which makes up over half of the total jaguar distribution. The total jaguar population in South America is estimated at approximately 148,000 individuals (95% CI: 113,000–183,000), with 56% of the population living in Brazil (Jędrzejewski et al. 2018, Jędrzejewski et al. 2023a, this Special Issue). Despite some countries having national jaguar action or management plans, few implement them; and conservation is largely carried out by researchers, conservationists and NGOs. This manuscript aims to provide an overview of jaguar legal status, trade, and large-scale conservation initiatives and management in South America. Information was collated through a survey distributed to in-country experts (co-authors), first-hand knowledge, reference searches and personal communication with experts in each South American range country.

Legal status

Jaguars are considered Near Threatened globally with a decreasing trend, by the IUCN Red List (Quigley et al 2018) largely due to their wide distribution and large population size in the Amazon. However, this does not necessarily reflect the situation in individual range countries, many of which list the jaguar in a higher threat category. Jaguars are listed as Critically Endangered in Paraguay (Giordano et al. 2017), Argentina (Paviolo et al. 2019), western Ecuador (Espinosa et al. 2011a), Caatinga and the Atlantic Forest of Brazil (Morato et al. 2018), Endangered in the Brazilian Cerrado (Morato et al. 2018) and Ecuadorian Amazon (Espinosa et al. 2011b), Vulnerable in the Brazilian Amazon and Pantanal and Brazil overall (Morato et al. 2018), Colombia (Rodríguez-Mahecha et al. 2006), Bolivia (Ayala & Wallace 2009) and Venezuela (Jędrzejewski et al 2015) and Near Threatened in eastern Colombia (Rodríguez-Mahecha et al. 2006) and Peru (SERFOR 2018). They have not been categorised in Suriname, Guyana, or French Guyana, and have been extinct in Uruguay since 1901. Some Red List assessments are old and consider different threat categories per subspecies, but jaguars are not clearly differentiated genetically or morphologically into subspecies (Eizirik et al. 2001, Ruiz-Garcia et al. 2006, Ruiz-García & Payán 2013).

Jaguars have been under strict protection from any type of international trade since their inclusion in CITES Appendix I in 1975. After the first hunting law prohibited hunting of all wild species in Brazil (Código de Caça - Lei 5197/67, 3/1/1967), Colombia followed, prohibiting hunting of all carnivores (Resolution 848 from August 6, 1973), and, over the last 40 years, most (Berzins et al. 2023) remaining South American countries also made it illegal to kill jaguars. However, there are some exceptions. Peru's legislation leaves potential loopholes, stating that firearms can be used to avoid attacks from wildlife and preserve human safety, pending notification of the government within 48 hours.

Despite the existence of legal frameworks in each country to protect jaguars and other wildlife, enforcement is weak, jaguar killing remains frequent due to conflict with livestock, fear, and an increasing demand for their body parts (see next section) and very few people have been prosecuted under these laws. Robust or standardised estimates of jaguar killing in South American countries are rare. Much of the killings go unregistered and unsentenced in almost all countries, but the number of dead jaguars and lack of enforcement is highest in Bolivia, Brazil, Venezuela, Panama, and Suriname (Arias 2021).

Several studies confirm that hunting is widespread even within protected areas PAs. In Brazilian PAs, the legal protection status is no guarantee for actual protection of jaguars (Ramalho 2012, de Carvalho & Morato 2013) and the same is the case in all of Venezuela (Jędrzejewski et al. 2017). Between 1995 and 2002 at least 70 jaguars were killed in areas around Iguaçu´ National Park NP (Crawshaw 2002), and from 1998-2008 at least 47 were killed in Northern Misiones, Argentina (Paviolo et al. 2008). In Paraguay, half of the 35 jaguars collared between 2002 and 2014 by McBride & Thompson (2018) were found dead (J. Thompson, pers. comm.), which is extremely concerning. These numbers are showing that some areas of trans-frontier landscapes in the "Corredor Verde" of Argentina and Brazil, and the Chaco region may be acting as sinks for jaguars (De Angelo et al. 2013, Romero-Muñoz et al. 2019).

Fig. 1. Jaguars in a burnt area in the Pantanal (Photo: M. Amend/WCS).

Trade and utilisation

Historically jaguars have been hunted for their pelts, with an estimated 182,564 jaguars killed between 1904 and 1969 in the central and western Amazon of Brazil alone (Antunes et al. 2016). Between 1946 and 1966, 12,704 jaguar skins were exported from Iquitos, Peru (Grimwood 1968). The ratification of the Convention on the International Trade in Endangered Species CITES in 1975 and the inclusion of all spotted cats in Appendix I, which prohibits any trade, proved effective to curtail the international fur trade (Payán & Trujillo 2006). Over the last two decades, trends have become uncertain. Morcatty and colleagues (2020) reported a significant increase in jaguar parts trafficked across both Central and South America between 2012 and 2018 using data on seizures from online news articles, technical reports, and police reports. However, a review of the UNODC's World WISE Database, which includes data from multiple official sources, showed that jaguar seizures were low in numbers and relatively stable between 2000 to 2018 (Arias 2021). Since seizures are a very incomplete measure of the actual extent of trade being conducted, the true extent of jaguar trafficking across the region remains unknown. Currently there is no consistent system in place across all the jaguar range countries to record, report and share information about trafficking. *Sensu* the CITES report, the most trafficked jaguar items are teeth, live animals, skins, and undefined products. Claws, tails, paws, and jaguar fat are also traded and used domestically (Arias 2021). Parts are used for ornamental, cultural, and medicinal purposes, and as a symbol of status. Verified evidence of international trade and links to China are limited, with clear indications of trade to China only from Bolivia and Suriname (Arias 2021, Polisar et al. 2023).

The drivers of jaguar parts trade are complex and multiple including domestic markets, traditional and cultural uses, illegal pet trade, poverty, economic incentives, human-jaguar conflict, demand from tourists, in-country Chinese private investment and Asian demand (Braczkowski et al. 2019, Morcatty et al. 2020, Arias et al 2021). Opportunistic poaching associated with domestic uses and markets, livelihoods, and conflict seem to account for the majority of killed and traded jaguars (Arias 2021). Furthermore, weak law enforcement is widespread. Institutions and authorities engaged in countering wildlife trafficking are understaffed and poorly trained and equipped while high personal turnover hinders retention of capacity and institutional memory. The countries most affected by trafficking of jaguar parts are Bolivia, Peru, Suriname and Belize (Arias 2021). In Bolivia, since 2014 a total of 900 fangs, and several skins, skulls and other jaguar parts have been seized, mostly en route to being smuggled to China (E. Aliaga, pers. comm. to N. Negrões, Villalva & Moracho 2019). Specimens detected likely represent a small fraction of the traffic, suggesting that overall numbers of jaguar killed are significant. Verheij (2019) reports that between 2009 and January 2018 seized specimens and parts correspond to that of at least 324 jaguars. In addition to links to China, jaguar trade in Bolivia is domestic and diffused. In the north of Bolivia 42% of participants possessed jaguar parts and 23% were commercially involved in the trade (Arias et al 2021). Evidence of the existence of organised groups supposedly involved in the trade (IUCN NL 2020) still needs to be further verified and corroborated.

In Suriname, sources report that over 80 jaguars were killed in 2017 and their parts trafficked (Verheij 2019). The country has registered jaguar paste seizures where jaguars are boiled into a mass then moved and sold in Chinese establishments and sent to China via the Netherlands (Verheij 2019). The use of this paste is a mystery, but is assumed to be medicinal, and might be reformed to be used as chao, see Nuwer (2018). There is unverified and informal information of jaguar parts traffic also extending to Ecuador, Paraguay and the border of Brazil with Bolivia. Peru has seized 38 jaguar fangs from 2000-2016 in Lima airport, as well as 18 skins, 11 skulls and 14 live jaguars in that same period (WCS 2018). There are no studies on the use of jaguar parts in Ecuador. In the last five years, there is suspicion that Chinese residents in Ecuador are increasing the demand on jaguar parts. However, there are no recent numbers on jaguar parts confiscated by national authorities; in 2014, jaguar parts were confiscated on five occasions by national authorities (S. Espinosa, pers. obs.).

When jaguars are killed incidentally, it is common that the skin and skull are removed. In many cases, the canines are extracted from the skulls (although some hunters like to keep an entire clean skull as a souvenir). These parts may be sold in local markets, with teeth and skins and decorative artifacts that include them being the most common items in many venues. If it is a mother, the cubs may be sold locally or to tourists, and sometimes voluntarily turned over to local authorities when they grow older, become dangerous and require more meat for food (Swank & Teer 1989, Payán & Trujillo 2006, Jędrzejewski et al. 2017). Jaguars killed due to conflicts with livestock may also end up in the illegal trade. The potential of income from selling body parts may create a perverse incentive for lethal control of conflicts, limiting uptake of the many non-lethal techniques that are now available. A question in need of further research, and potentially actions, is whether jaguar-killing associated with predation on livestock is feeding the illegal supply on body parts. More research is also needed to better characterise and quantify the extent of domestic demand and uses.

Management

Management of wild jaguar populations has been weak in South America and initiatives have seen pulses of implementation without a continuous systematic application and thus, results. Most management has been reactive to multiple causes of hunting and poaching. The most evident and widespread management has been indirect, consisting of improved livestock husbandry to prevent attacks on livestock and domestic animals (Castaño-Uribe et al. 2016, Hoogesteijn & Hoogesteijn 2010, Hoogesteijn & Chapman 1997, Jędrzejewski et al. 2017, Quigley et al. 2015). It merits mentioning that techniques have now been developed that span the spectrum of livestock operations from small farms embedded in forests (pigs and cows), to much larger commercial operations and across nearly all biomes where the species occurs (Valderrama-Vasquez et al. 2024). There has been enough characterisation of attacks on cattle, and currently the need is to further the understanding of efficacy of the solutions across the spectrum of operations and settings (Hoogesteijn & Hoogesteijn 2011, Hoogesteijn & Hoogesteijn 2013, Quigley et al. 2015, Villalba et al. 2016, Valderrama Vásquez et al. 2017).

In the mid-1970s Venezuela implemented a country-wide conflict management strategy that permitted hunting verified cattle-killers with a previous authorisation from the Ministry of Agriculture, however, the strategy was abandoned in 1976 due in part to abuses of the system (Hoogesteijn et al. 2002). In 1991 managers at a wild cat conference proposed to study jaguar sport hunting as an alternative to conflict and financial reparation to ranchers, and in 1996 Profauna – the Ministry of Environment at the time – officially proposed this mechanism to CITES. This proposal never prospered due to vigorous opposition from the public, NGOs and some voices inside Profauna (FUDECI 1991, Hoogesteijn et al. 2002). Between 1994 and 1998 the Ministry of Environment together with Safari Club arranged a translocation programme that moved 11 individuals in Venezuela. Hunters paid $6,000 USD to shoot the anesthetising dart and proceeds went to the affected rancher and Profauna (Hoogesteijn et al. 2002). There is currently some pressure from special interest groups to legalise sport and control hunting in Paraguay.

Translocations of jaguars have had mixed results (Miquelle et al. 2016, Rabinowitz 1986) and reintroductions of individuals have nearly all failed. Frequently reintroductions result in individuals killed by other jaguars or starved to death, there are few exceptions of successful examples (see following paragraph). In most cases the translocation or reintroduction aimed to solve cattle depredation problems, moving animals that were already accustomed to preying on livestock or to human presence. However, more recently, the adaptation and refinement of a soft-release protocol led to the successful reintroduction of two captive-reared jaguar cubs in the Pantanal (Gasparini-Morato et al. 2021).

Probably the most pro-active management strategies for jaguars are the current reintroductions to the Iberá wetlands of Argentina, and Onçafari's reintroductions and habituation interventions in the southern Pantanal. Six jaguars have already been reintroduced, together with a suite of other species previously extinct since 1950 (De Angelo 2011). Prior to their return, habitat conditions in a vast area were significantly improved through the removal of livestock, the increase of protection by the creation of a NP, and the reintroduction of several previously extinct prey species including the giant anteater *Myrmecophaga tridactyla*, the pampas deer O*zotoceros bezoarticus*, and the collared peccary *Pecari tajacu* (Zamboni et al 2017). The area also has large populations of wild capybaras *Hydrochoerus hydrochaeris* and Paraguayan caiman *Caiman yacare* offering a very good habitat for jaguars. The Iberá Rewilding Program has been designed and developed with the support of several researchers and is being adopted by government authorities, private conservationists and the general public as a true pilot for well-justified rewilding. In 2011 Onçafari began a project where two female jaguar cubs were introduced complementing the existing wild jaguar population in Caiman ranch in Pantanal, two females in Thaimaçu Lodge in the amazon and one adult male was sent to Iberá for programmed reintroduction at the end of 2021 (M. Haberfeld, pers. comm.). Reintroductions, followed with GPS-collars, have been completely successful, and the two females from Caiman Ranch have had their first litters. Sixty-eight jaguars have been habituated to human tourism observation from vehicles out of 187 identified individuals in this 530 km^2 ranch. Caiman ranch runs cattle raising operation (20,000 head) and two luxury hotels with a zero-hunting policy, applied antipredator measures and constant jaguar population dynamics monitoring in this (Hoogesteijn et al. 2015).

There is a long history studying jaguar behaviour, with implications for management and conservation, by collaring and monitoring individuals. This line of research was initiated by George Schaller and continued by the late Howard Quigley and the late Peter Crawshaw at the end of the 1970s (Crawshaw & Quigley 1991, Hoogesteijn & Mondolfi 1992, Schaller & Crawshaw 1980) and expanded upon by succeeding researchers and managers (Polisar et al 2003, Scognamillo et al 2003, de Azevedo & Murray 2007, Cavalcanti & Gese 2010). Today, approximately 120 jaguars have been collared and studied for general ecology (Harmsen et al. 2010, Paviolo et al. 2018), home range and behaviour (Scognamillo et al. 2003, Soisalo & Cavalcanti 2006, Morato et al. 2016, McBride & Thompson 2019, Thompson et al. 2021a). The information accumulated during the last decades, now with a strong component from camera trapping (Wallace et al. 2003, Maffei et al. 2004, Soisalo & Cavalcanti 2006, Tobler et al. 2013, Boron et al. 2016), is allowing greater understanding of individuals (Jędrzejewski et al. 2022, Stasiukynas et al. 2022) and populations (Morato et al. 2016, Thompson et al. 2021a), but little active management has ensued, at least further than published management (Quigley & Crawshaw 1992, Sanderson et al. 2002, Rabinowitz & Zeller 2010).

Several complementary management measures such as stocking and collecting DNA and disease research have been done. Jaguar gamete and somatic cells behave well when cryopreserved and science for conservation via assisted reproductive strategies is promis-

Fig. 2. Jaguar in a burnt area in the Pantanal (Photo: M. Amend/WCS).

ing, with some experiences in Brazil, Argentina and some international genome banks (Morato et al. 2001, Amstislavsky et al. 2017, de Araujo et al. 2017, Praxedes et al. 2019, Silva et al. 2020). However, it is necessary to continue working on the development of assisted reproduction techniques that can help us to increase the viability of captive and wild populations, and to start planning and managing gamete and gene banks on a regional basis to ensure the conservation of the most threatened subpopulations.

Concern for zoonotic disease transmission and bridging has received some research but is acknowledged without much management. Parasitoid zoonosis, identified through jaguar faeces, have been identified in deforestation and agricultural frontiers where jaguars can act as definitive or intermediate hosts in the jaguar-livestock-human transmission chain, highlighting the need for zoonotic management practices in conservation strategies and wild felid health management programmes (Uribe et al. 2021). This can also be seen jaguars being useful sentinels to alert people about the potential risk of exposure among human populations to parasitic tapeworms, cestodes, acantocephalans and nematodes through contact with untreated water, faeces and uncooked meat in jaguar territories. Recently, model predictions for SARS-CoV-2 spillback transmission from humans to animals, and secondary spillover from animal hosts back to humans included the jaguar due to its high zoonotic capacity (Fischhoff et al. 2021).

Conservation

The jaguar is widely recognised as a species of special conservation concern by academics, NGOs, and governments. It is an important keystone, umbrella, indicator, and flagship species (Olsoy et al. 2016, Thornton et al. 2016). Six South American countries, combined covering almost 80% of the current jaguar range (Jędrzejewski et al. 2023, this volume), have national action plans for jaguars: Argentina (Nación 2016), Brazil (Paula et al. 2012), Bolivia (Pinckert de Paz et al. 2020), Ecuador (Zapata et al. 2014), Paraguay (Secretaría del Ambiente et al. 2016), and Peru (Ministerio de Desarrollo Agrario y Riego & SERFOR 2022). In Colombia there is an outdated Programa Nacional para la Conservación de los Felinos Silvestres (Valderrama-Vásquez & Moreno 2006) that is being implemented partially by NGOs but without government funding. Venezuela, Guyana, French Guyana, and Suriname have no national strategies/action plans.

Several organisations and universities work on jaguar conservation along the jaguar range in South America, among these, the two that lead multi-country jaguar conservation programmes focusing on key Jaguar Conservation Units and corridors (Sanderson et al. 2002, Rabinowitz & Zeller 2010) have been Panthera and the Wildlife Conservation Society, with the World Wildlife Fund initiating a similar multi-national multi-biome programme at the time of writing. The San Diego Zoo Conservation Program is working in conservation of jaguars in Peru and Mexico, Guyra in Paraguay and its Chaco frontiers, and the Corridor Verde in the Brazilian and Argentinian Iguazu is a well-managed example of multi-country conservation. In recent years, there has been increasing consensus among governments, NGOs and academic institutions on the need to improve collaboration and maximise synergies to achieve greater impact for jaguar conservation. Regional collaboration facilitates knowledge exchanges, scaling up the application of conservation techniques, and enhancing local and transboundary efforts. The Jaguar Corridor Initiative overlaps with the Path of the Anaconda, a connectivity-based conservation initiative promoting conservation of the indigenous peoples of the Colombian Amazon (Payán & von Hildebrand 2016). Given growing evidence of the effectiveness of indigenous territories ITs in avoiding deforestation (Walker et al. 2020), it is important to articulate synergies with indigenous organisations more effectively and proactively, supporting their stewardship of Amazon forests and jaguar habitats.

Given the increasing and complex threats (Quigley et al. 2023) that jaguars face across the range, it is important to adopt a comprehensive conservation approach that spans all the relevant scales, from specific landscapes to the entire region. This understanding led to the Jaguar 2030 Roadmap, for the Americas, a multi-government jaguar conservation initiative supported by the United Nation Development Program UNDP, Panthera, WCS and WWF. Grounded in Panthera's Jaguar Corridor Initiative, which aims to connect Jaguar Conservation Units JCUs from Mexico to Argentina, the Roadmap strives to secure 30 jaguar landscapes and their connectivity by 2030, while leveraging large finances, and generating support for jaguar conservation through advocacy and public support.

Regionally, alliances and networks to increase cooperation for jaguar conservation are also growing, with examples in Bolivia, Brazil, Argentina, and Suriname. The Jaguar Alliance in Brazil was created in 2014 as a multi-institutional collaborative effort between Federal agencies, NGOs, and research institutions to strengthen the implementation of the National Action Plan for jaguar conservation, facilitate and amplify scientific studies and coordinate science-based conservation actions. In Argentina, a national committee and three regional sub-commissions (Atlantic Forest, Chaco and Yungas region) have been created to work on the implementation of conservation plans for the species. These committees are composed of members of the government, researchers and NGOs. In 2020, a National Jaguar Working Group was also formed in Suriname between different organisations and the Nature Conservation Division NCD of the Ministry of Spatial Planning and Forest Management to provide strategic direction and leadership to maximise jaguar conservation in Suriname. Lastly, the National Alliance for the Conservation and Protection of Jaguars in Bolivia was formed in February 2020 among several organisations and under the coordination of the General Directorate of Biodiversity and Protected Areas DGBAP of the Ministry of Environment and Water MMAyA. The alliance members formally committed to exchange information, coordinate jaguar conservation activities to maximise impact, and help implementing the National Jaguar Action Plan.

In Venezuela the tendency has been the opposite. Governance in wildlife protection has deteriorated due to an uninterested government (Jędrzejewski et al. 2011). The very promising conservation initiatives for jaguars such as those ensuring forest connectivity and secure jaguars within the state of Cojedes through interconnected ranches that promoted conservation such as Hato Pinero, Hato Socorro, Hato Corralito, Hato El Frio and Hato el Cedral have been dismantled and the properties expropriated by the Venezuelan government in 2009–2010, in some cases eliminating many conservation achievements (Rial 2011). The erosion of conservation safeguards has also been seen in Bolivia and Brazil.

Protected and managed areas for jaguar conservation

PAs per country merit a dedicated section as they are the vertebrae along the backbone of the jaguar corridor, and they are currently the safest havens for jaguars. PAs and NPs in South America often lack sustainable financial mechanisms, adequate governmental support or governance. Strengthening existing PAs is as important as creating new ones. PAs cover 29% of the current (2020) jaguar range in South America, and 32% of the jaguar population lives inside them. Additionally, ITs cover 20% of the jaguar range and harbour 23% of the jaguar population, which leaves 51% of the jaguar range area and 45% of jaguar population outside of legally PAs of any kind (Jędrzejewski et al. 2018, 2023a, 2023b, Berzins et al. 2023, Thompson et al. 2023). For details of population numbers of jaguars per country within PAs see Jędrzejewski et al. (2023a). Managed areas or under some other sort of land tenure regime can also be key strongholds for jaguars. Some indigenous areas, especially in the Amazon, can be very effective in conserving jaguars (Nepstad et al. 2006, Payán & Escudero 2015) as some multiple use areas (Polisar et al. 2016, Tobler et al. 2018).

In Colombia 21% of the jaguar population lies within PAs (Jędrzejewski et al. 2023a).

Fig. 3. Jaguar in a burnt area in the Pantanal (Photo: M. Amend/WCS).

The stronghold for jaguar conservation lies within a group of Amazonian parks whose core is Chiribiquete NP, covering 43,000 km^2 alone. Colombia is one of the few countries where new NPs are still being created. There is a critical need for at least three additional strictly PAs in Colombia: San Lucas, Perijá and Arauca-Casanare (Llanos; Payan et al. 2016). The first two would ensure connectivity for jaguars from the biogeographic Choco, crossing the Andes to the Orinoquia (Llanos), and Venezuela. The latter would join the eastern Andes to the Orinoco watershed. Currently, private reserves are havens for jaguars in the extensively ranched savannas. These PA priorities for jaguars are also highlighted as conservation vacuums in their representative biomes (Forero-Medina & Joppa 2010). However, the current internal violence, lack of state presence, and gold deposits make their creation a challenge that no government has been willing to undertake. An existing corridor without strong protection lies with the Darien gap joining Panamanian and Colombian jaguar populations through dense rainforests. This forest is currently threatened by a rapidly advancing destructive frontier driven by expanding oil palm plantations and by plans to connect both countries by the Pan American Highway.

In western Ecuador, about 17% (ca. 2,000 km^2) of the jaguar's current habitat is within the National System of PAs. In contrast, in Ecuador's Amazon region about (26% ca. 30,000 km^2) of jaguar habitat is under protection (Zapata et al. 2014). Jaguars are presumed extirpated from south-western Ecuador (Zapata & Araguillin 2013). Abundance of prey for jaguar is sufficient in large PAs in Ecuador, such as Yasuní NP (Espinosa et al. 2018). However, this is not the case in western Ecuador, where jaguar populations are at the brink of extinction (Saavedra et al. 2017, Zapata & Araguillin 2013).

Venezuela has 259,000 km^2 of PAs and there are no officially approved ITs. There are 46 NPs and 36 other PAs. Caura NP is the largest (75,340 km^2) and the youngest one (created in 2017; http://www.inparques.gob.ve/cms/main/galeria). However, the actual situation inside the NPs is uncertain due to underfunding, insecurity and lawlessness derived from illegal mining (Castillo 2020, deSousa 2020). For example, it is estimated that over 20% of the area of Canaima NP has been destroyed by illegal gold mining, and Caura and Yacapana follow in degree of disturbance from gold mining (Mongabay 2018, RAISG 2020).

Peru is estimated to have the second largest jaguar population after Brazil, with high densities in the Amazonian lowlands along the eastern flank of the Andes (Jędrzejewski et al. 2018, Tobler et al. 2013). There are 25 National PAs within the jaguar's distribution range in Peru covering an area of 171,400 km^2 or 28% of the range. ITs cover an additional 190,700 km^2 or 31% of the range (Jędrzejewski et al. 2023a) and together with regional and private PAs and buffer zones over 65% of the jaguar's range have some level of protection. Jaguar habitat in Peru is largely connected from north to south, with a series of PAs including the Pucacuro National Reserve, Pacaya Samiria National Reserve, Sierra del Divisor NP, Cordillera Azul NP, Alto-Purus NP, Manu NP and the Bahuaja-Sonene NP forming the backbone (Carrillo-Percastegui & Maffei 2016, Tobler et al. 2013). There is a strong connectivity along the Amazon basin to Colombia and Brazil and a noteworthy triple frontier international border population between Peru, Bolivia and Brazil. Jaguar conservation in Peru should focus on maintaining jaguar populations and connectivity outside of PAs, especially in logging concessions which make up the majority of the unprotected forest. Major threats to jaguars in Peru are deforestation due to the advancement of informal mining and agriculture, unsustainable hunting of prey, and killing due to conflict. The first two threats are moving eastward from the Andes foothills and the hunting is endemic to the indigenous and colonist settlements in the Amazon irradiating a depletion of jaguar prey outwards (Carrillo-Percastegui & Maffei 2016).

Brazil has over 1,330,000 km^2 of its jaguar range inside PAs and 995,000 km^2 inside ITs, which is proportionally more than any other South American countries (Jędrzejewski et al. 2023a). The Amazon is unique because over 50% of the biome is legally protected (Sollmann et al. 2008) and the majority of the forests are well connected representing a large continuous jaguar population (Nijhawan 2012). Only in the Amazon are the PAs large enough to have the potential for long-term jaguar conservation on their own as modelled by Sollmann et al. (2008). This extensive area constitutes the largest contiguous block of jaguar habitat within the species' range. Despite the many PAs located in the Amazon, the biome continues to be under threat. The deforestation Arc has aggressive mining, selective logging, predatory agriculture, general colonisation pressures, road penetration and man-made fires (Figs 1–3; Barber et al. 2014, Nepstad et al. 2001). For instance, near 1.8% of the jaguar population has been displaced by deforestation in the last five years in the Brazilian Amazon (Menezes et al. 2021). Private reserves play a key conservation role here (Negrões et al. 2011). More parks are needed in the states of Acre, Amazonas, Rondonia and Para to counter the advance of the deforestation arc. The PAs of the Pantanal, Cerrado, Caatinga, and Atlantic Forest are less numerous and smaller than the ones in the Amazon and probably insufficient for maintaining jaguar populations in the long term (Paviolo et al. 2016, Sollmann et al. 2008). The Atlantic Forest and the semi-arid Caatinga are isolated and have the most impacted potential corridors (Silveira et al. 2014). New PAs and well-defined functional corridors are crucially needed in central, southern, and eastern Brazil to maintain and/or re-establish connectivity between the fragmented jaguar populations of Caatinga (Morato et al. 2014, Jędrzejewski 2023c), Cerrado (Portugal et al. 2020), and Atlantic Forest which holds only a remnant 2.8% of its historic jaguar population (Paviolo et al. 2016). Maintaining connectivity in the Cerrado is particularly critical, given its central location, linking Pantanal, Caatinga, Amazon, and Atlantic Forest and high agricultural pressure. These would help ensure connectivity between the Amazon and the Pantanal.

Jaguar conservation in Brazil has several important transboundary dimensions. In the north and west, the Brazilian Amazon borders with all French Guiana, Suriname, Guyana, Venezuela, Colombia, Ecuador, Peru, and Bolivia (Berzins et al. 2023, Jędrzejewski et al. 2023b). Northern Roraima could play a key role connecting PA blocks with southeast Venezuela and southwest Guyana. In south-western Brazil the Pantanal grades into the Bolivian and Paraguayan Chaco (Thompson et al. 2023), which grades into the Chiquitanía of Bolivia which in turn grades into the Amazon and hence the Guiana Shield. All told, this complex exceeds four million square kilometers and is the planet's largest tropical reservoir of biodiversity and carbon. New parks are needed in the western flanks of Mato Grosso, where a PA would complement the Noel Kempff Mercado NP on the Bolivian border and in the Mato Grosso do Sul western limit to complement the San Matias Integrated Management district in that landscape. The Brazil-Bolivia area includes three JCUs and connecting corridors that provide over more than 1,500 km of shared border that are important to the long-term maintenance of those three core populations and for those to the south. The latter area is in much need of transboundary parks and international conservation cooperation. Exemplary research and conservation work has been done in the Corredor Verde between Argentina and Brazil where jaguar populations are recovering after being in a very critical situation at the end of the last century (Paviolo et al. 2015, 2016). However, the degree of isolation of this population and profuse hunting requires stringent transboundary conservation action to secure a long-term stable population of jaguars (De Angelo et al. 2013, Paviolo et al. 2006).

Approximately one-fifth (22.5%) of Bolivia's territory is covered by PAs. It also has 14 million hectares protected under Ramsar and 20 million hectares of forest owned and controlled by indigenous people. However, not all ecoregions/biomes are equally represented. The stronghold for jaguars lies in the eastern lowlands of the country in a unique latitudinal transitional from the Amazon through savannah-forest mosaics to Chiquitano dry forest into Pantanal and Chaco, all biomes apt for jaguars (Maffei et al. 2004, Silver et al. 2004, Romero-Muñoz et al. 2019). The Beni savannahs are largely unprotected, and are a hotbed for jaguar-cattle conflict, with large numbers of jaguars and pumas killed there each year. PA coverage should be extended to ensure survival for jaguars in this unique environment. At the same time, new PAs should be created in the Santa Cruz Department to ensure connectivity between the Noel Kempff Mercado NP and San Matias NP. Existing parks have lacked political support in previous administrations, suffering from chronic underfunding, understaffing and exploitation. Bolivian parks and the jaguar populations they harbor are threatened by new roads, legal and illegal mining, a new hydroelectric project, illegal colonisation, rampant hunting and lately, by man-made fires (Perz et al. 2013, Maffei et al. 2016, Romero-Muñoz et al. 2019). Given the important potential of Bolivian jaguars for long-term continental conservation, strengthening the governance and defense of NPs should be an international priority. The southeastern corner of Bolivia is in the Pantanal watershed, part of the greater Pantanal JCU and incredibly important as trans-frontier jaguar crossroads meriting effective conservation actions. The bi-national Bolivia-Paraguayan Gran Chaco and the trans-frontier areas with Argentina merit better integration of forest conservation and hunting regulation with the agricultural expansion that threatens to consume the biome.

Paraguay has a young national PA system, established in 1994, protecting close to 28,000 km^2, or about 6.9% of Paraguay's land area (Cartes & Yanosky 2020). However, land disputes, indigenous land claims, administrative errors, land invasion, and flooding from reservoir developments, have reduced PAs by at least 3,500 km^2, while >4,200 km^2 of PAs have been downgraded to less strict categories of protection (Cartes & Yanosky 2020). In the Atlantic Forest of eastern Paraguay, the only surviving jaguars are confined to the private Mbaracayu and Morombi reserves (Paviolo et al. 2016, McBride & Thompson 2019). Both these reserves are under severe threats from illegal logging and hunting, and land invasion for campesino farmland and illicit marijuana production. In western Paraguay jaguars are found in >21,100 km of PAs in the Gran Chaco and Pantanal, which constitutes about 5% of the land area west of the Rio Paraguay. Agricultural expansion has been rapid in the remaining stronghold for jaguars in northeastern

Paraguay in the Chaco. Still linked to large PAs in south-eastern Bolivia, this core component of the Gran Chaco and the Pantanal-Chaco-Chiquitana-Amazon. This merits actions that include ranching with more effective conservation than has taken place to date.

Argentina holds three populations of jaguars in about 85,000 km^2 of jaguar habitat that should contain between 200 and 300 jaguars (Paviolo et al. 2019). All trans-frontier, the populations are the focus of research and conservation initiatives. Jaguars still exist in Salta, Jujuy, Formosa and over the Chaco with a remnant population in the Misiones province (Perovic & Herrán 1998, Di Biteti et al. 2016). Chaco populations are in a very critical situation (Altrichter et al. 2006, Quiroga et al. 2014). PAs cover 28% of jaguar range in the country, but its proper implementation is not fully effective, and poaching problems still exist. Major threats include increasingly eroded lands and habitats from intensive agriculture and livestock, added to expanding arid lands and indiscriminate hunting, even in PAs (Altrichter et al. 2006, Di Biteti et al. 2016, Martinez Pardo et al. 2017). Argentina's 2016 National Conservation Plan for jaguars combines previous regional jaguar conservation plans in Yungas, El Chaco and Paranaense forest regions. This plan seeks to maintain and restore natural jaguar populations in northern Argentina through four lines of action: scientific research, landscape connectivity, habitat protection, and education (Nación 2016). It is noteworthy to mention the reintroduction programme for jaguars in the wetlands of Iberá (Zamboni et al. 2017).

Discussion

This summary of jaguar legal status, utilisation, management, and conservation gives insight into the current state of the jaguar and its needs in South America. The jaguar is legally protected in most of the range countries, but all lack strict enforcement and real protection on the ground for the species. PA violations, illegal killing of jaguars and trade in their parts (illegal in every country), has, thus far, resulted in few convictions. Even when enforcement is active, hunters and poachers have been able to make the most of legislative loopholes and exemptions. Recent reviews of illegal wildlife trade (Morcatty et al. 2020, Arias 2021) have alluded to the role that inadequate public investment in conservation and correspondingly weak commitments to wildlife law enforcement play in allowing almost unfettered levels of domestic trade in jaguar parts. That concern extends to the often-urgent need to better defend PAs from a variety of illegal uses.

NPs have been and still are a cornerstone of jaguar conservation in the continent, but hampered, with a few exceptions, by underfunding, understaffing and a lack of governance and political will. The resulting lack of adequate enforcement capacities by park rangers has weakened their impact. There is a key, time-sensitive, opportunity to work closer between indigenous reserves and territories to strengthen overall conservation and connectivity. This would build on the overall success in conservation governance already achieved. Exceptional ranches and other private properties have also played key conservation roles in many parts (Hoogesteijn & Chapman 1997, Hoogesteijn & Hoogesteijn 2010, Hoogesteijn et al. 2015, Payán & Boron, 2019, Tomas et al. 2019). Financing the operation of NPs and fostering key private protection should be a priority for national governments and funding agencies. The latter is noteworthy, given that 51% of the jaguar's current distribution is outside PAs and ITs.

Even the larger, more developed countries such as Brazil and Argentina have challenges adequately addressing poaching and illegal incursions into PAs. All this emphasises the political work needed to improve the situation for jaguars and the habitats they occupy and use. The best-protected population of jaguars may be the one in the Pantanal, as a product of the financial incentives provided by jaguar-viewing tourism that motivates local people to value and protecting the species that sustain a large chunk of their livelihoods (Tortato et al. 2017).

The CITES prohibition in the mid-1970s worked well countering a growing international threat but appears to have left a less prominent level of domestic trade intact within each country. We currently lack robust and standardised estimates of jaguar killing in South America. However, that is a parameter whose detection fraction may continue to challenge efforts to measure it. Most killings go unregistered by government agencies and few entities apart from academic and NGOs are paying attention. The current extent of jaguar trafficking across the region remains unknown, with official records likely underestimating this threat. Recent investigations have revealed that the trade in jaguar body parts is largely diffused, opportunistic and domestic, with limited concrete evidence of trade to China from Bolivia and Suriname (Arias 2021). The trade merits more research and inter-institutional and international coordination, in addition to research on the extent of the domestic demand and uses and links with human-jaguar conflict. Multi-faceted approaches are needed to stop trade including better law enforcement, behaviour change, and conflict management.

Management of wild jaguars has mainly focused on reactive hunting to depredation events. There is currently a long list of alternatives to reduce attacks and several experiences developing throughout South America (Castaño-Uribe et al. 2016, Knox et al. 2019). In the coming years the challenge will be to strengthen and implement on a much larger scale the local initiatives of NGOs, researchers and governments to promote actions to reduce jaguar attacks on livestock and their consequent persecution. Currently there are a few noteworthy examples of habituation schemes, like the one done by Onçafari aimed to stimulate tourism viewing in southern Pantanal, the Porto Jofre region jaguar oriented tourism activities in the Northern Pantanal, and the rewilding of jaguars in the wetlands of Iberá in Argentina.

Conservation of jaguars in South America has been relatively well fed by research data (Schaller & Crawshaw 1980, Hoogesteijn & Mondolfi 1992, Quigley & Crawshaw 1992, Medellín et al. 2002, Rabinowitz & Zeller 2010, Castaño-Uribe et al. 2016, Boron et al. 2023, Morato et al. 2023). There is very worthwhile accumulated and growing information on spatial ecology from GPS collared individuals spearheaded by valiant projects in different countries of South America (Thompson et al. 2021b). These data are essential to design and actively manage conservation actions for the future of the species with more frequent needs of translocations and gene pool variation. Amazonia lacks strong data on ecology and jaguar killing, with a few notable exceptions.

The Jaguar 2030 Roadmap marks a milestone for the species. Ideally it joins and justifies government and private partner conservation actions for jaguars. The pathways include all the needed key points, from addressing public opinion to development planning to science, with a strong focus on core areas and connectivity, and it is probably the best and most comprehensive drafted plan to save the species to date. Recently the CITES and Convention on Migratory Species CMS Secretariats have joined the 2030 Coordinating Committee. Given their direct interaction with signatory countries, this should help ensure uptake and implementation. Additional entities such as the diverse components of the IUCN can also engage, promote and execute the Road Map. The role of NGOs has been evident in the drafting and promotion of the document and can be heightened through additional collaboration with governments and conventions (Convention on Biological Diversity CBD, CITES, CMS) to make the plan a reality.

A key pathway involves the development of financially sustainable mechanism for jaguar conservation and currently this has seen development in certified timber and non-timber extraction (Polisar et al. 2016, Paviolo et al. 2018, Tobler et al. 2018), new jaguar tourism initiatives outside the Pantanal (Hyde et al. 2023) and a carbon credits scheme to secure forests along the Jaguar corridor Initiative (Hyde et al. 2022). The latter consists of a South American tripartite relationship between ISA, South Pole and Panthera for carbon bonds emission along key forest and plantations along the corridor that currently includes more than 2,860 km^2.

It is noteworthy to highlight the importance of transboundary cooperation and action, especially among the trans-frontier hotspot for jaguar gene flow in the Panama - Colombia Darien, among the Amazonian country political boundaries and between the Bolivian and Brazilian Chiquitano-Pantanal-Cerrado frontier. These political boundaries, if unchecked, act as loopholes in legislation, smuggling and general lack of governance when they could instead be playing a key role in strengthened connectivity through international collaborative conservation. The political differences among countries that affect jaguars weaken the effective application of laws and regulations that could protect jaguars on the large scale need to be transcended. Where jaguar trade is truly international in scope, it needs to be addressed collaboratively at both ends, source and destination.

Emerging threats like jaguar parts smuggling and man-made fires merit special attention and effective action. These constitute the new threats building on top of the old and traditional ones that our history or research and conservation hasn't been able to solve. The collaborative synergy sparked by the IUCN SSC Cat Specialist Group and San Diego Zoo Wildlife Alliance to launch this special issue is an example of the power needed to face jointly, among conservationists and researchers, current questions and summarise immediate needs for the species. Let us hope this mobilises more joined-up action. If jaguar conservation aims at being effective at a large scale, in an ever more populated world, it needs to be efficiently streamlined from high level agreements through reliable and systematic funding to applicable and scalable effects on the ground, within a matrix of PAs, complemented with effective corridors, strong values associated to jaguar survival and local people buy-in.

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A global perspective on trade in jaguar parts from South America

Starting in 2010 and accelerating in 2014, reports of trade and seizures of jaguar *Panthera onca* parts surfaced from several countries in South America. In this paper we summarise knowledge to date including official reports, peer-reviewed publications, public articles, seizure records, online searches, and market surveys in source countries in South America and big cat consuming countries in Asia. We found widespread records of domestic use and commerce in jaguar parts, in many cases without effective enforcement of existing laws to provide a substantial deterrent. We found less abundant solid records of trade from South America to China, with the exception of Bolivia where 95.4% of the historic interceptions of jaguar canines were oriented towards China, and Suriname where seizures in airports testify to international trade. International trade is particularly onerous as it can drive domestic killing of jaguars at an increased level due to higher prices and diversified markets. More material may be shipped to Asian markets than we have detected and we recommend vigilance in all potential mediums for transport (passenger aircraft, air freight, postal services, courier services, and marine shipping). We present a summarised review of relevant legal structures. The depth and breadth of domestic commerce that we recorded from diverse sources suggest the need for increased enforcement of existing laws, coupled with behaviour change and livelihood alternatives. All jaguar killing starts at the local level, and when there is a local national market for jaguar parts there is less incentive to pursue the means and methods for coexistence already tested and proven in much of the species' range.

The jaguar, known for its golden rosetted coat and cultural symbolism, has been considered a valuable and sought-after species throughout the history of Latin American societies. Archaeological records show that jaguar body parts travelled long distances across the Caribbean Sea, potentially transported as prized items of exchange between Amerindian and Caribbean societies, as early as the Ceramic Age (500 BC to AD 1500; Laffoon et al. 2014). During the 18th century, there are records of approximately 2,000 jaguars being exported annually from Buenos Aires to Europe for the fur industry (Swank & Teer 1989). Jaguar trade reached unprecedented commercial levels during the first three-quarters of the 20th century, when the spotted cat fashion trend reached its peak. In Brazil, an estimated 180,000 jaguars were killed during this period (Antunes et al. 2016), causing a widespread population decline. In response to the imminent extinction risk posed to jaguars and other spotted cats by the fur trade, in 1975, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) listed these species under Appendix I, prohibiting their commercial trade across international boundaries (CITES 2017, Reuter et al. 2018).

Even though by the end of the 20th century, international jaguar trade was virtually over, low-scale but widespread jaguar trading continued to occur domestically, commonly as a by-product of killing caused by opportunistic encounters between people and jaguars or human-jaguar conflict, as well as for subsistence and cultural use (Arias & Lambert 2019, Arias et al. 2020, 2021a). However, starting in 2010, reports of trade and seizures of jaguar body parts surfaced from several countries across the jaguar range, suggesting a re-emergence of international jaguar trade (Kernam 2010, Nuñez & Aliaga-Rossel 2016). Between 2014 and November 2023, 825 jaguar canines have been seized in trafficking cases linked to Chinese individuals in Bolivia and in mainland China. Other similar cases were registered in the region, including the sale of jaguar body parts in physical and online markets, and the preparation of jaguar paste in Suriname for alleged export to China (Lemieux & Bruschi 2019, Verheij 2019, SERFOR & WCS 2020). These seizures and reports mobilised attention on the issue. Subsequent reports and publications have shed light on the drivers and dynamics of the trade (e.g. Morcatty et al. 2020). This team of international experts explored the state of the evidence on this threat in 2023, focusing on its geographical characteristics and nuances. The paper starts with preliminary results of a seven-language investigation of online trade in jaguar parts, transitions into specific country analyses and legal considerations, and closes with recommendations for future actions.

Online investigations of jaguar trade conducted 2019–2020

Between May 2019 and March 2020, a multinational team of researchers conducted systematic searches for online trade of jaguar parts in seven languages (Spanish, Portuguese, Vietnamese, Chinese, French, Dutch, English; Polisar et al. 2023). The team searched for offers of sale of jaguar parts and processed items, as advertised, through multiple platforms, accessible via search engines, online marketplaces, video-sharing, social media and weblogs (blogs). The results were collated in a standardised database including the platforms, assessed country locations of posts, jaguar part and product type, prices and other trade information where available, and corresponding images of jaguar parts and products were visually reviewed, where available. Platforms showing jaguar parts varied across countries and languages. Methods such as standardised collection and metrics of effort facilitated structured searches, subsequent analyses and interpretations, and revealed the most productive search terms, search engines, and platforms for potential future searches. Following data collection, experts from Noel Kempff Mercado Natural History Museum NKM Museum in Bolivia with expertise identifying and classifying jaguar parts resulting from a successful prosecution of a jaguar trafficking case in Santa Cruz visually verified images as jaguar (Figs 1–3). The analyses presented here incorporate the results of image review, yet should be still considered preliminary.

Raw results included a total of 230 posts motivated by trade in jaguar parts; other posts referred to sharing news about jaguars, or posting images of parts but with an unclear motivation, or wearing items, and these were not included. From the 230 posts, 71 posts contained images that were identified as definitely jaguar. We sampled a ten-year period and found that the numbers of posts increased over time from 2009 to 2019, which may be an artifact of posts removed or becoming moribund with time, or an increase in trade. Excluding duplicate posts, posts were present on 31 distinct platforms, and the posts with images verified as jaguar were present on 12 platforms, comprised of 10 online marketplace sites (18 posts or 25.4% posts) and 2 social network sites (53 posts or 74.6% posts).

The most widely used language in posts was Spanish. In our searches 98.6% of all posts accompanied by verified jaguar images were in Spanish, Chinese, and Portuguese. Whilst Vietnamese language searches identified 31 posts without duplicates, none of the posts accompanied by an image were deemed to be jaguar.

The location was assessed by researchers for 193 of all posts, with records from at least 17 countries (plus one subset indicating posts derived from one of two countries, but unclear which), however, only 64 posts from at least 9 countries included images that were definitely jaguar, the most prolific being Brazil, Mexico and Bolivia. For the 437 parts that were counted in posts, 15 categories of body parts were recorded, with teeth being the most popular item traded (156 posts totalling 367 teeth), followed by skins (Fig. 4), entire or fragments (37 skins, 1 skin piece and 1 skin scrap spanning at least seven countries), claws (12 posts of 14 claws), heads (nine posts counting nine heads) and additional posts related to parts including bones, bodies and live animals. Where the probable country of the post could be assessed (through platform addresses, stated business geo-tag and other contextual information, but not physically verified by researchers), jaguar skin posts were confined to jaguar range countries, with highest prevalence in Brazil, Peru, Bolivia, and Mexico. Meanwhile, posts advertising teeth were most prevalent in countries including Brazil, Mexico, Bolivia, China and Vietnam. However, following image verification, those proportions changed with Mexican posts representing over one quarter of all teeth counted (26.8%), Chinese posts one quarter of teeth (25.4%), Bolivia around one-fifth (16.9%) and Brazil approximately one-tenth (12.7%). Vietnamese posts included tiger, leopard, and bear teeth in posts obtained from searches targeting jaguar, illustrating some of the challenges of search terms across geographies and languages, even with native speakers conducting the research. Whilst searching in Chinese, and less intensively in Dutch, we encountered very few records of medicinal oil/paste, a product reported from Suriname (Kerman 2010, Lemieux & Bruschi 2019, World Animal Protection 2018).

Fig. 1. Jaguar, puma, and ocelot canines seized from trafficking (Photo D. Rumiz, NKM Museum).

Bolivia National/International Trade - from reports/records 2014–2022

The recent international trade in jaguar parts, especially canine teeth, was first reported in Bolivia in July 2014, when Bolivian scientists who were camera trapping for jaguars in Madidi National Park heard local radio advertisements offering to buy jaguar teeth in the nearby Beni Department. This was immediately reported to the Ministry of the Environment and Water, which coordinated with multiple authorities, including the Bolivian postal system, resulting in the detection of several packages containing jaguar teeth, addressed to locations in China. Simultaneously, customs officials stopped two individuals in El Alto International Airport in La Paz travelling to China with jaguar teeth. Subsequently, three high profile legal cases of jaguar teeth trafficking involving individuals of Chinese descent recently naturalised in Bolivia, further increased national and international attention towards the threat of jaguar teeth trade (WCS, WWF & Panthera 2016, Bale 2018, Franco 2018, León 2018), and led to increased investigations on the matter, including academic and journalistic efforts, NGO investigations, and enforcement operations in Bolivia (Nuñez & Aliaga-Rossel 2016, Verheij 2019, Arias et al. 2021a,b, CITES 2021, Earth League International 2021).

Efforts by the Wildlife Conservation Society to systematise official data on illegal wildlife trade in Bolivia now include data provided by 62 institutions, including the Ministry of the Environment and Water, the Bolivian Forestry and Environment Police POFOMA and most of the Departmental governments and wildlife rescue centers in the country, and reveal that since mid-2014 there are a total of 83 verifiable jaguar trafficking cases in Bolivia, with two additional cases of jaguar parts seizures in China coming from Bolivia. Of these, 32 cases (37.6%) are of jaguar teeth, amounting to 825 jaguar canines, making teeth the most trafficked part. Additionally, 27 of the 83 cases so far, and 95,4% of Bolivian seized canines, are directly linked to China. Online analyses in Bolivia have revealed 24 additional posts mainly on social media, across the Bolivian lowlands. Although most recent cases of jaguar parts trafficking in Bolivia occurred between 2014 and 2019, two cases were reported in 2022 and 3 cases in

2023, all involving jaguar teeth. One of these involved 4 men of Chinese descent.

Previously, jaguar populations were recovering in protected areas in Bolivia (Mongabay 2018), with indigenous territories (Polisar 2021), forestry concessions (Polisar et al. 2017), and cattle ranches (Polisar 2021, Polisar et al. 2022), all demonstrating real potential for the conservation of jaguar populations. However, conflicts between jaguars and livestock owners are likely to be fueling part of the supply of jaguar teeth, responding to the high prices being paid for jaguar canines, teeth, heads, claws and skins. Similarly, local people's attitudes towards jaguars are mixed, with some indigenous groups publicly declaring to be against the illegal wildlife trade and in favor of jaguars (CIPTA 2019, CRTM 2019), whilst other local actors have admitted their fear of jaguars and willingness to kill them (Knox et al. 2019; Arias et al. 2021a). Aside from cattle ranching, other forest dependent livelihoods (e.g. wild meat hunting, farming, non-timber forest product collection) have been associated with jaguar killing (Arias et al. 2021a). Moreover, a high proportion of rural households in north Bolivia buy, sell and use jaguar body parts for a wide range of purposes, from decorative (jewelry, accessories, furnishings) to medicinal (Arias et al. 2021b). Although illegal, these traditional uses continue in the Beni Department, where it was shown recently that inmates of the Trinidad prison buy wildlife skins to make wallets, bags and belts (Elwin et al. 2023). These handicrafts are commonly sold to tourists in town markets, but are also bought in bulk by foreign middlemen for export. Four cases of wildlife parts seized in La Paz, Santa Cruz, and Riberalta, with support from the Noel Kempff Mercado Natural History Museum for forensic identification during 2022-2023, included jaguar teeth or skin pieces. Illegal trade in jaguar teeth, alongside habitat loss and recent increases in frequency and intensity of Amazonian fires, are currently the largest threats to jaguar populations in Bolivia (Romero-Muñoz et al. 2019).

Suriname National/International Trade - from reports/records 2005–2022

Nearly 93% of Suriname's territory is covered by contiguous rain forest (FAO 2015) that extends over the border with Brazil, French Guiana and Guyana. Suriname has numerous reports of jaguar trade, which suggest high rates of removal of jaguars and reports of hunters selling jaguar teeth in Paramaribo dating back to 2005 (Kernam 2010, World Animal Protection 2018, Lemieux & Bruschi 2019, Verheij 2019). Several incidents support the assertion that the trade in jaguar body parts in Suriname may be more pronounced than in neighboring countries. According to CITES (2021), at least 60 jaguar teeth and a smaller number of other body parts have been officially seized by the authorities from 2009 to 2020, 14 of which came from 3 seizures made at international airports, indicating international trafficking. According to news and published reports on seizures, at least 11 jaguars were killed in Suriname between 2012 and 2018; three of the reports involved jaguar body parts claimed to be destined to China, comprising two canines and four bodies or meat (Morcatty et al. 2020). Verheij (2019) estimated that at least 17 jaguars were killed between 2007 and January 2018 due to trafficking, and put an emphasis on the involvement of both the Chinese diaspora and Chinese visitors in this trade. Trafficking was apparent from the seizures of seven teeth in the Amsterdam airport in 2010 and 19 teeth in the Paramaribo airport in 2018 (Verheij 2019) and 5 teeth also at Paramaribo airport in 2019 (Anonymous 2019). However, the intensity of the trade may be even higher. One informant estimated over 80 jaguars killed in 2017 alone (Verheij 2019).

Following information from hunters and traders interviewed in 2009 that the main consumers of jaguar parts were Chinese (Kerman 2010), subsequent research on the trade and trafficking of jaguars in Suriname has focused largely on the Chinese communities living in Suriname, or on Chinese nationals that visit the country (Lemieux & Bruschi 2019, Verheij 2019). Jaguar body parts reportedly have diverse uses for Chinese people in Suriname, from medicinal application of the meat and bones, especially skulls, to jewelry made from teeth (Kerman 2010). Earth League International (2020) offered an online platform where wildlife trafficking information can be anonymously reported. With regards to the trade in jaguars in Suriname, reports were received of alleged killing and sale to Chinese buyers of jaguars from the North-west Nikerie and Wageningen region, as well as the area close to the international airport in the period 2017-2020. Two Chinese-owned shops in the capital were singled out as selling jaguar parts, meat and jaguar paste.

As early as 2010, records emerged of Chinese traffickers requesting suppliers for entire carcasses for producing medicinal powder or paste (Kerman, 2010, Verheij 2019, Lemieux & Bruschi 2019). According to Verheij (2019), local informants also stated that teeth and processed medicines were transported by passengers in flights to China as well as in timber containers transported by ships. Jaguar teeth are used in necklaces and gold jewelry and thus bought and sold in jewelry shops in Paramaribo (Kerman 2010). An indirect factor elevating this trade is that poorly patrolled new access roads to logging and gold mining sites have opened up previously inaccessible forested regions, facilitating the establishment of trafficking routes. Recent independent reports state that vendors actively approach villagers, loggers, gold miners and hunters soliciting jaguar body parts (Lemieux & Bruschi, 2019, Verheij 2019). In March 2021, a baby jaguar was offered for sale on social media in Suriname with an asking price of USD 2,500, and in October 2021 videos were posted on TikTok of a freshly killed jaguar; it was unclear if this animal entered the trade (Fig. 5).

We did not locate much evidence of online trade in Suriname in our study conducted May 2019-March 2020, and found no posts advertising medicinal jaguar paste or powder. Verheij (2019) reported several advertisements selling jaguar canines found on a Facebook group in Suriname between 2016 and 2018, and 13 canines that resemble jaguar teeth posted on WeChat, an online platform used by the Chinese community. Only 57.8% of Suriname's population has access to the internet. It is the country with the third lowest internet penetration in South America (Miniwatts 2019), and thus online advertisements may not be a primary medium for the trade of jaguar body parts, especially close to source areas.

Peru National/International Trade - from reports/records 2014–2019

The upper Amazon of Peru probably holds the second-largest jaguar population after Brazil (Carrillo-Percastegui & Maffei 2016). In recent years, deforestation and gold mining in the Amazon have aggravated the perils faced by jaguars (Swenson et al. 2011) as more people penetrate previously inaccessible areas. Jaguars are sometimes killed due to livestock loss, a pattern that is likely exacerbated as cattle ranching and small-scale agriculture expand (Tobler et al. 2013). Both killing and trade seem to take place despite laws prohibiting killing of jaguars and trade in their parts. Teeth, claws, and skin (whole or in parts) continue to be traded openly in local markets across Peru, a situation that strongly indicates that more active, committed, and courageous enforcement of existing laws is needed to change the situation.

Research on jaguar trade in the Peruvian Amazon carried out between October 2018 and January 2019 found 102 jaguar parts sold in 12 of the 19 localities studied, including Iquitos (Loreto), Pucallpa (Ucayali), Puerto Maldonado (Madre de Dios) and Puno (Puno; SERFOR & WCS 2020). Sales were most prevalent in the Amazon towns of Iquitos and Pucallpa, with a few teeth found in Lima. A journalist, Berton (2018), researched jaguar trade in three markets in Iquitos for seven days and found 44 canines, four skulls, five skins, and 70 claws. According to Berton (2018), between 2000-2015 Peru's National Forestry Service (also known by its Spanish acronym 'SERFOR') seized 11 live jaguars and parts and products as 9 skulls, 14 skins, and 38 canines – the last product encountered in one confiscation event in March 2015. The implication is that approximately the same amount of material was encountered by journalists in one week in one city as the national authorities had confiscated in more than 30 incidents. If true, more effective enforcement is needed. Based on official international seizures found in the UNODC World Wise Database, Peru stands out as the most frequent source of jaguar body parts (CITES 2021). Braczkowski et al. (2019) identified links between 'ayahuasca' tourism and jaguar related trade, and that in tourism hubs jaguar body parts are openly sold on markets, with vendors offering to help with export.

Fig. 2. Jaguar fangs (canines; Photo D. Rumiz, NKM Museum).

Brazil National/International Trade in Jaguar Parts – from reports/records 2010–2019

Brazil contains around 60% of the Amazonian rainforest and 66% of current jaguar range (de la Torre et al. 2018). Although Brazil has been suggested as a potential source of wildlife for international traffic (Phelps et al. 2010), little is known about the intensity of trade and the impact of illegal wildlife trade on wild populations.

During online investigations, we recorded a total of 42 unique online advertisements of jaguar parts in Brazil in the last decade, involving 84 counted parts (72 teeth, 10 skins and two bodies; Polisar et al. 2023). Advertisements focused on handcrafts containing canines, such as sculptures and necklaces, and skins, such as coats, carpets or wall decorations, potentially aimed at a domestic market. Most of the online advertisements were encountered on online marketplaces located through commonly used search engines or social media. However, seizure reports and news indicate that there may be an existence of an international market for jaguar body parts from Brazil (6.5% of the seizure reports; Morcatty et al. 2020). This suggests that stakeholders supplying international markets may use alternative methods to trade jaguar body parts, other than advertising online or risking exposure in open fairs. Further research on that matter is merited.

In an examination of reported seizures and news available online, the majority seemed to be domestic trade in comparison to the international trade, accounting for near to 80% of the individuals (46/57) and body parts seized (65/82; Morcatty et al. 2020). Skulls represented 33% of the seizures (27), followed by leather items 46.3% (38) and bodies 8% (6; Morcatty et al. 2020). However, 56% of the skulls seized in recent years were directed to international markets. Apart from skulls, all the remaining body parts seemed to supply the domestic market (Morcatty et al. 2020). In 2016, 16 killed jaguars were seized in the countryside in Pará state by authorities who raised strong concerns about links to wildlife trafficking. The official, though unpublished, database of the Brazilian government reports ca. 50 infraction notices involving jaguars in Brazil, however, most of those do not provide any details on the type of infraction (whether trade or killing due to conflict with livestock; Brazilian government, unpubl. data). Only four records explicitly stated that pieces of skin and handcrafts were seized. The fine in one case was USD 2,400 (10,000 Brazilian Real). In an investigation of open-air markets throughout the Brazilian Amazon and in South-eastern Brazil conducted by members of our team in 2019, only a few pieces containing jaguar skin or teeth in handcrafts were found. The sellers expressed fear of fines and prosecution due to the illegality of the trade, confirming their awareness of the laws, but the persistence of material offered in those venues suggest enforcement is ineffective.

In Brazil, selling an unauthorised piece of a native and protected species is a crime independent of source, and the buyer may also receive the same penalties as the trader in case of proven purchase. Simply liking or sharing a post advertising the trade of jaguar body parts, or complimenting the piece that is for sale, is also breaking the law. The article 287 in the Penal Code (Law nº 2.848/1940) states that public communication (apology or incitation) of a criminal act is liable to punishment. Enforcement of all regulations across all scales, local, national, and international is important. As a response, a Federal Task Force was formed in 2019 aiming towards an integrated approach for counter-wildlife trafficking in Brazil.

Current knowledge of status and trends in illegal trade in the remainder of South America

Although detected in a much lesser degree, trade in jaguar parts exists in other South

American countries. During online investigations, we recorded posts offering visually confirmed jaguar parts linked to other countries, such as three posts in Venezuela and one in Uruguay (Polisar et al. 2023). Additionally, seizure reports of illegally owned jaguar body parts included three cases in Colombia, four in Paraguay, and one each in Ecuador and Venezuela in the last six years (Morcatty et al. 2020).

Source South American countries with relatively high levels of corruption and Chinese private investment and low income per capita had 10–50 times more jaguar seizures than the other countries (Morcatty et al. 2020). Likewise, the links between jaguar trafficking, human-jaguar conflict, and other criminal activities such as drug or weapons trafficking have been raised in countries like Brazil and Guatemala (Arias et al. 2020, CITES 2021). Regarding online trade, internet penetration has proven to be a critical factor influencing online wildlife trade listings (Nijman et al. 2023). the lower internet penetration combined with extent of jaguar range within a country may be a factor leading to a low detection of online jaguar trade and seizure records. The three countries adjacent to Brazil of Colombia, Venezuela, and Guyana have low internet penetration (63.2%, 53% and 50.5%, respectively) yet individually and as a block contain a considerable proportion of current jaguar range. Paraguay and Argentina have high internet penetration (89.6% and 93.1%, respectively) but contain a relatively small proportion of total jaguar range (Miniwatts 2019, de la Torre et al. 2018). The few online trade records we detected for Suriname, compared to other reports emphasising interviews and market searches (Kernam 2010, World Animal Protection 2018, Lemieux & Bruschi 2019, Verheij 2019) suggest a high degree of variability in the role of online platforms in jaguar part commerce. This seems potentially significant in the largely porous, remote, and unpatrolled common international boundaries of Brazil, Guyana, Venezuela, Colombia, Ecuador, Peru, and Bolivia, which have likely low internet penetration. Increased physical vigilance by national and local authorities in border areas is merited to prevent possible illegal trade threats from emerging in future.

In French Guiana records are maintained by the police division of a governmental agency titled "Office Français de la Biodiversity" (French Biodiversity Office), that works mainly by checking online social networks. The jaguar is not protected by a governmental decree (i.e. at the National – French – level), but by a local decree, meaning that killing a jaguar is not a criminal offence, but punished by a fine. Between 2018-2022 the division recorded one intentional killing), and traffic of jaguar parts that involved one skin, 72 teeth (in seven different judiciary cases), and eight claws.

China and Vietnam

In parts of Asia, Asian big cat parts and products are consumed for multiple purposes, including skins for décor, taxidermy and non-financial bribes, teeth and claws for jewelry, and bones for steeping in tonics, carving, and traditional medicine including 'glue' or 'paste' (EIA 2018). Previous research has indicated China and Vietnam to be significant markets for tiger trade (Gratwicke et al. 2008, Wildlife Justice Commission 2016, Wong 2016, Indenbaum 2018).

Verheij (2019) noted in Suriname, "there are indications that Chinese individuals were buying jaguar parts as early as 2003", and transnational trafficking has been generally viewed as an emerging trend. Kerman (2010) noted for Suriname that jaguars were sold to Chinese nationals as early as 2005. Aside from the seizures made in Bolivia and Suriname, which included Chinese cities as destinations for jaguar body parts seized at post offices or airports, there are few examples of confirmed seizures of jaguar body parts within Chinese territory. According to the recent study on jaguar trade conducted by CITES (2021), China was identified as the destination country in just three out of 76 (4%) jaguar seizures reported by UNODC's World Wise Database in the past two decades, involving less than 10 jaguar specimens (body parts or live animals; CITES 2021). In that same study, internet searches yielded information on another three seizures involving a total of 137 teeth (CITES 2021). Detections commonly feature teeth, and are generally related to Chinese nationals either within Latin America or shipping into China (Franco 2018, Kerman 2010, Leon 2018, Nuñez & Aliaga-Rossel 2016, Verheij 2019).

While many news articles have suggested that a wide variety of jaguar body parts (including bones, meat, and organs) are being used in the context of Traditional Chinese Medicine (TCM) in China, official seizure evidence is mostly limited to teeth, and there is scant official evidence of the use of jaguar parts in TCM, making 'Wenwan' (subculture of collecting sophisticated items) a more likely driver of the trade (Li et al. 2022). In China, news reports suggest two pieces of alleged jaguar bones seized in 2014; 1,490 grams of jaguar bones and paws in 2014 (Anonymous 2014). The only official seizure made in China, referenced above, involved 119 jaguar teeth and 13 jaguar claws seized in 2015, the latter resulting in a custodial sentence of 4.5 years and a fine equivalent to USD 7,200 (He 2016). In 2019, nine 'American lion' teeth from Peru were seized, later identified as puma (Verheij 2019). It is unclear if suspects arrested at airports were in possession of jaguar parts for personal use, or intended to supply consolida-

Fig. 3. Hat with jaguar skin (Photo D. Rumiz, NKM Museum).

tors in other jurisdictions. This has occurred against the backdrop of increasing trade in big cat teeth in recent years, including on Asian online platforms (Indenbaum 2018). Despite the Suriname-China links suggested by some reports, there is scant information from seizures within China reflecting known links to Suriname.

Online research may be challenging as Chinese language does not clearly distinguish among leopard, cheetah, clouded leopard, and jaguar, for example using the same character "豹" across species. Chinese media also may confuse common names when reporting trade in big cats. The Vietnamese language presents similar challenges for online research: online traders of big cats in Vietnam refer to tigers and lions and products from these two species and all others big cats as "báo".

Jaguar parts featured in Chinese-language online posts cited "the Americas" as the source to indicate jaguar parts, and both Chinese and Vietnamese platforms featured discussions about how to differentiate the teeth of different big cats. Notably, genuine jaguar teeth were less likely to occur in Vietnamese than Chinese posts; visual review of Vietnamese posts verified no images of jaguar parts, however Chinese posts did contain jaguar teeth. We encourage and recommend online research that includes additional countries in Asia.

Legal considerations to control and eradicate jaguar trade in and from South America

The killing of jaguars that eventually enter international trade are preventable at the local level, within each country. National legal frameworks and their local implementation play an important role in deterring opportunistic killings and accidental takes; they can also reduce the human-carnivore conflict that may lead to killing jaguars, or to opportunistic trade of parts and products in the underground market (Fukushima et al. 2021).

All jaguar range countries have entered the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Jaguars are listed in Appendix I of CITES, which prohibits commercial international trade of live animals, parts or products. According to this, jaguar trade across South American borders is forbidden in the terms of the Convention, though there is no similar homogenous framework for in-country legal provisions.

Other international instruments, such as the Convention on Biological Diversity CBD and the Convention on the Conservation of the Migratory Species of Wild Animals CMS, also contribute to setting international standards for the maintenance of robust wildlife populations. Implementation of international instruments relies solely on each country's development and enforcement of their national and subnational – where applicable – legal frameworks.

Hunting and in-country trade laws, though not specifically covered in CITES, are oftentimes contained in the same legal instruments approved to comply with said Convention. Such instruments can contribute to curbing in-country trade, provided they include clauses to address capacity-building and robust implementation among the local authorities. Importantly, comparability of the legal frameworks in adjacent countries is needed as these instruments may be applicable to jaguars (potentially, the same individuals) across borders. Legal measures can be heightened when acknowledging that consequences extend beyond conservation issues, impacting economic, health, and security ramifications associated with illegal activities (Cardoso et al. 2021). A range-wide review of national legal frameworks within countries in the jaguar range by Kretser et al. (2022) offers insights on the legal trends informing national laws and suggests legal best practices and ways to strengthen existing laws related to trade of jaguar parts. Recently, the enactment of Law N° 1525 for the Protection and Conservation of the Andean Condor, Kuntur Mallku *Vultur gryphus* in Bolivia, included an additional provision that categorises illegal wildlife trafficking as a criminal offense within the Penal Code of Bolivia.

How countries design and enforce administrative and criminal penalties has far-reaching implications for jaguar conservation, especially in areas where subsistence hunting takes place, and where human-wildlife conflict is escalating. Administrative penalties are applied to infractions of regulations and may be enforceable by countries' wildlife authorities; criminal penalties are enacted by criminal courts. Penalties (and the probability of them being enforced) need to be high enough to deter opportunistic killings, not only among the local population but most importantly to middlemen that have access to international underground markets. All South American countries include both administrative and criminal penalties for illegal killing of endangered species, such as jaguars. However, many of the penalties are calculated based on each country's minimum wage (Ecuador, Peru, Colombia) and might be insufficient to deter hunters that supply trade for the international market.

All countries require hunting licenses for sport hunting of wildlife, but not all require licenses for subsistence hunting, and many allow for killings under the umbrella of self-defense (Kretser et al. 2022). Hunting licenses are granted by local or national officers in the executive branch – often times a regional manager, or a national-level directorate – and while it is unlikely that a public official would grant a permit to hunt jaguars, some of the existing frameworks have not made it entirely illegal.

The legality of jaguar killings is delicate, as only Paraguay and Argentina have national level laws that place the species in a special category, and it would require Congress to pass a new law in order to lift the protections. In contrast, the majority of South American countries (except Bolivia, French Guiana and Suriname), place jaguars in a special management category by listing them alongside all the endangered species in the country. While such lists are potentially efficient management strategies, they present certain weaknesses: they often rely on the global conservation status of the species, rather than the national status, and they are typically infra-legal level regulations; that is, vulnerable to being modified by a low-level executive order.

Most countries allow for subsistence hunting, particularly for Indigenous Peoples and/or local communities. Each country's enforcement determines whether wildlife parts and by-products can be traded after allegedly hunting for subsistence reasons. Local non-monetary trade of meat and animal by-products within rural communities is quite common. However, subsistence hunting of game species for food should not enter commercial trade. Market hunting to satisfy urban demands for cash returns is usually detrimental to game populations (Robinson & Bennett 2000, Greenberg 2014) and presumably, also to the jaguars that depend on those prey species (Polisar et al. 2003, Novack 2005, Foster et al. 2014, McNab et al. 2019). For jaguar conservation, the case is clear; no commercial trade of jaguar parts should be legal. Allowing any trade in jaguar parts leaves a door open for abuse, fraudulent interpretation of the law and the potential rapid decline of jaguar populations.

Fig. 4. Jaguar skin (hide; Photo O. Torrico, WCS Bolivia).

For human-wildlife conflict where some flexibility to address chronic losses exists, few laws ensure such flexibility is not abused, since it potentially provides a window to legitimise killing for trade. To stop wildlife parts and by-products originating from legal self-defense or depredation control killings from entering the market – and therefore creating an incentive to cover up illegal hunting for trade – countries could adopt provisions similar to Peru: where the forest authority is in charge of disposing of the remains of legally-killed jaguars (with prior governmental authorisation). While enforcement is not yet ideal in Peru, such a legal mandate would simplify authorities' efforts to confiscate dead jaguars, thereby preventing parts from entering illegal trade.

Given the complexity of these issues only a combination of policies, deterrence mechanisms and reinforced implementation efforts have a chance at stopping illegal trade (Fukushima et al. 2021). Since legislation in each country already regulates against trafficking in the parts of threatened and endangered species, including jaguar, the primary need is to enforce existing laws more actively and effectively in both rural areas where the killing happens and urban areas where demand for parts may exist. At the same time, given that a considerable proportion of jaguar killings are associated with opportunistic encounters between humans and jaguars, human-jaguar conflict, and subsistence/cultural practices, it is essential to include behaviour change, awareness building, and alternative livelihoods efforts into the mix of interventions to deter jaguar trafficking (Arias et al. 2021a). Finally, tech companies must bear responsibility for illicit transactions on their platforms, as they play a role in facilitating illegal wildlife trade (Morcatty et al. 2022), including transactions involving jaguars.

Discussion and Conclusions

Recent questions regarding trade in jaguar parts have included: 1) is the extent of Asia driven trade in jaguar parts, especially teeth, echoed in additional countries but thus far poorly detected? 2) what are the relative proportions of domestic and international commerce? 3) what needs to be done to halt the trade? In this review we found: 1) widespread evidence of domestic commerce in several countries, mostly unimpeded by law enforcement; 2) a narrower band of evidence of international transport of jaguar parts (which by definition are collected on local and national levels before export), including to Asia. Teeth were the most common part traded. All South American countries in the jaguar range have some evidence of jaguar trade, but international trade is particularly concerning in Bolivia, Peru, Suriname and Brazil due to potentially higher volumes; 3) ambiguity as to how much domestic trade enters international trade.

The number of interceptions of jaguar parts in China has been low but concerning nevertheless due to the amount of body parts traded, and seizures in South America with direct links to China, which indicate that jaguar body parts may have entered that country without being seized. Online searches revealed jaguar parts on Chinese platforms and advertised in Chinese, yet in low numbers. Thus far, online and interception records of material coming from Suriname and other potential source countries in South America to China do not match the volume implied in some published reports focused on source countries. Two conclusions may be drawn: 1) trade in jaguar parts may be coming into China from several sources in South America, but has been difficult to detect, record and disrupt; 2) while not diminishing the gravity of existing and potential South America to Asia trade in jaguar parts, currently domestic commerce in jaguar parts in source countries may exceed international commerce. Conclusion 2 emphasises the dramatic need for improved national level education and enforcement within South America to curb all commerce in jaguar parts. Both conclusions (1 & 2) represent grave threats. More investigative efforts are needed to examine jaguar trafficking from South America to Asia, and wherever encountered, disrupt it. Given international travel between the two regions, and the frequency of legitimate commercial shipments that provide opportunities to smuggle wildlife parts, increased vigilance and additional investigations are recommended.

While it remains necessary to investigate the illegal trade in jaguars in China, the growing evidence of international trade in jaguar body parts points towards a wider geographical scope. In particular, some North American and European countries, including the United States, Mexico, Germany and France have been found to have some of the highest numbers of official jaguar seizures (CITES 2021). These markets have received less attention than China, and they are not well understood in terms of their drivers or scale. Several jaguar seizure events in range countries have taken place in touristic areas frequented by foreign and national tourists, suggesting that tourism may be an underestimated driver of jaguar trade (Braczkowski et al. 2019, Arias et al. 2020, CITES 2021).

Using online searches, we identified records that law enforcement could review for actionable information, and recommend additional online research in future to locate illegal trade to curb the threats to wild jaguar populations. Comparing the preliminary results of our online searches to other sources (Kerman 2010, Lemieux & Bruschi 2019, Verheij 2019, SERFOR & WCS 2020, World Animal Protection 2018) and team member experiences in the upper and lower Amazon, we note that even when sampling bias is avoided in online searches, variation in consistent electricity/internet across regions and trading contexts preferred among vendors means that online searches should be complemented by on-the-ground market reconnaissance and searches by mandated agencies. The greater Amazon includes nine of eighteen jaguar range states; the scale of the forest and porous international boundaries suggest that more research is advisable and greater vigilance and enforcement even in the more remote areas will be very important.

Recognising the international nature of the trade in jaguars, since November 2021 Suriname has deployed two specifically-trained jaguar detecting dogs at the international airport and other border posts. Increased enforcement in domestic commerce in Peru seems a priority. However, seizures without prosecution may elevate killing to replace stock lost. Tackling markets at all levels will require improvements in enforcement, surveillance efforts tracking different transportation routes, as well as improvement of capabilities and commitments to investigate and effectively prosecute wildlife poaching and trafficking cases.

The prevalence of jaguar parts in trade that we encountered, some of which may have originated in lethal responses to human-jaguar conflict, illustrates the importance of more effectively regulating local and national trade, so there are no disincentives to finesse coexistence due to a market that motivates killing jaguars for profit (Reuter et al. 2018). We also recommend greater efforts at effective outreach and investment that elevate the uptake of non-lethal conflict mitigation, as well as economic alternatives integrated with conservation that generate incentives to maintain live wild jaguars and intact natural wildlife communities.

A key issue that we identified, and which has also been raised by other attempts to collate and systematise information on jaguar trade (e.g. CITES 2021), was the lack of a centralised and reliable information on the matter. Reports of jaguar trade come from diverse sources varying in their quality and verification status, while data on official seizures made by enforcement authorities may be missing or unpublished. This has challenged the separation of facts from anecdotal information, and has presented challenges in evaluating the actual scale and trends of jaguar trade. The recommendations generated during the meeting of the jaguar range states in Cuiaba, Brazil, 18–22 September 2023 offer cause for optimism. Greater international collaboration to combat illegal cross-border trade is one of seven themes to be considered in a continental jaguar action plan. In addition, the CITES Standing Committee has requested that the Secretariat prepare terms of reference for the creation of modular system for monitoring illegal killing of jaguars and illegal trade in their parts and derivatives, which provides an opportunity to improve our capacity to evaluate the trade, and disrupt it (CITES 2023a, 2023b).

Almost all sampling includes some form of bias. Seizure data may be biased towards countries with greater enforcement capacity and reporting practices. Online searches may be biased towards areas with better electricity and internet accessibility. In this regard, there is a great value to proactive and carefully designed investigations that intentionally reduce bias (Arias 2020, Arias 2021a, Arias 2021b, Morcatty et al. 2020, Earth League International 2021) to support conservation. Cooperation between independent and academic researchers and national authorities, that include collaborative "methods and information transfers" can elevate knowledge and enable the interceptions that are important to disrupt the trade. Our recommendations are strengthened monitoring of physical and online markets to identify threats, supported by mandated law enforcement using existing mechanisms to disrupt trade in jaguar parts at all levels, local, national and international, whilst exploring multi-faceted approaches that do not criminalise vulnerable communities. Law enforcement should be complemented by social awareness, behaviour change and alternative livelihood programs that reduce the incentives to poach and trade jaguars.

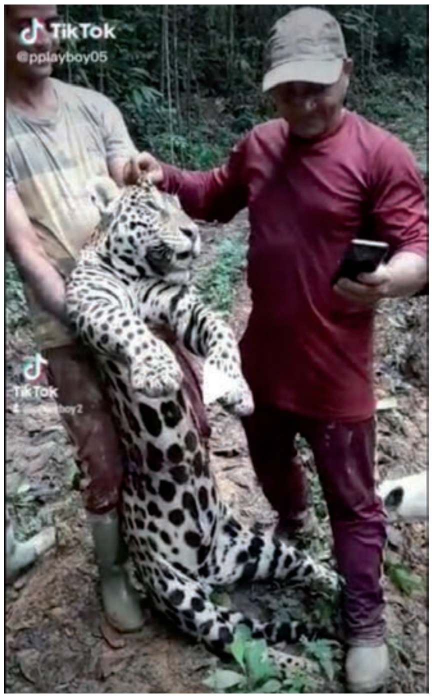

Fig. 5. Screenshot of a TikTok video posted in October 2021 of a freshly killed jaguar in Suriname's interior; the video remained online for several months after posting but has now been taken down (credit: pplayboy05/TikTok)

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Ex situ conservation of jaguar

Jaguars *Panthera onca* have been managed under human care for centuries for a variety of purposes. Until recently, jaguar management in zoological collections has tended towards a generic big-cat style, often to the detriment of species-specific psychological and behavioural considerations. Prospects for the jaguar's importance as a representative of eco-systems in which it lives, however, have improved. There are now four programmes (ALPZA, JAZA, AZA, and EAZA) that identify population sustainability, best practice animal care and jaguar welfare as primary objectives. Animals have (infrequently) been exchanged among EEP, SSP and ALPZA studbook institutions based on genetic and demographic recommendations. Both the SSP and EEP recognise that their animals serve as refugium populations, against a time when wild jaguars are so few that reintroduction could become necessary. Ex situ conservation includes significant potential to utilise data contained in studbooks and other documentation kept by zoos to inform and support field data and analysis. The EEP and SSP management teams collectively possess decades, if not centuries, of professional expertise with jaguar care and management. Accredited zoos have blended field and ex situ activity for some time as the OnePlan Approach has crystallised. There is reason for optimism: as there is a widening conservation niche for zoos, and a brighter, more robust outlook for jaguars.

Jaguars have been managed under human care for centuries for a variety of purposes. Spanish accounts of first contact with Mesoamerican civilisations mention jaguars kept by rulers and elites in menageries and for sacrifice (Schele & Miller 1986, Tedlock 1997). Down to the present day, the species has been held in private hands for a variety of other reasons, including as pets, status symbols, or as non-releasable animals rescued from unhealthy or dangerous captive conditions (S. Johnson, pers. comm.). Although none of these circumstances necessarily constitutes species conservation per se, just as some noteworthy professional jaguar hunters are recognised as contributors to conservation, some dedicated private holders have improved the understanding of jaguar behaviour and husbandry.

Since at least the last quarter of the 19th century, the species has also been managed in zoological parks with varying degrees of focus and success (AZA 2019). Whether kept as part of the 'complete set' of big cats, as a geographic representative or an apex predator, the jaguar's story in zoos has never been complete. Unlike tigers and lions, whose better-known ecological roles are frequent themes in popular culture and nature literature, the historically superficial and often inaccurate knowledge of jaguar traits and relationships continues to hinder meaningful conservation. The evolution of the modern wildlife conservation ethic – whose beginning dates to the publication of A Sand County Almanac by Aldo Leopold in 1949 – outpaced both the ability to manage jaguars sustainably ex situ and the emergence of a clear picture of wild jaguar ecology. As a result, the species has spent more than 60 years caught between perception as a menace to livestock and elevation to status as an ecological icon.

Until recently, jaguar management in zoological collections has tended toward a generic style, often to the detriment of species-specific psychological and behavioural considerations. One recommendation made by a veteran mammal curator when the first jaguar husbandry guidelines were written in 2003 was, "Take the tiger manual and make a global search/replace with the word 'jaguar'." While largely effective in terms of diet, security and other material parameters, that traditional approach had produced generations of zoo jaguars being treated symptomatically for chronic stress-related conditions without identifying the underlying causes. The recommendation for the husbandry manual was rejected but it remains evident that continued investigation into jaguar psychological welfare in zoo situations is necessary. Nevertheless, much of what is known first-hand about the jaguar life cycle, anatomy, physiology and other aspects of its particular biology comes from observations recorded and documents kept by professional zoos. This information serves as a foundation and comparative tool for field study and conservation.

In Latin America, zoos are frequently required to accept jaguars rescued or confiscated by wildlife authorities. While this is justifiably considered an ex situ conservation role, it can be complicated by negative impacts on animal welfare when over-crowding occurs or jaguars with health and behavioural conditions arrive unexpectedly. Managing this practice as a mutually beneficial partnership in which wildlife agencies and zoological institutions plan and prepare for the placement of jaguars could measurably improve their welfare while establishing collaborative networks to manage genetically and demographically healthy populations. The direct benefit would be to strengthen the services provided by zoos and, indirectly, positive attention from the public, conservation NGOs and other collaborators could generate support for habitat management and law enforcement.

Fig. 1. Asociación Latinoamericana de Parques Zoológicos y Acuarios Jaguar Studbook.

Professional animal management practices and data collection in zoos

Resulting from a burst of field research over the past two decades and focused interest in better zoo care for jaguars, prospects for the jaguar's importance as a real representative of the many ecosystems in which it lives have improved. In fact, the capacity to maintain ex situ populations is not in question and a number of resources are available to support the effort. For example, studbooks established and managed by zoo and aquarium associations document population histories through birth, death and pedigree data entry on individual animals. They are the foundations of collaborative species management programs, and four are kept for jaguars: in Europe, Japan and the Americas. Two zoo breeding and population management programs for the species are active as well.

The regional jaguar studbook for the Asociación Latinoamericana de Parques Zoológicos y Acuarios ALPZA (Fig. 1) is the newest, initiated in 2009 to consolidate zoo population data across the Americas outside Canada and the USA and represents 28 institutions. Studbook coordinator Lic. Adrián Sestelo, Fundación Bioandina, Argentina, identified it as the first step toward developing breeding plans across Latin American zoos that conserve ex situ genetic diversity for the species, while promoting cooperative management on a regional scale (ALPZA 2010).

A regional studbook for the Japanese Association of zoos and Aquariums JAZA has been kept since the early 1980s. JAZA maintains its JAZA Collection Plan JCP for rare species conservation. The jaguar is categorised in the Plan as a studbook species. The population manager investigates the regional population dynamics and publishes a studbook every year. JAZA member zoos work together to increase the population and its genetic diversity by means of domestic transfers and introduction of founders from abroad (JAZA 2019).

The European Association of Zoos and Aquaria EAZA maintains a regional studbook containing records dating back to the early 20th Century overseen by an EAZA Ex situ Programme EEP with 40 participating institutions. Anne Rikke Winther Lassen, Randers Regnskov Tropical Zoo, Randers, Denmark, is the studbook keeper and coordinator with the support of an EEP Species Committee representing nine EAZA zoos. Jaguar EEP members individually support in situ conservation and research for jaguars. The goal of the Jaguar EEP is to maintain a healthy population fulfilling the need of EAZA zoos to hold jaguars for exhibition, education and conservation research (R. Biddle former Jaguar EEP Coordinator and Studbook Keeper, pers. comm.).

The Association of Zoos and Aquariums AZA maintains a regional studbook including data back to the 1870s from zoos and facilities within and outside AZA. It manages a Species Survival Plan SSP with 46 AZA member institutions. Stacey Johnson, Roger Williams Park Zoo, United States of America, is the studbook keeper and SSP coordinator with the support of a management group and advisors representing four AZA zoos plus several retired professional colleagues and Jaguar SAFE (Saving Animals From Extinction) coordinator, representing 36 partner zoos and with the support of a management committee presently representing two AZA zoos (S. Johnson, pers. comm.).

All four programs identify population sustainability, best practice animal care and jaguar welfare as primary objectives. In its most literal sense this is the conservation of those animals in human care. Although infrequent, animals have been exchanged among EEP, SSP and ALPZA studbook institutions based on genetic and demographic recommendations.

Both the SSP and EEP recognise that their animals serve as refugium populations, against a time when wild jaguars are so few that reintroduction could become necessary. Their

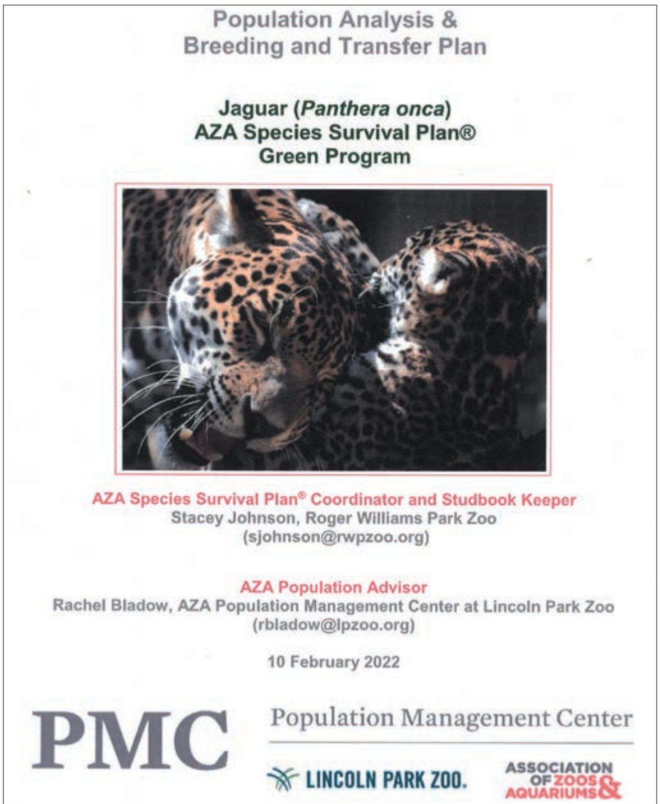

Fig. 2. Association of Zoos and Aquariums Jaguar Species Survival Plan® Breeding and Transfer Plan.

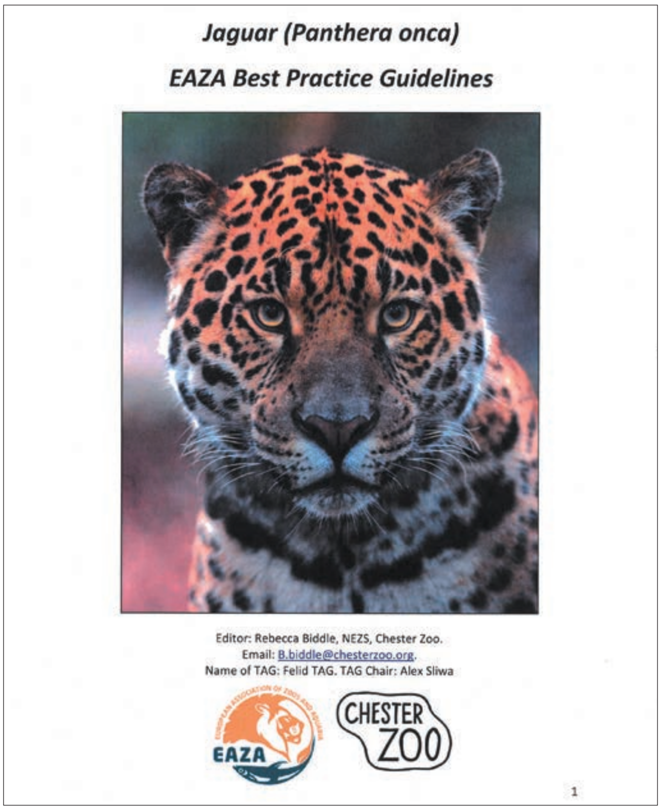

Fig. 3. European Association of Zoos and Aquaria Jaguar Best Practice Guidelines.

Fig. 4. Pronatura Península de Yucatán, Fort Worth Zoo, and the Instituto de Ecología of the Universidad Nacional Autónoma de México collaborated from 2004-2010 to estimate jaguar population density in and near the Ría Lagartos Biosphere Reserve (Photo: PPY-FWZ-IEUNAM).

Fig. 5. Participants in the IUCN SSC Cat Specialist Group workshop to draft a conservation strategy for South American jaguars, San Diego Zoo Safari Park, California, November 2019 (Photo: IUCN SSC Cat Specialist Group).

attention to genetic diversity and age distribution targets the conservation of an ex situ resource while keeping an eye on the potential for future in situ population rescue (Fig. 2).

Living jaguar somatic cells can be cryobanked reliably (M. Houck, pers. comm.), and the SSP is taking initial steps to identify and freeze a subset of its population to preserve genetic diversity. Semen has also been banked at several institutions and as assisted reproduction technology procedures (e.g. artificial insemination, in vitro fertilisation and embryo transfer) are developed for the species, gametes can be frozen and used in jaguars as they have been in domestic species. Again, such management may serve to ensure living zoo populations as well as offer insurance against wild population collapse in the future. Ex situ conservation includes significant potential to utilise data contained in studbooks and other documentation kept by zoos to inform and support field data and analysis. With varying levels of completeness, information on longevity, health, reproduction, behaviour, body size and other physical characteristics has been kept for over a century. Combined, the robust dataset in the four regional studbooks' historical populations represents more than 2,000 individuals.

The EEP and SSP management teams collectively possess decades, if not centuries, of professional expertise with jaguar care and management. The SSP produced a comprehensive, peer-reviewed Jaguar Care Manual in 2016 (AZA 2016); and the EEP produced its Best Practice Guidelines in 2019 (EAZA 2018; Fig. 3) with an additional Veterinary Guidelines document in preparation at the time of this writing.

Scientific investigation in laboratory and field lead to conservation action

Among professional zoos and aquaria, alliances of institutions with aligned interests may arise external to recommendations and requirements of association membership. For example, the Zoo Conservation Outreach Group ZCOG is a coalition of zoos and aquariums that promotes wildlife and habitat conservation throughout the Americas. ZCOG delivers technical, material, and financial support to institutional zoo colleagues and conservation programs in Latin America and the Caribbean Basin, and develops conservation leadership capacity through scholarships and training. Their conservation and research projects span numerous species and ecosystems, and have included jaguar monitoring in Brazil's Amazon, Atlantic Forest, and Cerrado biomes (D. Hilliard, pers. comm.).

Initiated for defined purposes or through the individual interests of investigators, scientific studies requiring long-term data and/or sample collection have been undertaken by zoos and their academic partners for decades. For example, post-mortem reproductive tissue samples have been collected from female SSP jaguars since the mid-1990s, first by the University of California, Davis, and now by Michigan State University. Results include numerous publications on female jaguar susceptibility to reproductive cancer. Subsequent research on mammary cancer in *Panthera* species has been supported by post-mortem and biopsy sampling of jaguars and by studbook pedigree data. Research into assisted reproduction techniques and technology for jaguars is presently underway, conducted by the Cincinnati Zoo and supported by numerous Jaguar SSP institutions.

In addition to grant-funded, large-scale research, many zoos have agreements with educational institutions to offer opportunities for experiential training to budding scientists from across a range of ages and levels, whether on-site data collection and analysis, through funding field programs or in combination. AZA has its Conservation Grants Fund, which offers financial resources for peer-reviewed proposals submitted by individual members, several of which have gone to jaguar projects since the turn of the century (AZA 2022).

Individual zoos have long worked singly or have banded together to support prioritised jaguar conservation endeavours (Fig. 4). Two additional present examples are the Randers Rainforest Zoo, Denmark, providing operating costs to the Bigai Biological Project in Ecuador (R. Biddle, pers. comm.) and the Jaguar SSP/ SAFE funding two full-time wildlife rangers for the Cockscomb Basin Wildlife Sanctuary in Belize (S. Johnson, pers. comm.).

The previous examples illustrate how accredited zoos have blended field and ex situ activity for some time as the OnePlan Approach has crystallised. Yet for decades, zoos already provided financial resources to universities, NGOs and individuals for a variety of jaguar programs and projects – especially since the advent of digital camera traps as a relatively inexpensive, highly effective, means of data collection. They have also served as controls and test sites for other emerging field techniques including hair collection and faecal genomic analysis. Their expertise in animal care, medicine, immobilisation and transportation is readily available and occasionally utilised by government agencies. So, as zoos continue to dedicate more resources and expertise to conservation and science the distinction between ex and in situ blurs. Regional zoo and aquarium associations that make accreditation a condition of institutional membership require increasingly rigorous attention to planning, execution and assessment of scientific investigation and conservation action (AZA 2022, EAZA 2022a, 2022b). A growing number of these zoos and aquaria employ trained scientists whose mandate is to conduct programs connecting their institutions with the natural world and to publish it in the scientific literature.

Finally, the workshop that led to this publication is an example of coordinated ex situ jaguar conservation leading to meaningful results for the species in situ. San Diego Zoo Wildlife Alliance responded to a need identified by the Cat Specialist Group for a multilateral South American conservation action plan with objectives, goals and funding to gather experts from range countries at its Beckman Center for Conservation Research (Fig. 5). Facilitated by the Specialist Group's co-chairs, whose stipend was provided by the Albuquerque BioPark, the workshop was the first meeting of its kind and was a deliberate first action to link the emergence of a coordinated conservation strategy with a regional zoo association's species conservation program. This plan is the blueprint for AZA's Jaguar SAFE programme for the coming decade (Fig. 6). While not every goal in the plan falls within the capability of Jaguar SAFE members, they can support most of them and, indeed, are positioned uniquely to achieve others.

Fig. 6. Jaguar SAFE (Photo: AZA).

Identifying and acting upon opportunities presented in this workshop to share ideas, expertise and resources among academic, government, NGO and professional zoo colleagues offers reason for optimism: a widening conservation niche for zoos, and a brighter, more robust outlook for jaguars.

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Past, present and future of the jaguar: review of threats, solutions, and research and conservation needs

Jaguars *Panthera onca* in South America are now found in only about half of the area they occupied in the early 20th century, and the rate of their decline is still high. The two most important drivers of the current decline are: a) deforestation and other habitat transformation and fragmentation, and b) killing jaguars related to conflicts with cattle ranching. Other important threats include illegal hunting and trade in jaguar body parts, increasing road density, and the rapid expansion of uncontrolled mining. Among the most important conservation achievements obtained so far are legal regulations that have eliminated legal jaguar hunting and trade in their parts in all countries, and the establishment of a network of protected areas across the jaguar range. The most urgent problems to solve are effective solutions to stop deforestation and stop the killing of jaguars in areas of conflict with cattle ranching. More protected areas are needed; however, it is also necessary to improve the functioning of protected areas. Ecological corridors have to be properly identified and implemented. Other important needs include enforcement of laws to eliminate the illegal jaguar hunting and trade, implementation of a system of environmental education, and the development of ecotourism. A coherent and effective common system of nature protection across South America would help to achieve the conservation goals. A number of international conventions and agreements support the conservation of jaguars, and in the recent years, significant new international initiatives have arisen to elevate the profile of jaguar conservation. We present and discuss needs for research, conservation solutions, and actions to stop the decline of South America's jaguars.

Jaguar population decline and its current situation

In the last 120 years, the range of the jaguar in South America decreased from about 14.9 million km^2 to 7.9 million km^2, and jaguars now occur in 52.9 % of their historic range (Sanderson et al. 2002, Jędrzejewski et al. 2023a). Moreover, not all of the area identified as jaguar current range is equally suitable for jaguars. Only 6.6 million km^2 (44% of South America's historic jaguar range) has been classified as an extant range with confirmed presence and well-preserved jaguar habitats (Jędrzejewski et al. 2023a). The rate of shrinkage of the jaguar's range remains high. The current (2020) estimate of jaguar distribution is 14% and 25% lower than the IUCN Red List assessments for 2015 and 2000, respectively (Caso et al. 2008, Quigley et al. 2018, Jędrzejewski et al. 2023a). The total estimated current jaguar population size in South America is 148,100 individuals (CRI: 112,900–182,700) with an average density of 1.9 jaguars/100 km^2 (Berzins et al. 2023, Jędrzejewski et al. 2023b, Thompson et al. 2023).

Overview of threats and their relative importance for jaguar decline

Current threat recognition

Habitat transformations, human-jaguar conflicts, hunting, and reduced natural prey availability have been proposed as the most important drivers of jaguar decline (Quigley & Crawshaw 1992, Nowell & Jackson 1996, Zeller 2007, de Oliveira et al. 2012, Jędrzejewski et al. 2017a, Quigley et al. 2018). However, recent studies have increased our understanding of the mechanisms leading to jaguar extirpations and range decline and they show that the strength of these factors vary. A number of studies on jaguar distribution showed that high forest cover, water abundance, high primary productivity (indicating high potential prey biomass) and the presence of protected areas are important factors that favour jaguar occurrence, while high human population density, high road density, large proportion of farmlands and pastures in the landscape, high degree of environmental degradation and habitat fragmentation have negative impacts on jaguar's distribution (Rodríguez-Soto et al. 2011, De Angelo et al. 2013, Olsoy et al. 2016, Paviolo et al. 2016, Jędrzejewski et al. 2017a, 2018, 2023a, 2023c, Morato et al. 2018, Portugal et al. 2019, Thompson et al. 2020, 2021a). Forest cover was one of the strongest positive factors in the jaguar distribution models at the continental scale (Jędrzejewski et al. 2018, 2023a), indicating that deforestation and other habitat transformations are indeed the main threat for jaguars. In the analysis of jaguar historical records, the largest declines of jaguar population coincided with the periods of the highest levels of deforestation and human expansion (Altrichter et al. 2006, Jędrzejewski et al. 2017a).

Habitat loss and degradation

The deforestation rate is increasing in several parts of the jaguar range causing disappearance of jaguars (Jędrzejewski et al. 2023a). For example, between 2001 and 2020, the Amazon region lost more than 543,000 square kilometers (9%) of forest, an area the size of France (Zanon 2023), with the highest deforestation rates in the Brazilian Amazon, followed by Bolivia, Peru and Colombia, overlapping significantly with the jaguar distribution (Fig. 1). The main factor driving current deforestation in South America is increases in the area of pasture and agricultural crops, mainly soybeans (Barona et al. 2010, Romero-Muñoz et al. 2020a, Menezes et al. 2021). The deforestation process is often carried out with the help of burning (Fig. 2), which often turns into uncontrolled large-scale wildfires that can have a profound additional impact on jaguar populations (de Barros et al. 2022). Deforestation causes direct loss of jaguar habitat; however, in the case of the Amazon, which has a significant impact on hydrological cycles and plays an important role in stabilising the global climate, this could also lead to disastrous consequences for the planet (Marengo et al. 2011, Lovejoy & Nobre 2018).

Deforestation is carried out in both private and public areas and is a complex process occurring within contrasting legal conditions in different countries. Effective protected areas are by far the best tool to prevent deforestation. Combating deforestation outside protected areas requires legal changes in many countries and significant strengthening of land management and timber supply control policies (Menezes et al. 2021, Barlow et al. 2016, Lambin et al. 2018, Trancoso 2021). Economic alternatives to deforestation and incentives for conservation should be fostered (Fearnside 2008). A global convention on stopping deforestation would possibly help (Erthal Abdenur et al. 2020, Rannard & Gillett 2021). Large-scale land conversions also occur in non-forest habitats, such as the Llanos (Fig. 3).

Legal logging and forest management, although not aimed at clearing forests, also generally have a negative impact on ecosystems, leading to profound changes in forest structure and loss of biodiversity, as well as a decrease in the density of many carnivores and their prey (Jędrzejewska et al. 1994, Putz et al. 2000, Gibson et al. 2011). However, the impact of logging depends on its intensity and post-logging practices (Burivalova et al. 2014). Low intensity selective logging in large contiguous forests does not cause the disappearance of jaguars (Tobler et al. 2018), although other trophic levels and general biodiversity may be affected (Tobias 2015).

Habitat fragmentation and increasing road density

Fragmentation of jaguar habitat and populations is increasing across South America, driven by deforestation to increase grazing land for cattle, agriculture and human settlements, and the development of infrastructure, mainly the road network (Petracca et al. 2014, Cullen et al. 2016, Jędrzejewski et al. 2017a, 2018, 2023a, 2023c, Thompson & Velilla 2017, Espinosa et al. 2018, Menezes et al. 2021, Martinez Pardo et al. 2022). Small and isolated animal populations, including jaguars, lose genetic diversity and have decreased chances of survival (Shaffer 1981, Soule & Simberloff 1986, Haag et al. 2010). Connectivity of jaguar habitats is still high only in the central core of the jaguar range, mainly in the Amazon and Guyana Shield (Jędrzejewski et al. 2023c), although fragmentation is increasing rapidly even there. Beyond this central core, connectivity between already fragmented jaguar populations is generally reduced, with examples of isolated sub-populations in the Atlantic Forest, the Caatinga, the Cerrado, the Llanos, and areas along the Andes. The impacts of fragmentation are exacerbated by the high and constantly growing density of roads in several parts of the jaguar range (Jędrzejewski et al. 2023c). Designating and protecting ecological corridors along with restoring habitats, building special passages for animals along roads and protected areas are the best tools to deal with the problem of fragmentation (Glista et al. 2010, González-Gallina et al. 2018, Hilty et al. 2020).

Human-jaguar conflicts, hunting and trading

The illegal killing of jaguars is a significant threat to their populations across the species range. The two main circumstances in which jaguars are killed are conflicts with cattle ranching and subsistence hunting, whose motivations for killing jaguars sometimes overlap, but have very different impacts on jaguar populations. Human-jaguar conflicts and the resulting retaliatory (or preventive) killing of jaguars occur in areas where livestock farming overlaps with the jaguar's range; in these areas, jaguars often kill livestock (mainly cattle), and ranchers kill jaguars (Hoogesteijn et al. 1993, 2002, Zimmermann et al. 2021). Conflict often follows deforestation and conversion of land to pastures (Fig. 4). In intense conflict areas, all jaguar mortality may be caused by humans (McBride & Thompson 2018). The retaliatory killing uses specialised methods and tools, for example, following jaguars with hunting dogs, waiting and shooting at prey carcasses, imitating jaguar roars and shooting when they come, using baited cage traps and poison. As a result, it can be very effective in eliminating jaguars and often leads to local jaguar extermination (Jędrzejewski et al. 2017b). Retaliatory killing, especially when related to deforestation, is one of the main drivers of jaguar range decline (Castaño-Uribe et al. 2016).

Jaguar killing can also be associated with hunting activities. Hunting in most of South America is for subsistence, with a goal to

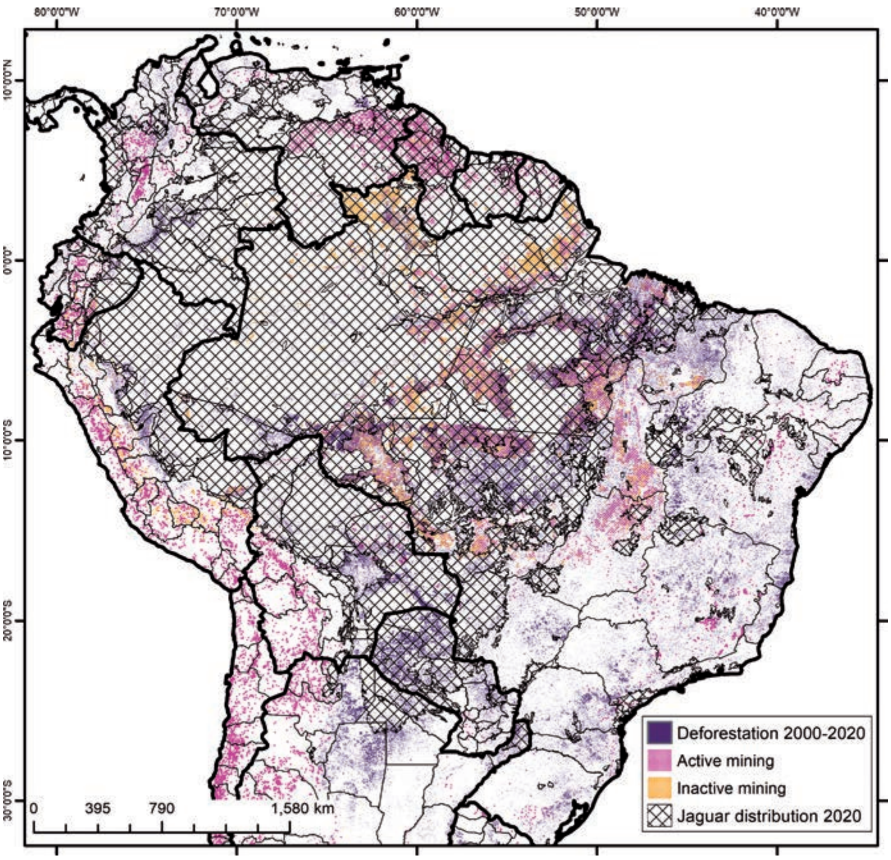

Fig. 1. Deforestation from 2000 to 2020 and areas with mining activities compared to the estimated jaguar distribution in South America in 2020. Mining areas are divided into active (with ongoing mining operations) and inactive (with concessions already granted or applied for). In the case of deforestation, the marked areas correspond to the actual deforested area. In the case of mining, general areas of mining activity are marked, not specific places of destruction; on the other hand, not all mining areas have been mapped yet and likely several are missing here. Mining areas often overlap with protected areas (see Jędrzejewski et al. 2023c). Sources: https://glad.earthengine.app/view/global-forest-change, https://www.raisg.org/es/mapas/ , https://mrdata.usgs.gov/. Jaguar range after Jędrzejewski et al. (2023c).

Fig. 2. Deforestation takes place through logging and fires and often encroaches deep into primary forests. Imataca Forest, Venezuela (Photo: W. Jędrzejewski).

collect meat and other products for family use and/or for sale (Redford and Robinson 1991). Most hunters focus on common game species rather than jaguars, but they may kill jaguars during chance encounters, so these hunts are opportunistic. Killing jaguars by subsistence hunters is very widespread (Fig. 5), it occurs over large, usually forested areas and the total numbers of jaguars killed can be high (Jędrzejewski et al. 2017b, Knox et al. 2019). However, because subsistence hunters do not usually focus on jaguars, on a large scale this type of jaguar hunting tends to be of low intensity (the number of jaguars killed per unit area is not high), and the overall impact on jaguar populations is generally low (Jędrzejewski et al. 2017b). Additionally, the beliefs of many indigenous groups do not allow the killing of jaguars which reduces jaguar hunting over vast areas (Espinosa et al. 2018). However, when opportunistic hunting overlaps spatially with retaliatory killing or habitat transformations – their synergistic effect may contribute to rapid local extinctions of jaguars (Jędrzejewski et al. 2017b, Romero-Muñoz et al. 2019). In some habitats, such as the flooded "várzea" forests of the central Amazon, jaguars become easy prey for hunters when they sleep in trees, and hunters may intentionally look for such jaguars, which increases the hunting rate and impact in jaguar populations (Ramalho 2012). Hunters may also focus on jaguars and their impact on jaguar populations may increase when they are further motivated by increased prices for jaguar-derived products (skins, fangs, meat), for example due to increased local or international trade, as happened in the 1950s through 1970s (Swank & Teer 1989, Payán & Trujillo 2006). Jaguar parts, especially skins, skulls, and fangs are often sold on local markets across South America, sometimes at high price and several lines of evidence suggest that this trade is widespread (Braczkowski et al. 2019, Arias et al. 2021, CITES 2021). Recently, several reports on the impact of an Asian market on the demand for jaguar parts, and potential increases in prices of jaguar body parts and rates of jaguar hunting throughout South America have been published (Morcatty et al. 2020, IUCN-NL 2023a, 2023b, Polisar et al. 2023a, 2023b); however, there is not yet enough information to quantify the total current effect of this new jaguar hunting incentive on jaguar populations.

Despite the fact that jaguars rarely attack humans, the reason for killing jaguars often stated in interviews is the fear and the belief that they may pose a threat to humans, which indicates the need for greater educational efforts (Marchini & Macdonald 2012, Hoogesteijn et al. 2016, Payán et al. 2016, Zimmermann et al. 2021).

Mining and petroleum extraction

Rapid growth of mining areas, especially gold mining and oil extraction is a growing problem across much of South America, especially in the Amazon and Guiana Shield region. It has been identified as one of the primary threats for jaguar populations in Bolivia, Brazil, Colombia, Ecuador, Guyana, Peru, and Venezuela (Berzins et al. 2023, Jędrzejewski et al. 2023b, Thompson et al. 2023, Bogoni et al. 2023). Mining has a number of negative impacts on jaguars and on nature in general. Mining causes large-scale deforestation, soil degradation and erosion (Fig. 6), contamination of ground waters and rivers, mostly with mercury, increased human encroachment, increased road density and high traffic in the forested areas, increased hunting pressure that includes jaguar hunting, bush-meat and jaguar body parts trade, increased crime, and decreased respect for the law. Most of these impacts occur in the core areas of the jaguar's range, in areas until recently considered pristine, and often also inside protected areas, including national parks (Fig. 1). For example, intensive mining has destroyed large areas within Brownsberg Nature Park in Suriname, the Iwokrama International Centre and Kaieteur National Park in Guyana, the Amazonian National Park in French Guiana, in Canaima, Caura, and Yacapana National Parks in Venezuela, Yanomami Indigenous Land in Brazil, and Serranía de San Lucas in Colombia (Rahm et al. 2017, RAISG 2020, Bogoni et al. 2023). Contamination with mercury is a particularly alarming problem as mercury is a powerful neurological toxin, both for humans and wildlife, including jaguars (May-Júnior et al. 2018). Oil extraction threatens the largest protected areas in Ecuador, Yasuní National Park and Cuyabeno Wildlife Reserve, which are the main strongholds for jaguar conservation in that country (Espinosa et al 2016, 2018).

Prey depletion

The reduction in the availability of potential prey due to hunting and other human activities has been suggested as one of the important factors limiting the distribution and density of jaguar populations (Miranda et al. 2018, Thompson et al. 2020). In many areas with a larger human population, low animal numbers are obvious, but subsistence hunting can importantly reduce the abundance of many large mammal species even deep in large forests (Redford & Robinson 1991 Benítez-López et al. 2017, 2019). The impact of hunting is generally lower in protected areas (assuming they are better safe-guarded than unprotected areas), but even there it is often present (de Carvalho & Morato 2013). Prey depletion is greater where road densities are higher, as roads increase accessibility to habitats for hunters and make hunting easier (Espinosa et al. 2014, 2018). Especially dangerous is the synergistic effect of hunting and environmental changes when they occur in the same areas, as it quickly reduces the distribution of many species of potential prey and may affect jaguar densities (Gallego-Zamorano et al. 2020, Romero-Muñoz et al. 2020b). However, more research is needed to assess whether, on a range scale, the impact of reduced prey availability is an important driver of jaguar range decline.

Climate change

Water abundance together with ecosystem productivity are among the crucial factors driving jaguar occurrence, density, and home range size (Jędrzejewski et al. 2018, 2023a, Thompson et al. 2021a, Morato et al. 2018, 2023). Expected climatic change and increasing aridification of lands can potentially have a strong direct and indirect effect on jaguars. Jaguars in arid and less productive environments are more sensitive to human impact and are extirpated faster than in humid and more productive habitats (Jędrzejewski et al. 2017a).

Relative importance of threats

A survey conducted among experts from the Cat Specialist Group (SSC IUCN) identified deforestation and habitat loss as the main threat causing jaguar population decline today (Berzins et al. 2023, Jędrzejewski et al. 2023b, Thompson et al. 2023). Human-jaguar conflicts, mining, road network development, and habitat fragmentation were identified as the other most important threats. Subsistence or opportunistic hunting of jaguars was assessed as important but usually not causing changes in jaguar distribution. In that survey, prey depletion was indicated as very important only in Ecuador. Other important factors listed by the group of experts included logging, lack of knowledge, low jaguar acceptance due to conflict or fear, poor law enforcement, and expansion of human settlements (Berzins et al. 2023, Jędrzejewski et al. 2023b, Thompson et al. 2023). However, one should be careful in interpreting the common understanding of threats and distinguish direct threats resulting from human activities (such as deforestation or killing jaguars) from the social or political determinants of such activities (such as lack of ecological education or poor law enforcement). The three most important threats that have proven to be the main causes of the continued decline of the jaguar range are habitat transformations (mainly deforestation), habi tat fragmentation and the killing of jaguars due to the development of cattle ranching (Table 1). Other threats obviously influence jaguar density and other population parameters, but probably do not currently significantly influence jaguar distribution. To address each threat, a different set of protective measures must be implemented (Table 1).

Review and evaluation of the most important jaguar conservation tools and approaches

Legal regulations to protect jaguars

The introduction of legal regulations aimed at protection of jaguars in individual countries at the end of the twentieth century, initiated by the CITES convention, largely stopped the international trade in jaguar skins and contributed to a decrease in the intensity of jaguar hunting throughout their range. Today, the jaguar is fully or partially protected by law in all countries. Hunting for jaguars and commercialisation of their parts are prohibited or limited to specific cases of problem individuals (e.g. those that attack livestock or are threat to humans) under special permits; however, licenses for hunting such individuals are practically not issued. Under existing legal regulations, the legal hunting for this species in jaguar range states is virtually nonexistent (Kretser et al. 2022).

However, it must be acknowledged that despite all these laws, illegal jaguar hunting and retaliatory killing, as well as trade in jaguar parts in local markets, are widespread and possibly increasing in some countries, showing that law enforcement is largely ineffective (CITES 2021). A larger problem is the lack of effective regulations to stop deforestation and other forms of destruction of jaguar habitats outside protected areas, especially within private lands.

Protected areas and indigenous territories

Protected areas, especially large ones, are the most important conservation tool to ensure the long-term persistence of jaguar populations (Table 1). They are the most effective tool to prevent deforestation and other habitat transformations, fragmentation, and reduce hunting rates (Naughton-Treves et al. 2005, Sollmann et al. 2008, Olsoy et al. 2016, Benítez-López et al. 2017, Jędrzejewski et al. 2018, 2023a). Indigenous territories are also of great conservation importance and help to protect jaguars (Figel et al. 2022, Bogoni et al 2023). In South America, protected areas and indigenous territories cover 29% and 20%, respectively (49% in total) of the total area of the jaguar range, which is an important conservation achievement. However, protected areas and indigenous territories are not evenly distributed throughout jaguar range in South America. The percentage of their area inside jaguar range is fairly high in Ecuador, Brazil, Bolivia, Peru, Colombia, French Guiana, and south-eastern Venezuela, while it is low in Paraguay, Argentina, north-western Venezuela, Suriname, and Guyana. In respect to ecoregions, the lowest share of protected areas is found in the Llanos in Venezuela and Colombia (13%) and in the Pantanal in Brazil, Bolivia, and Paraguay (19%; Jędrzejewski et al. 2023b, 2023d, Thompson et al. 2023).

However, designating a high percentage of protected areas does not mean a full conservation success. Even in the Brazilian Amazon, where a total of 56% of the jaguar's range is protected in some way, we must remain vigilant and prevent the destruction of the remaining 44%, which is a real threat and if it happens it will be a catastrophe for the entire ecosystem and for the jaguar population. Efforts should be made to ensure that the entire area of the Amazon and other most valuable and most sensitive ecosystems that have been preserved to this day, receive adequate

Fig. 3. Large scale habitat transformations occur also in open jaguar habitats, like The Llanos. Oil palm plantations, Colombia (Photo: R. Hoogesteijn).

Fig. 4. Deforestation, the subsequent conversion of land into cropland and cattle pasture, and the resulting conflicts with jaguars emerging from remaining forests and attacking cattle are the main reasons for the decline in the jaguar's range. Imataca Forest, Venezuela (Photo: W. Jędrzejewski).

protection and management to maintain their ecosystem integrity.

Not all categories of protected areas actually guarantee jaguar conservation (RAISG 2019). Probably national parks that combine area protection with local engagement and environmental education are the form of protection that best guarantees long-term conservation of jaguars. The size of protected areas is also important - if they are too small, their significance for the protection of jaguars is reduced. An important problem of protected areas is that many of them are not properly managed. Efforts should be made to ensure that protected areas, especially those located in more threatened regions, have and implement protection plans, employ properly trained staff, and conduct public education activities. Importantly, their educational and conservation impact must go far beyond the borders of protected areas.

Scientific research

Scientific research is at the heart of all nature conservation activities. Scientific research allows us to understand natural processes, detect human influences, set conservation goals, and often also indicate practical methods of protection. Researchers are most often the ones who initiate conservation campaigns and actions (Robinson 2006).

Jaguar conservation is also science-based, and many jaguar conservation programmes have been initiated by scientists and based on their research (e.g. Sanderson et al. 2002, Polisar et al. 2022). Recently, scientific research has resulted in an important increase in knowledge of jaguar biology and ecology and understanding of threats and mechanisms leading to jaguar population decline (reviews in: Berzins et al. 2023, Morato et al. 2023, Jędrzejewski et al. 2023a, 2023b, 2023c, Thompson et al. 2023). It is very important to maintain the link between jaguar conservation and scientific research, and to financially support jaguar science in parallel with conservation efforts. It would be desirable if large conservation funding institutions, as well as other responsible bodies (governmental and academic), also had their own specific programmes supporting jaguar research and monitoring, which could function as a metric of biodiversity and ecosystem conservation success (Polisar et al. 2022).

Education programmes and campaigns

Social sciences studies indicate that three main factors influence people's attitudes towards the illegal killing of jaguars: level of education, perception of the jaguar as a threat to human life, and level of fear from being persecuted by law if someone hunts a jaguar (Marchini & Macdonald 2012, St. John et al. 2015, Boron and Payán-Garrido 2016, Engel et al. 2016, Porfirio et al. 2016). Therefore, appropriate educational programmes at various levels of schools and through media campaigns can help protect jaguars by building public awareness, and in particular increasing understanding of the need to protect jaguars, reducing fear of jaguars, learning methods of protecting cattle against jaguar attacks, and also resulting in a lower level of social acceptance for jaguar hunting and deforestation (Baruch-Mordo et al. 2011, Marchini & Macdonald 2020). Several educational and promotional efforts have been made throughout the jaguar range in South America. For example, the Jaguar Forever educational program has been implemented in various Latin American countries and hundreds of students have participated (WCS 2006, Álvarez & Zapata-Ríos, 2022). Another example is the International Jaguar Day that has been publicised and celebrated in many countries all over the world (International Jaguar Day 2020). Nevertheless, studies measuring effectiveness of these efforts are needed.

Jaguar Conservation Units and Jaguar Corridor

The concept of the Jaguar Conservation Units JCUs was developed over 20 years ago by the Wildlife Conservation Society WCS to prepare a comprehensive science-based jaguar conservation program. In 1999, 35 jaguar experts from various countries across jaguar range prioritised 51 JCUs that were defined as areas with a stable prey community and believed to contain a population of resident jaguars large enough (at least 50 breeding individuals) to be potentially self-sustaining over the next 100 years (Sanderson et al. 2002, Zeller 2007).

The identification of these JCUs has stimulated the creation of new protected areas and led to the protection of many fragmented jaguar populations (Paviolo et al. 2016). JCUs were also the basis for analysing ecological connectivity and proposing a network of ecological corridors, known as the Jaguar Corridor (Rabinowitz and Zeller 210). They were also used in several other important ecological analysis related to jaguar conservation and its role as umbrella species for biodiversity conservation (Olsoy et al. 2016, Thornton et al. 2016).

However, it should be remembered that the concept of these units was born at the very beginning of efforts to protect jaguars throughout their range, when jaguar distribution was rapidly diminishing and the highest priority seemed to be the protection of most important or endangered populations (Sanderson et al. 2002). At the time, data was limited and knowledge about the distribution of jaguars was incomplete, and sometimes even incorrect. The JCU concept also did not take into account subsequent knowledge about the genetic structure of the population on the scale of the entire range of the jaguar (Lorenzana et al. 2020). The JCU designation process was affected by the composition of

Table 1. The main threats to the jaguar population, distinguishing whether they only affect population density or also cause local extinctions and reduction of the jaguar distribution (see text for explanations and evidence). For each threat a set of conservation measures is recommended.

Threats	Impact on densities	Impact on distribution	Recommended conservation measures
Deforestation and other habitat transformations	Yes	Yes	1. Protected areas 2. Law changes and law enforcement 3. Land management policies 4. Timber/soy/meat supply control 5. Incentives for local conservation and building public awareness
Habitat fragmentation and road network development	Yes	Yes	1. Ecological corridors 2. Habitat restoration 3. Protected areas 4. Constructing animal crossings on roads
Mining	Yes	?	1. Law enforcement 2. Protected areas and strengthening their protection 3. Territorial planning policies 4. Political decisions
Conflicts with cattle ranching and retaliatory killing	Yes	Yes	1. Introducing methods of protecting cattle against jaguar predation 2. Education and governmental assistance programs 3. Financial incentives for conservation in private lands 4. Development of ecological tourism
Killing jaguars in subsistence hunting	Yes	Currently no, potentially yes	1. Education programs and building public awareness 2. Incentives for local conservation 3. Development of ecological tourism 4. Law enforcement 5. Preventing and combating illegal trade
Prey reduction	Yes	Generally no, locally yes	1. Control of hunting activities; 2. Incentives for local conservation and alternatives for hunting; 3. Law enforcement.

the individual experts, their subjective experiences, and decisions made by them. Despite multiple subsequent attempts to verify and expand JCU areas (Zeller 2007, Panthera 2017, International Jaguar Day 2020, WWF 2020), many important jaguar populations still remain outside this network. The disappearance of those jaguar populations that are outside the JCUs would be a great loss for conservation, would mean a decline in jaguar numbers and range, and increase fragmentation of the range wide population. According to the Kunming-Montréal Global Biodiversity Framework, today's approach to biodiversity conservation should focus on preserving all existing biodiversity and halting or reversing biodiversity loss (Joly 2023). Thus, jaguar conservation should aim to protect the entire population throughout its range and prevent any part of it from being further reduced or fragmented, assuming that all surviving populations are equally important.

The concept of a network of jaguar corridors, initially designed to connect JCUs and collectively known as the "Jaguar Corridor", was introduced in the early 2000s to connect jaguar populations from Argentina through Mexico and enable dispersal and gene flow throughout the species' range (Rabinowitz and Zeller 2010). This innovative concept helped elevate the profile of jaguar conservation and attract resources which led to impacts in strategic areas and initiated processes still underway. The initial analyses and designation of these corridors were based on the JCU as nodes (centers) to be connected and therefore missed important jaguar populations and potential connections between them. Recent analyses, based on a larger and more contemporary set of field data, a more complete jaguar distribution estimate, and additional environmental variables, provide a different and more complete picture of the jaguar connectivity network (e.g. Thompson et al. 2020, Martinez Pardo et al. 2022, Jędrzejewski et al. 2023c). Thus, the localisation of ecological corridors and their prioritisation used in recent conservation initiatives, such as the Jaguar 2030 Roadmap (2018), should be verified and corrected.

Management of human-jaguar conflict

In each jaguar-range country, there are projects, mostly local, led by non-governmental organisations, aimed at mitigating human-jaguar conflicts and reducing the rate of jaguar predation on cattle. However, in South America, no country has any governmental system aimed at mitigating conflicts, in contrast to most European countries and some USA states, which have governmental programmes paying compensations to farmers for livestock losses caused by carnivores. Compensation programmes appear to be moderately effective as they have a snowball effect and implementation of methods to prevent jaguar attacks and incentives to encourage local conservation are more recommended (Muhly & Musiani 2009, Bautista et al. 2019). For jaguars and pumas in South America, better solutions would include training and supporting farmers and ranchers to implement preventive measures, that requires assistance programmes in conflict-affected areas (Hoogesteijn & Hoogesteijn 2010, 2014, Castaño-Uribe et al., 2016, Koprowski et al.

2019). Possible financial incentives include special certifications to help commercialise products, such as the Jaguar Friendly™ eco-label for ranches that do not kill jaguars, implement conflict mitigation measures and protect habitat, with successful examples from Colombia and Costa Rica (Koprowski et al. 2019, Dickman et al. 2023). Other possible incentives could include tax credits, environmental service payments and technical assistance and support to develop and promote ecotourism (Table 1).

Eco-tourism and jaguars

Promoting the development of ecotourism can help sustainably manage jaguars' habitats and protect them. On cattle ranches in the Pantanal, Brazil, the financial gains from ecotourism focused on jaguar sightings exceed the losses from jaguar attacks on cattle by several dozen-fold, which contributes to greater acceptance and protection of jaguars by cattle ranchers (Hoogesteijn et al. 2015, Tortato et al. 2017, 2021). Ecotourism on cattle farms has also developed in Los Llanos, e.g. in Hato Piñero and Hato Cedral in Venezuela, which resulted in conservation programmes and virtually eliminated hunting and clearing of forests in those areas, and contributed significantly to the survival of the jaguar population in the region (Polisar et al. 2003, Olmos Yat Sing and González-Fernández 2008, Jędrzejewski et al. 2014, 2023d). The opportunity to observe jaguars, or at least their footprints, is one of the elements that attracts tourists to the tropical forests throughout the Amazon, giving local communities the opportunity to earn extra money and shaping a positive attitude towards jaguar's protection. The development of ecotourism should be an important element of national jaguar conservation strategies.

Reintroduction programmes

Reintroduction programmes may be considered in areas where adequately sized, well-preserved habitats still exist, but jaguars have disappeared due to previous extermination or intensive hunting. An example of a successful action of this type is the reintroduction of jaguars in the Iberá region of Argentina (Zamboni et al. 2017, Avila et al. 2022).

National conservation strategies

Developing and then legalising a jaguar conservation strategy in each country is important for planning the best conservation solutions and achieving successful conservation outcomes. Such national plans also activate and involve governmental and scientific institutions, non-governmental organisations and private business sectors in conservation activities. At the moment, only four countries in South America (French Guiana, Guyana, Suriname, and Venezuela) still do not have national jaguar conservation plans.

Fig. 5. Subsistence hunters seeking other game species may sometimes hunt and shoot jaguars. This type of hunting, which usually occurs in vast forests, is widespread, however, has less impact on the jaguar population than retaliatory killing of jaguars in cattle areas. Bolivar state, Venezuela (Photo: W. Jędrzejewski).

International efforts for jaguar conservation

Global conventions

The three main global conventions that directly or indirectly affect jaguar conservation and related legal regulations in each country are: (1) Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), (2) the United Nations Convention on Biological Diversity CBD, and (3) the Convention on the Conservation of Migratory Species of Wild Animals CMS that is also known as the Bonn Convention (Trouwborst 2015, Kretser et al. 2022).

CITES regulates international commercial and non-commercial trade in endangered animal and plant species and obliges ratifying countries to implement appropriate legal regulations. CITES entered into force in 1975 and by 1996, jaguar hunting and trading was prohibited or strongly restricted in most of jaguar range countries across South America (CITES 1973, Kretser et al. 2022). The CITES Secretariat remains very active in undertaking various initiatives for jaguar conservation (e.g. CITES 2021).

The CBD is a United Nations treaty signed in Rio de Janeiro in 1992 aiming at the conservation of biological diversity and its sustainable use around the world. It obliges countries to revise and update national biodiversity strategies and action plans and to reduce the loss of habitats and improve the protection status of threatened species (CBD Secretariat 2016). An important addition to CBD is The Kunming-Montreal Global Biodiversity Framework (GBF), adopted by the Parties to the Convention on Biological Diversity during the 2022 United Nations Biodiversity Conference. The GBF aims to conserve and sustainably use biodiversity and halt and reverse biodiversity loss and includes specific goals and targets for halting species extinction, reducing extinction risks, maintaining genetic diversity, maintaining or restoring the integrity and connectivity of ecosystems, and significantly increasing the area of natural ecosystems by 2050 (GBF 2023, Joly 2023).

The CMS is an environmental treaty of the United Nations established in 1979 with the purpose to strengthen the conservation of migratory animals that cross national borders in their life cycle. In 2020, the jaguar was listed in Appendix I and II of this Convention, which obliges the parties to undertake commitments to protect target species, especially in transboundary areas, and to cooperate internationally to further achieve these goals (CMS

Annex I and II, 2019). In South America, only Colombia, Guyana, Suriname and Venezuela are not parties to this convention (CMS Secretariat 2020).

International organisations, programmes and initiatives

Many national and international organisations, governmental and non-governmental, are working to halt the decline of jaguars and ensure their long-term persistence. While three of the most prominent are the Wildlife Conservation Society WCS, Panthera, and World Wildlife Fund WWF, there are many other organisations, large and small, with merit in jaguar conservation.

The Jaguar 2030 Conservation initiative aims to achieve jaguar conservation on a range wide scale. It was launched in 2018 during the conference of parties of the UN Convention on Biological Diversity which was attended by the jaguar range state governments, international organisations (UN Development Program, UN Environmental Program, and CITES and CMS Secretariats), and non-governmental organisations (WWF, WCS, and Panthera; UNDP 2020). Central to the initiative is the Jaguar 2030 Roadmap, a living document, located on a UNDP website that, so far, has been endorsed by sixteen countries. Objectives of the Roadmap include strengthening the Jaguar Corridor by securing 30 priority jaguar landscapes by 2030, stimulating sustainable development, reducing jaguar-human conflicts, and increasing the security and connectivity of core protected habitats (Jaguar 2030 Roadmap, 2018. UNDP 2020). The Jaguar 2030 Initiative launched the International Jaguar Day (on November 29 each year) to promote jaguar conservation as an umbrella species for biodiversity conservation (International Jaguar Day 2020).

In September 2023, a meeting of 16 jaguar range States, represented by relevant government representatives, was held in Cuiabá, Brazil. It was organised by the CITES Secretariat in cooperation with CMS, the Jaguar 2030 Coordination Committee (which includes UNDP, UNEP, UNODC, Panthera, WWF, and WCS), the Amazon Cooperation Treaty Organization, and the government of Brazil. The parties agreed to collaborate and take actions to reduce the loss and fragmentation of jaguar habitat, mitigate or prevent negative interactions between humans and jaguar, monitor and reduce the illegal killing and illegal trade of jaguars, and monitor their population. They also agreed to work to raise funds for jaguar conservation and organise an intergovernmental platform to support jaguar conservation. It was also decided that CITES and CMS will work closely for jaguar conservation (CITES 2023).

Fig. 6. Gold mining is a rapidly growing threat, already widespread in jaguar core habitats. Mining causes large-scale deforestation, soil degradation and erosion, and mercury pollution of groundwater and rivers. Bolivar state, Venezuela (Photo: I. C. Ríos Málaver).

An important international organisation that puts forward many initiatives to protect wild cats, including jaguars, is the Cat Specialist Group (CSG) of the IUCN Species Survival Commission. CSG initiated or collaborated to prepare several conservation strategies and action plans for wild felids across the world, including jaguars in Americas (e.g. Nowell & Jackson 1996, Desbiez & de Paula 2012, SAJCAT 2023).

Information gaps, research needs, and conservation issues

Solid, science-based, up-to-date and defensible information on jaguar biology, ecology, and conservation situation is critical to conservation strategies, awareness raising, capacity building and education programmes, and to justify management and funding decisions made by national governments. Updated information on jaguar distribution, density and abundance, mortality and threats are high priority. There is a great need to develop a cost-effective and easy-to-implement standardised monitoring system for the entire jaguar range (Thompson et al. 2021). Standardisation of monitoring methods should include the collection of information on jaguar absence locations along with the jaguar presence records in order to refine distribution maps. Jaguar conservation will benefit from more long-term studies of population dynamics and demographic parameters (e.g. reproduction and mortality), movement and dispersal across habitats and ecoregions.

Various information and studies indicate that the jaguar population is genetically diverse and may consist of genetically distinct subpopulations inhabiting different ecoregions (Hoogesteijn & Mondolfi 1996, Lorenzana et al. 2020). Such population divisions likely result from genetically based adaptations to hunting different prey and living in different environmental conditions, analogically to other carnivores (Pilot et al. 2006, 2012). More local, regional and range-wide genetic analyzes based on larger genetic samples are needed. The results of such analyzes will have an important impact on our understanding of conservation needs and future conservation plans. A common obstacle to jaguar genetic research is that the authorisation procedures for such research resulting from CITES regulations and the Nagoya Protocol on Access to Genetic Resources equate scientific research with for-profit corporations seeking to exploit genetic resources, which often makes it very difficult, and sometimes impossible, to conduct genetic research for conservation and scientific purposes. This situation has to be changed quickly for the good of the species.

We also need a better understanding of the varying impact of hunting on jaguar populations in different countries and habitats, as well as the mechanisms that can lead to increased hunting rates and the factors that drive the ability of jaguar populations to compensate for human-caused mortality. It is important to develop an international system to monitor the illegal killing of jaguars and the local and international trade in jaguar parts, in line with CITES Decisions 19.110 and 19.111.

Another important need is to improve and implement human-jaguar conflict mitigation methods, which should include not only prevention of jaguar attacks of livestock, but also incentives to protect jaguars and their habitats. Application of conflict management systems in each country is desirable. A related need is to recognise the key role of private lands for jaguar conservation in many parts of the species' range and to develop conservation programmes targeting owners and users of these areas. Programmes for private lands should address both killing jaguars and deforestation and help developing alternatives (e.g. ecotourism).

It is also important to identify regions where jaguars have been eradicated but habitats can be maintained and restored so jaguars can eventually be reintroduced to these areas. It is particularly important to identify areas where environmental restoration and area protection would increase large scale ecological connectivity to improve the situation of isolated jaguar populations, and to act to institutionalise long-term protection of these key sites. On roads and highways with high traffic, which may constitute a serious barrier to jaguar movements, special passages for animals should be planned and constructed.

Recently, several political and organisational initiatives have been taken and several international high-level meetings have been organised to help protect jaguars (Polisar 2023). While these "top down" efforts are very important to secure funding of large-scale programmes, it is also crucially important to ensure the involvement of local organisations and stakeholders, including indigenous territories, ranching associations and conservationists, to build alliances and gain local community support for jaguar conservation in each jaguar-range country.

International cooperation is necessary to increase the effectiveness of all conservation activities. It is particularly important to develop a common, coherent conservation system across South America capable of countering the most important threats today, such as deforestation, the killing of jaguars on private cattle ranches, and illegal mining. Increased international cooperation should also include: 1) the joint monitoring program; 2) efforts to strengthen ecological connectivity and protect jaguar corridors; 3) stop illegal hunting and trading; 4) increase exchange of information and experiences; and 5) work towards more equally distributed research and conservation funding. Particular attention should be paid to adequate funding for both research and conservation activities in poorer countries. These expectations seem to be met by the commitments declared under the Kunming-Montreal Global Biodiversity Framework (GBF 2023), which announce the launch of financial instruments related to CBD and GBF as part of the eighth edition of the Global Environmental Facility (GEF-8). This funding is to support programmes that can directly and indirectly help protect jaguars and their habitats (GEF 2023). It is important that the funds also have impacts at local levels. Increasing public investments in biodiversity conservation in each jaguar range country would help. Finally, strategies for innovative jaguar landscape conservation funding that involve public-private partnerships are emerging and have great potential.

One obstacle for jaguar conservation funding comes from the fact that several donors prioritise species that are recognised by the IUCN Red List of Threatened Species as highly threatened (CR, EN, VU categories), while jaguar is listed as NR (near threatened) under this list. This policy should be changed. The high rate of jaguar decline, the importance of jaguars in neotropical ecosystems as well as the importance of the jaguar as an umbrella species should be significant arguments to convince funding agencies and organisations to include jaguar conservation into high priority list.

Conclusions – the need for solutions

We have to conclude that despite numerous conservation initiatives and introduction of regulations and other conservation tools in the last thirty years, South America as a whole has proven ineffective in combating degradation of jaguar habitats and stopping jaguar decline. The likely reason is that all these conservation efforts have been rather dispersed and lack systemic cohesion. This is particularly clear in comparison with the European Union, where the common sustainable development strategy, supported by uniform EU-wide legislative solutions (e.g. Birds Directive, Habitats Directive, and the extensive system of protected areas known as Natura 2000) largely contributed to stopping the decline in the number of large carnivores and even to their population growth and return to areas where they were previously exterminated (Chapron et al. 2014, Boitani & Linnell 2015, EC Environment 2023). The creation of a common and coherent conservation system for the whole of South America would ensure greater efficiency in biodiversity protection and would help meet the obligations arising from international environmental conventions (CITES, CBD, CMS) as well as climate change and the Kunming-Montreal commitments.

A second important reason for the failure to meet jaguar conservation goals is probably that the dominant conservation measures do not correspond to the current threats. The prevailing conservation initiatives over the last thirty years have been directed at combatting the hunting and trade of jaguar parts, while more recently deforestation and other environmental changes have been the major cause of jaguar population decline. While the efforts of many countries to establish a significant number of protected areas are to be greatly appreciated (though not equally in all countries), the fight against deforestation outside protected areas has not been adequately addressed. In addition to deforestation, the retaliatory killing of jaguars (as part of the human-jaguar conflict) also contributes to the current decline in jaguar distribution. Insufficient actions have been taken in this area, especially by national governments.

Given the current status of the jaguar and the above overview of threats, tools and conservation initiatives, we propose the following hierarchy of key conservation objectives that should be included in a common conservation policy to halt further decline and range reduction of the species:

1. Stopping deforestation and habitat transformation;
2. Strengthening protected areas, improving their management, and increasing their number and size;
3. Better management of human-jaguar conflicts, supporting the development of ecotourism and the conservation of jaguars on private lands;
4. Improvement of wildlife law enforcement for better control of the illegal jaguar hunting and trade;
5. Strengthening and protection of ecological connectivity;
6. Halting the development of uncontrolled mining and the destruction it causes in core jaguar habitats.

The history of the extinction of many species teaches that even very numerous and widely distributed species can become extinct in a very short time. Large carnivores are particularly vulnerable. In the early 20th century, lions *P. leo* and tigers *P. tigris* were relatively numerous and widespread, while today they are on the brink of extinction (Nicholson et al. 2023, Goodrich et al. 2022). The jaguar's range has already decreased by about 50% and the rate of population decline is still high, probably even accelerating. Only the combined efforts of governments, international and conservation organisations, scientific institutions and individual activists will prevent further decline of this species.

Jaguars inhabit a wide variety of tropical environments, which in turn are home to a huge number of other species. The presence of jaguars in a given area is an indicator of good habitat conservation and high biodiversity, while the absence of jaguars indicates significant transformation, destruction and loss of biodiversity (Thornton et al. 2016). By protecting jaguars, we protect numerous other species as well as whole ecosystems and their natural processes. When we protect the Amazon - the lungs of the world and a regulator of global climate, and other biomes within jaguar's South American range, we are protecting our home - the planet where we want life to survive, and humanity with it.

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SOUTH AMERICAN JAGUAR CONSERVATION ACTION TEAM

Regional conservation strategy for the jaguar in South America

The jaguar *Panthera onca* has been classified as Near Threatened in the 2017 IUCN Red List assessment (Quigley et al. 2018). However, jaguar population is declining fast: only in the last 20 years its range has decreased by about 20% (Sanderson et al. 2002, Jędrzejewski et al. 2023a) and the decline rate is likely speeding up. Jaguar conservation programs must aim to stop this negative trend. They also have to respond to all important threats identified by the studies presented in this volume that include: (1) deforestation and other habitat transformations carried out to enlarge livestock pastures and agricultural crops, (2) the killing of jaguars due to conflict with cattle ranching, (3) the killing of jaguars by hunters in natural areas, often related to the trade and trafficking of jaguar skins or other body parts, (4) habitat fragmentation and development of transportation infrastructure that disrupts the jaguar movements and gene flows, (5) development of mining, especially gold mining, that takes place in protected areas and destroys jaguar core areas (Berzins et al. 2023. Jędrzejewski et al. 2023b, Thompson et al. 2023). The studies also pointed to other problems, such as the small number of protected areas in some ecoregions (e.g. in the Llanos), poor law enforcement in most countries and the low level of ecological awareness and knowledge regarding jaguar biology and conservation problems. Any conservation plans also need to take into account the genetic differences among the jaguar populations inhabiting different ecoregions. This indicates a need to protect all jaguar populations with their unique, genetically inherited adaptations to exploit different habitats prey populations (Roques et a. 2016, Lorenzana et al. 2020). Other challenges are the necessity for more scientific research, continuous monitoring of jaguar populations across the continent and the need to expand international cooperation related to jaguar conservation.

Consequently, the IUCN Cat Specialist Group has set as a high priority to establish a long-term South American jaguar conservation strategy. In November, 2019, representatives with expertise in jaguar ecology, biology and conservation from all eleven South American range countries, plus three wildlife conservation non-governmental organisations, gathered to 1) review and assess the status and conservation needs of jaguars in South America, (2) update its current and historic distribution range maps, (3) develop a Regional Conservation Strategy as a baseline for future conservation work in this region and (4) identify priority actions for each country. This chapter is the result of the third objective in that list.

Planning process and workshop procedures

The development of the Conservation Strategy followed the IUCN Guidelines for Species Conservation Planning (IUCN SSC Species Conservation Planning Sub-Committee 2017) and, more specifically, the Strategic Planning Cycle as explained in the Cat SG's Cat Conservation Compendium (Fig. 1; see Breitenmoser et al. 2015).

The conservation status and needs of the jaguar in South America were reviewed by three regional working groups of experts ahead of the workshop and the results presented at the jaguar regional planning meeting that took place on 18–21 November 2019 (see Appendix II for a list of participants).

The status presentations served as information input for drafting the Range-wide Strategy for the Conservation of the jaguar. The draft version of this Strategy was developed in a participatory, multiple step approach according to the "Zielorientierte Projekt Planung" ZOPP (Fig. 2; see Breitenmoser et al. 2015), including the status reviews and analyses of Threats (Table 1) and resulted in the development of a logical framework (LogFrame; Table 2).

Following Breitenmoser et al. (2015), the strategic planning process included six steps:

1. Development of a Vision, which is a wishful perspective for the next 25–50 years, describing the ideal future scenario for the subspecies. It reflects an optimistic view of the future of the jaguar and is meant to be a source of inspiration;
2. Development of a Goal, which is a more concrete intention than the Vision. It is a feasible, realistic and measurable long-term aim (10 years) for the conservation of the jaguar;
3. Performing a Threat Analysis by analysing the Strengths, Weaknesses, Opportunities and Threats (SWOT analysis; Table 1);
4. Development of Objectives based on the Threats and Weaknesses. Objectives support reaching the Goal, directly address important Threats and Drivers, they are impact- and result-oriented, and realistic, achievable, and measurable;
5. Formulation of Results based on the Strengths and Opportunities. Results are the concrete achievements or direct outcomes needed to reach every Objective. Results are the direct outcome of the implementation of a Logical Framework (LogFrame) and should be SMART (Specific, Measurable, Achievable, Relevant and Time-bound);
6. Development of a number of clear and feasible Activities = Actions to achieve each Result, with a defined Actor, Indicator and a Timeline (Table 2). Implementation of Activities/Actions is the ultimate goal of the strategic planning process (Breitenmoser et al. 2015, IUCN – SSC Species Conservation Planning Sub-Committee 2017).

SWOT analysis

Evaluation of Threats faced by the jaguar across its range is crucial for the strategic planning of its conservation. Additionally, however, gaining an understanding of current Strengths, Weaknesses, and Opportunities can strengthen the conservation approach and is critical in order to identify appropriate measures to mitigate Threats and achieve conservation Objectives. Therefore, a SWOT analysis was performed during the workshops, during which the participants discussed Strengths, Weaknesses, Opportunities and Threats within their subjective Workgroup (WG). Subsequently, the outcomes were discussed in the plenary session and ranked in order to determine their relative importance (Table 1).

Weaknesses are shortcomings or gaps which hamper the conservation of jaguars. Based on the discussions, it became clear that poor regulation and law enforcement (both presence and prosecution), as well as a lack of biological/social science, knowledge and/or information are deemed some of the most important weaknesses (sum scores of 4). These weaknesses were followed by the suboptimal collaboration between institutions/NGOs and limitations to reach decision makers (sum scores of 3; Table 1).

A threat is a direct or indirect factor threatening the conservation of jaguars. Direct killing, whether this was retaliatory killing, out of fear, out of prevention, casual killing or as a result of trade or trafficking was ranked to be an important threat, together with habitat loss, resulting from mining, agriculture, ranching, infrastructure, and fires (sum scores of 4). Habitat loss due to unsustainable logging and urban development was ranked as relatively less important (sum scores of 2), followed by prey base depletion, climate change, civil unrest and direct killing of jaguars for hunting (Table 1). The weaknesses and threats discussed were later utilised in order to formulate Objectives

Strengths are qualities of this group supporting the conservation of jaguars. The strengths deemed most important (sum scores of 4) were those of increasing scientific interest in order to provide advanced knowledge and experience for jaguar conservation, the acceptance of the jaguar as a flagship species, followed by the improved management/awareness of PAs and increased landscape protection, cohesive communities of jaguar experts, conservationists and high levels of commitment, and the resilience of jaguars as a species (sum scores of 2; Table 1).

Opportunities were the present chances that we have to conserve jaguars. The opportunities deemed most relevant (scores of 2) were those of the current momentum, the Post 2020 Global Biodiversity Framework and other conventions, the timing and international attention, the opportunity to have the jaguar serve as a flagship species, the growing trend of (eco)tourism, the increased availability of technology and the increased demand for sustainable and environmentally-friendly products. The other opportunities were cumulatively ranked as 1. Together, these opportunities and strengths were utilised in order to phrase realistic Results and set realistic priorities (Table 1).

The strengths, weaknesses, opportunities, and threats discussed can be divided into eight general themes: (1) knowledge, information, data collection, and distribution; (2) direct killing; (3) monitoring of jaguars; (4) prey depletion; (5) habitat loss and degradation; (6) regulation and law enforcement; (7) cooperation; and (8) awareness and education. These themes were used to guide the development of Objectives, related Results and finally Activities, with their respective Actors, Indicators, and Timelines (Table 2). The four workgroups (Appendix II) each had the task to define 1–3 Objectives for their assigned themes, formulate related SMART Results and Activities, and then add Actors, Indicators and Timelines for each of these Activities throughout the 3rd, 4th and 5th day of the workshop.

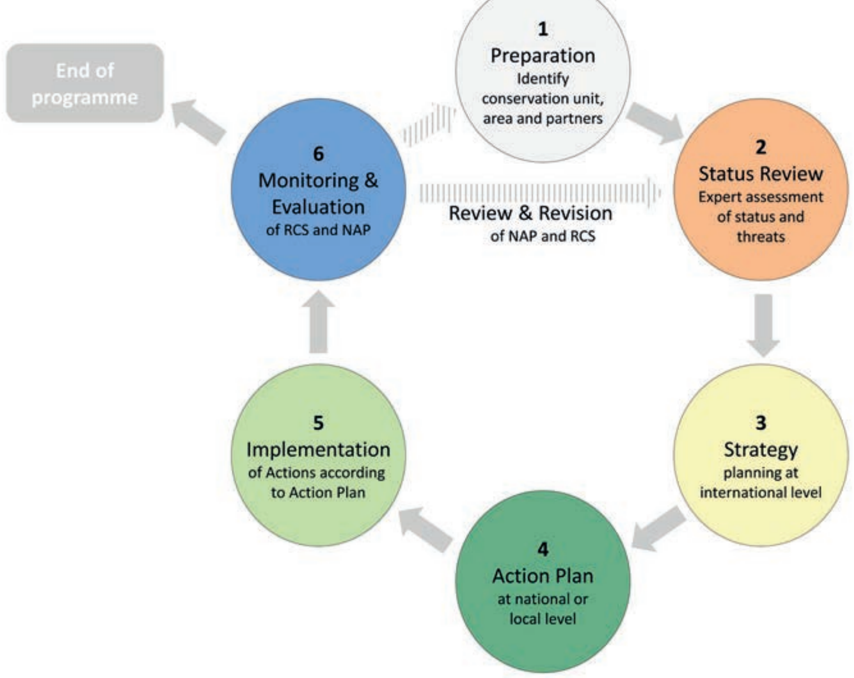

Fig. 1. The Strategic Planning Cycle. The preparatory steps (Points 1 and 2) are important for sensible planning, which is the first step to successful conservation. The actual planning process (done in participatory workshops) is covered by Points 3 and 4. The ultimate goal of the whole proce-dure is the implementation of conservation actions (Point 5), but these will only be successful if properly planned and subsequently monitored and evaluated (Point 6). The purpose of the whole participatory process is not to have a plan but the effective implementation of conserva-tion measures. This circle implies that conservation is an adaptive process (Breitenmoser et al. 2015). RCS stands for Regional Conservation Strategy.

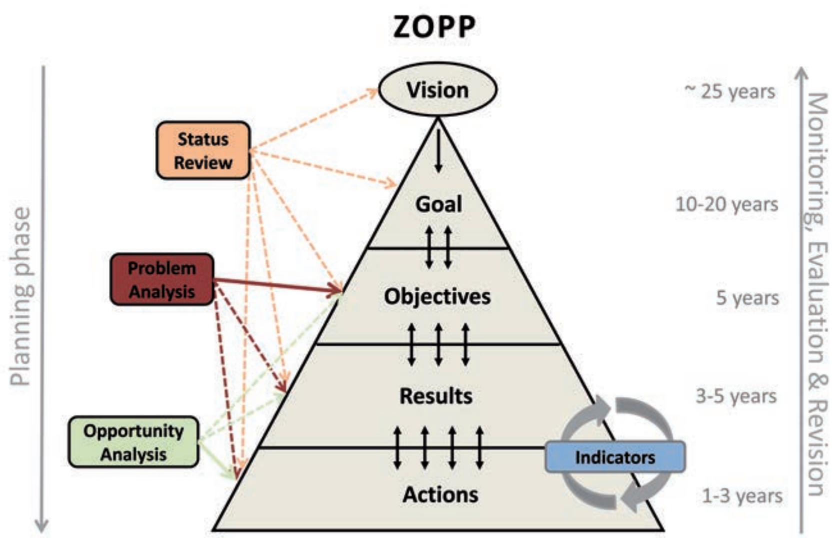

Fig. 2. The ZOPP ("Zielorientierte Projektplanung" goal-oriented project planning) pyramid as a scheme to explain the planning process in a participatory workshop. The ZOPP is an analytical process (Breitenmoser et al. 2015).

Table 1. Overview of the discussed weaknesses, threats, strenghts and opportunities, and their relative importance according to the four WGs, the higher the sum, the more important a respective weakness/threat/strenght/opportunity is deemed. Weaknesses, threats, strenghts and opportunities are ordered according to their ranked importance.

Weaknesses	**WG1**	**WG2**	**WG3**	**WG4**	**Sum**
Poor regulation & law enforcement (presence & prosecution)	X	X	X	X	4
Lack of biological/social science [4] knowledge/information	X	X	X	X	4
Suboptimal collaboration between institutions/NGOs	X		X	X	3
Limitations to reach decision-makers [2]		X	X	X	3
Corruption	X		X		2
Poverty/Lack of alternative/sustainable livelihoods and opportunities for people	X	X			2
Poor land-use planning	X		X		2
Inadequate capacity (knowledge, patrol, PA management)	X		X		2
Political instability/Slow political traction / poor governance / poor will	X		X		2
Lack of education and awareness and misconception of general public		X		X	2
Lack of suited PAs and proper management of PAs, and PADDD		X	X		2
Inadequate resources/investments – limited funding	X				1
Lack of biodiversity mainstreaming into different sectors		X			1
Lack of political will [3, 4]					0
Poor communication / lack of multidisciplinary cooperation					0
Threats					
Direct killing – retaliatory (livestock, dogs)	X	X	X	X	4
Direct killing – trade/trafficking	X	X	X	X	4
Habitat loss – infrastructure (hydro, transport, urbanisation)	X	X	X	X	4
Habitat loss – mining	X	X	X	X	4
Habitat loss – agriculture (palm, soy, …)	X	X	X	X	4
Habitat loss – ranching	X	X	X	X	4
Direct killing – fear/preventative/casual	X	X	X		3
Habitat loss – fire	X		X		2
Habitat loss – unsustainable logging	X		X		2
Habitat loss – urban development			X	X	2
Prey base depletion – sustenance and commercial hunting	X		X		2
Prey base depletion – same causes as above (habitat loss and direct killing)	X				1
Prey base depletion – invasive and feral species			X		1
Climate change		X			1
Civil unrest		X			1
Direct killing – hunting (sustenance/trophy)					0
Strengths					
Increase in scientific research/interest in jaguar range countries	X	X	X	X	4
Charismatic jaguar accepted as a flagship species	X	X	X	X	4
Improved management/awareness of PAs and increased landscape protection		X		X	2
Cohesive community of jaguar experts, conservationists/commitment		X		X	2
Resilience of the jaguar as a species			X	X	2
Increasing collaboration, information exchange between different actors		X			1
Existing legal frameworks protecting jarugaars across most countries		X			1
Private sector awareness in conservation		X			1
Existing conservation planning exercises		X			1
(Increased awareness from) international conventions			X		1
Conservation will			X		1
Cultural value of jaguars			X		1
Opportunities					
Current momentum	X			X	2
Post 2020 Global Biodiversity Framework, Conventions		X	X		2
Timing and international attention (funding and political leverage)			X	X	2
Jaguar as a flagship species, symbol	X			X	2
Growing (eco)tourism	X	X			2
Increased availability of technology	X	X			2
Increased demand for sustainable, environmentally friendly products	X	X			2
Attention of Cat SG		X			1
Carbon trade	X				1
Increasing (urban) public concern about environmental issues		X			1
Exchange of experience and lessons from other species, regions, etc.		X			1
Low human population density across jaguar habitats		X			1
Wide-ranging species			X		1
Indigenous movements to protect traditions/elevated voice of indigenous to protect	X				1
Increased attention to the role of private reserves in conservation		X			1

Regional Conservation Strategy

The ***Vision*** for the jaguar is the following:

A network of healthy jaguar populations coexisting with humans across their native South American habitats.

The ***Goal*** is

By 2035 priority landscapes will have stable jaguar populations and functional connectivity among them based on effective coexistence.

Objectives and Results

To work stepwise towards the Goal and counter the Threats and Drivers, nine Objectives, 30 related Results, and 100 related Activities were formulated within the eight themes described below. See Table 2 for the LogFrame with Objectives, Results and Activities with their respective Actors, Indicators, and Timelines.

Knowledge, information, data collection and distribution concerns the need to improve the understanding and data base on the ecology of the jaguar and the social science aspects (human-dimen-sion, conflicts) associated with its conservation to guide and prioritise effective conservation measures for the species.

Objective 1: **To fill knowledge gaps in jaguar ecology and social science aspects associated with jaguar conservation.**

Result 1.1: Knowledge gaps in jaguar ecology and social science aspects associated with jaguar conservation are identified by 2025.

Result 1.2: Funding is secured for research specifically filling the knowledge gaps identified under Result 1.1 by the end of 2025.

Result 1.3: Identified knowledge gaps, identified by Activity 1.1.4, are 50% resolved by 2028 and 100% resolved by 2033.

Result 1.4: Knowledge on the effect of disease(s) on wild jaguar populations is improved and demonstrated by at least two scientific publications per year by 2033.

Result 1.5: Necropsy manual for jaguar health, and for collection and storing of genetic samples from recently killed jaguars developed and distributed (Activity 1.4.4) by mid-2025.

Direct killing addresses the conflicts between humans and jaguars and how to mitigate those as well as the direct killing of jaguars by humans in retaliation, or for the legal or illegal use and trade; and the lack of law enforcement, political awareness and capacity to tackle these issues.

Objective 2: **To understand and reduce human-caused mortalities of jaguars**

Result 2.1: National protocols for addressing human-carnivore conflict in all South American jaguar range countries have been produced and begun implementation by the end of 2027.

Result 2.2: National/local social marketing campaigns are underway in all South American range countries to change attitudes towards/perceptions/social norms of jaguars by 2026.

Result 2.3: A minimum decrease of 10% in jaguar killing and trafficking though increasingly effective law enforcement, prosecution and other deterrents is documented by 2027; and a minimum decrease of 50% (compared to 2021 levels) by 2033.

Result 2.4: Sale of jaguar parts and products on local markets has been eradicated in South America by 2029.

Result 2.5: International airports in all range countries display information for tourists on jaguars and the illegality of all trade in (products of) jaguars by 2025.

Result 2.6: Social marketing campaigns to discourage use of jaguar parts have been implemented in at least two Asian markets by 2027.

Monitoring of jaguars tackles the lack of knowledge on jaguar population sizes, distribution and trends and the need to develop standardised methodologies and reference sites across its range for the long-term monitoring of the species across its South American range.

Objective 3: **To evaluate spatial and numerical trends in jaguar populations and the efficacy of conservation interventions.**

Result 3.1: Standards for data collection, management and communication to be utilised throughout this Strategy are established by mid-2025.

Result 3.2: An evaluation of existing data for spatial and temporal trends in jaguar distribution and abundance is underway by the beginning of 2026, with the goal of a first scientific publication by 2027.

Result 3.3: Baseline data on jaguar population status for unstudied areas in all South American range countries is published by 2031.

Prey depletion refers to the necessity to ensure an adequate prey species abundance to maintain a healthy jaguar population and satisfy the human needs.

Objective 4: **To ensure adequate prey species abundance for jaguars and humans.**

Result 4.1: Sustainable use of natural resources, jaguar-friendly agricultural production methods, and other forms of natural resources harvest are established to measurably begin ensuring a stable and abundant prey base in jaguar habitat by 2031.

Habitat loss and degradation addresses the need to conserve habitat and prevent habitat loss and degradation by identifying priority jaguar areas at regional and national level including those and corridors into land use plans as well as by efficient management of protected areas.

Objective 5: **To minimise loss, degradation and fragmentation of jaguar habitat.**

Result 5.1: At least five multilateral lending institutions include specific criteria for conserving priority jaguar landscapes in their agricultural, natural resource extraction, and real estate (larger than 10 hectares), loan eligibility requirements by 2026 (see also Jaguar 2030 – Conservation Roadmap for the Americas).

Result 5.2: Regional and national land use plans incorporating priority jaguar landscapes and corridors are adopted by all South American range countries by 2031 (see also Jaguar 2030 – Conservation Roadmap for the Americas).

Result 5.3: Verifiable measures for efficient management of protected jaguar habitat are in use across all South American range countries by 2031.

Result 5.4: In priority jaguar landscapes, production areas (agriculture, ranching, logging/forestry and mining) incorporate best practices compatible with jaguar presence/movement by 2031.

Result 5.5: Infrastructure in priority jaguar landscapes allows jaguar movement and can be demonstrated not to increase mortality of jaguars by 2029.

Result 5.6: All South American jaguar range countries implement fire risk maps, prevention and response protocols by 2031.

Regulation and law enforcement covers the problem of gaps in legislation and law enforcement in regard to the protection of jaguar, prey and their habitat and the shortfalls in resources to tackle these issues.

Objective 6: **To improve regulation and law enforcement regarding jaguars, prey and habitat protection.**

Result 6.1: For all South American countries, national gaps in legislation that apply to jaguar protection are identified by relevant authorities before the end of 2026.

Result 6.2: For all South American range countries, national shortfalls in resources for law enforcement related to jaguar conservation are eliminated by 2028.

Objective 7: **To promote decision making and political will towards jaguar conservation.**

Result 7.1: Natural resource management authorities and national decision-makers in all South American range countries can be demonstrably seen as allies for jaguar conservation by 2026.

Cooperation concerns the need to improve the cooperation across the distribution range of the jaguar in South America by creation of regional and national networks including researchers, institutions, governments, NGOs and local people (see also Jaguar 2030 – Conservation Roadmap for the Americas).

Objective 8: **To unite forces for jaguar conservation.**

Result 8.1: Regional and national networks for research, monitoring, and management of jaguars and their habitats in South America are implemented by 2025.

Result 8.2: Multilateral and bilateral cooperation among governments in South America to improve knowledge, enforcement and joint actions towards jaguar conservation are developed by 2026.

Result 8.3: In all South American range countries, improved management of landscapes, law enforcement and joint actions for jaguar conservation via better intra-government cooperation and communication are developed by 2026 and fully implemented by 2031.

Awareness and education addresses the need to enhance globally, regionally and locally the awareness and education for the species by producing education materials and guidance documents and by promoting the value and cultural significance of the jaguar so that it is recognised as a positive symbol.

Objective 9: **To make jaguars universally recognised as a positive symbol.**

Result 9.1: A continental scale education and awareness project under a common logo "All4Jaguars" (Todos por los jaguares, Allen voor de jaguar, Tudo para jaguares) is launched using nature conservation materials that follow local education standards and featuring jaguars and used in schools across all South American range countries by 2031.

Result 9.2: The jaguar is shown to be one of the most loved South American wildlife species by 2033.

Result 9.3: Presence of jaguars is utilised by all South American range country environment and agriculture agencies as a positive indicator of ecosystem health by 2031 (linked to Results 2.2, 2.6, 3.1, and 5.1–5.5, Activity 7.1.1).

Activities

Implementing conservation measures is the ultimate purpose of the planning process. Activities were hence defined to reach the Results, Objectives and ultimately Goal and Vision. Sets of Activities were developed by the working groups and discussed in the plenary to meet the respective Result. Typical timeline for an Activity is 1–3 years. Activities need to be very specific, including an actor and timeline, but ideally also selected methods, monitoring and assessing progress, and a budget. To define such details was not possible during the workshop. The simple LogFrame presented below (Table 2) hence will need to be further refined.

Table 2. Activities (three digit numbers) by Objectives and Results. Actor indicates the responsible implementer(s). Indicator signifies the outcome that should have been achieved. Time line is the expected date for finishing or the approximate period for implementing the respective Activity.

Activity	Actor	Indicator	Timeline
Theme. Knowledge, information, data collection and distribution			
Objective 1. To fill knowledge gaps in jaguar ecology and social science aspects associated with jaguar conservation			
Result 1.1. Knowledge gaps in jaguar ecology and social science aspects associated with jaguar conservation are identified by late 2025			
Activity 1.1.1 Working group identifies the major types of scientific data gaps currently present and sets a minimum of three specific, measurable, achievable, relevant and time-bound goals to close the gaps for each type identified		SAJCAT Working Group established and key contacts in each range country recruited to participate in activities	mid 2024
1.1.2. Design, and distribute to university researchers, non-governmental organisations (NGOs) and government scientists, a digital questionnaire on knowledge gaps in jaguar ecology and social science aspects of jaguar conservation	SAJCAT	Questionnaire sent to key contacts in all range countries	September 2024
1.1.3. Achieve a survey return rate of 100% and tabulate survey response data			January 2025
1.1.4. Develop and share document on survey results for revision and final approval to all participants (presented in Cat News)		Report/publication	October 2025
1.2 Funding is secured for research specifically filling the knowledge gaps identified under R.1.1 by the mid of 2025			
1.2.1 Inform and influence donor and NGO awareness on research priorities, as identified in A. 1.1.5, for jaguar ecology and social sciences associated with conservation	SAJCAT, identified group, Cat News editors, IUCN	Gaps specifically included in lines of funding	August 2024
1.2.2 Assemble teams and prepare proposals, including possible consortium	NGOs, researchers, institutions	No fewer than 20 proposals submitted that target identified gaps	November 2024
1.2.3 Using materials produced in A. 1.2.1, and 1.2.2, assemble a detailed list of no fewer than 20 sources of probable funding based on topics identified in 1.1.5, and associating each potential funder with a member of SAJCAT.	SAJCAT	List of sources published in platform (see A. 1.3.1)	December 2024
1.2.4 Formalise a host (e.g. one of the wildlife conservation NGOs) for this strategy and create a multi-institutional conservation fund to address the identified gaps/priorities	SAJCAT with leading NGOs	Funds available	July 2025
1.3 Identified knowledge gaps, identified by A. 1.1.5, are 50% resolved by 2028 and 100% resolved by 2033			
1.3.1 Create open online jaguar research and conservation platform within IUCN that is moderated by Working Group 1 of the SAJCAT (The platform is to become a source of information on all organisations/researchers/funders, publications, priority research locations and topics, with automated # projects per priority topic)	SAJCAT WG 1, under the auspices of the Cat SG to set up platform with information from NGOs, researchers, institutions, donors	Platform launched	2024

Activity	Actor	Indicator	Timeline
1.3.2 Conduct research and publish on specific topics to fill all knowledge gaps identified by A. 1.1.5.	SAJCAT, key contacts from 1.1.1, NGOs, academic institutions, range country environment agencies	Publications and reports filed with the platform of A. 1.3.1	2025–2033
1.4 Knowledge on the effect of disease(s) on wild jaguar populations is improved and demonstrated by at least two scientific publications per year by 2033			
1.4.1 Create summary of existing information from published and grey literature and formulate research hypotheses	San Diego Zoo, WCS, SAJCAT	White paper published in Cat News and posted to jaguar conservation platform (1.3.1) on existing information and proposed research needs	September 2024
1.4.2 Establish a consortium and develop a plan to evaluate domestic and wild vectors, transmission, and prevalence of pathology in jags, including an evaluation of impacts on populations	San Diego Zoo, WCS, SAJCAT, wildlife health professionals	Research proposals	End of 2025
1.4.3 Obtain funding and execute relevant research/studies according to the plan from 1.4.2 across South American biomes	San Diego Zoo, WCS, SAJCAT, wildlife health professionals, government agencies	Number of publications on impacts of disease on wild jaguar populations	End of 2031 (and ongoing)
1.4.4 Analyse, summarise, publish results of studies, and generate a protocol for long-term monitoring of health in jags (linked to R. 1.5)	Researchers, colleagues in wildlife health	Number of published papers and long-term monitoring	End of 2033
1.5 Necropsy manual for jaguar health, and for collection and storing of genetic samples from recently killed jags developed and distributed (A. 1.4.4) by mid 2025			
1.5.1 Review literature on existing guidance for jaguar health check and collection and storing of genetic samples	San Diego Zoo, WCS, AZA Jaguar Species Survival Plan	White paper published in Cat News, possibly AZA connect, and posted to online jaguar conservation platform	End of 2024
1.5.2 Review and edit white paper and develop necropsy manual	San Diego Zoo, WCS, colleagues	Finalised manual available through Cat SG and posted to online jaguar conservation platform	June 2025
Direct killing			
2. To understand and reduce human-caused mortalities of jags			
2.1 National protocols for addressing human-carnivore conflict in all South American jaguar range countries have been produced and begun implementation by the end of 2027			
2.1.1 For all South American countries, compile, evaluate and tabulate existing protocols, including information on content, origin (e.g. legislation, executive action or agency regulation), implementation, functionality and effectiveness	A coordinator with SAJCAT	Review paper on protocols is published in Cat News	End of 2024
2.1.2 Share existing protocols on the jaguar conservation platform (A. 1.3.1)	SAJCAT members (sharing protocols), Cat SG (uploading)	Protocols available on platform	Time of platform launch
2.1.3 Identify key stakeholders in each range country without a protocol and organise WGs to develop protocols	SAJCAT country representatives	List of stakeholders and their potential roles	End of 2024
2.1.4 Facilitate enhancement of existing protocols and advocate for production and approval of new protocols at appropriate levels in all South American countries	SAJCAT country representatives with identified stakeholders	Approved protocols established in all range countries	Mid 2026

Activity	Actor	Indicator	Timeline
2.1.5 Establish training resources and programs to implement protocols in all South American countries	SAJCAT, NGOs, IUCN, governments	Annual reports recording the number of agents trained and the number of times protocol(s) are applied in response to conflict reports in each country; resources available for conflict response per country	Starts with completion of 2.1.4, and is indefinitely
2.2 National/local social marketing campaigns are underway in all South American range countries to change attitudes towards/perceptions/social norms of jags by 2026			
2.2.1 Share existing initiatives and materials for wildlife awareness campaigns, with emphasis on jags, on platform created under Activity 1.3.1.	SAJCAT group, NGOs, researchers and institutions, IUCN	Materials available through platform (1.3.1)	Time of platform launch
2.2.2. Utilising the survey results document from Activity 1.1.4 and the human-carnivore conflict review paper from Activity 2.1.1, organise a working group of social scientists to identify and prioritise a minimum of ten desired human behaviour changes to be affected at appropriate scales (e.g. individual, local, regional, national)	Social science researchers	Reports/publications identifying priority areas for behavioural change	Beginning of 2025
2.2.3. Facilitate the creation of three international alliances (North-west, North-east, Central-South) to develop and implement behaviour change campaigns using the report output from Activity 2.2.2.	NGOs, governments, researchers, civil society, special interest groups	Number of target audiences and persons reached with campaigns	End of 2025
2.3 Document a minimum decrease of 10% in jaguar killing and trafficking though increasingly effective law enforcement, prosecution and other deterrents by 2027; and a minimum decrease of 50% (compared to 2021 levels) by 2033			
2.3.1 Review, analyse and document existing legal frameworks and enforcement activities for jag conservation across all South American range countries	WCS, Panthera, WWF-FVSA, IFAW	Publication in Cat News & availability on online jag conservation platform (1.3.1)	2024 (with platform launch)
2.3.2 Establish a working group to identify anti-trafficking and anti-poaching training practices and levels for law enforcement and judicial officers in all South American range countries	SAJCAT WG 1		End of 2024
2.3.3 Working group from A. 2.3.2 confirms application of training, resources and field practices against trafficking and poaching in all South American range countrie.			Mid 2025
2.3.4 Develop legal and law-enforcement training resources targeted to reduce jag killing and trafficking and make them available throughout South America	SAJCAT WG1, NGOs, governments, Interpol	Training materials adopted by all range countries	Beginning of 2026
2.3.5 Advocate for budget allocation and contributions for adequate support and implementation of training materials developed in A. 2.3.3.	SAJCAT, NGOs, governments	Amount of funds available for enforcement; # people trained per country, # enforcement incidents	End of 2026
2.3.6 Compare the numbers of jaguar killing and trafficking of 2023 to that documented in 2026 and 2032	SAJCAT WG 1	Report on # jaguar killings and trafficking in 2023 compared to that in 2026 and 2032 available	2033
2.4 Sale of jaguar parts and products on local markets has been eradicated in South America by 2029			
2.4.1 Conduct an informal survey of field scientists, NGOs, journalists and wildlife agency field officers to Identify and compile a list of the main markets, businesses and traders selling illegal wildlife products at national levels in each range country	SAJCAT WG1, Researchers, NGOs, governments, journalists	List of main markets, businesses and illegal traders, and estimates of annual value traded, made available to range country wildlife agencies and judiciaries	End of 2024

Activity	Actor	Indicator	Timeline
2.4.2 . Facilitate the adoption of official action plans by each range country to eliminate trafficking in jaguar parts and products	SAJCAT WG1, Researchers, NGOs, governments, journalists	Action plans adopted by every range country	End of 2025
2.4.3 . National wildlife authorities utilise action plans generated by A. 2.4.2 to confiscate contraband materials of significant actors and successfully prosecute them according to applicable laws	Governments (law enforcement)	# apprehensions, material confiscated and penalties	Start of 2026 (and ongoing)
2.5 International airports in all range countries display information for tourists on jags and the illegality of all trade in (products of) jaguars by 2025			
2.5.1 Design universal displays against South American wildlife trafficking for airports in representative languages (limit wording)	Graphic designer, SAJCAT supervisor, national CITES authorities	Design approved by SAJCAT and national CITES authorities	End of 2024
2.5.2 Design an airline screen announcement per jaguar range country destination with information on products not to buy	Graphic designer, SAJCAT supervisor,	Video approved by SAJCAT	End of 2024
2.5.3 Identify airports, airlines, and actors to install and fund the displays	SAJCAT, national CITES authorities	List of formal agreements with airports and airlines to display for agreed-upon duration	Mid 2025
2.5.4 Produce and distribute displays	Depend on 2.5.2	Number of airports with display	October 2025
2.6 Social marketing campaigns to discourage use of jaguar parts have been implemented in at least two Asian markets by 2027			
2.6.1 Using results and connections with social scientists engaged in achieving R. 1.2 and 1.3, conduct research on the jaguar market and target audience in Asia to evaluate what has already been done to discourage use of jaguar parts	SAJCAT WG1, social scientists from 1.2 and 1.3	Report on markets and audiences produced	End of 2024
2.6.2 . In collaboration with Asian counterparts who can advise on platform, language, design and cultural values, design social marketing campaigns to discourage use of jaguar parts	Social marketing group under supervisions of SAJCAT and Asian counterparts, WildAid, IFAW	Social marketing product	End of 2025
2.6.3 Assess the effectiveness of the campaign		Number of platforms and locations where campaign is launched	Beginning of 2027
2.6.4 Adapt and renew (or discontinue) the campaign	SAJCAT, Asian counterparts, social marketing group	Campaign updated or discontinued	Mid 2027
Monitoring jaguars			
3. To evaluate spatial and numerical trends in jaguar populations and the efficacy of conservation interventions			
3.1 Standards for data collection, management and communication to be utilised throughout this Strategy are established by mid-2025			
3.1.1 Develop standardised methods for data collection so that results can be integrated and compared with each other across the jags' range (interviews, camera trapping, disease, etc.)	SAJCAT, facilitated by WG1	Methods developed, results integrated and compared	Mid 2025
3.2 An evaluation of existing data for spatial and temporal trends in jaguar distribution and abundance is underway by the beginning of 2026, with the goal of a first scientific publication by 2027			
3.2.1 Make longitudinal estimations of jaguar population numbers and distribution in all range countries/important areas (Jaguar Conservation Units JCUs)	SAJCAT, Academic institutions, NGOs		October 2024
3.2.2 Elaborate standardised methodology for monitoring of distribution and population numbers/trends/densities	SAJCAT coordinated by M. Tobler	Manual produced as appendix to peer-reviewed publication	Beginning of 2025
3.2.3 Select and establish long-term monitoring sites across the jaguar range, representing all significant biomes and geographic regions, which will utilise the methodology published in Activity 3.2.2 for a minimum of five years	SAJCAT, researchers, NGOs, governments	Lists of sites with confirmed and funded projects	Mid 2025

Activity	Actor	Indicator	Timeline
3.2.4 Implement standardised methodology, as elaborated under A. 3.2.2. at all selected long-term monitoring sites (as defined under A. 3.2.3)	Researchers across jaguar range with SAJCAT WG1 monitoring and reporting progress to the Cat SG	Semi-annual notes published in Cat News of sites with established monitoring programmes	Beginning of 2027
3.2.5 Quantify conservation interventions by category, actors and financial investments. Associate conservation interventions to five-year population trend investigations undertaken in A. 3.2.4.	Researchers, governments, Paviolo et al.	Review of publications on impacts of interventions on jaguar populations	2031
3.3 Baseline data on jaguar population status for unstudied areas in all South American range countries is published by 2031.			
3.3.1 Identify areas lacking data on jaguar population presence, distribution, abundance and/or density published in scientific literature since 2000.	SAJCAT, coordinated by WG1	List of areas published in Cat News	End of 2024
3.3.2 . As of 2024, recruit projects to obtain presence data, estimates of population size and distribution from areas lacking information, as identified by A. 3.2.2, following standardised methods as defined under A. 3.1.1., and with the goal of initiating at least two studies per year	Researchers, NGOs, facilitated by SAJCAT	# publications, # sites researched	2025–2031
Prey depletion			
4. To ensure adequate prey species abundance for jaguars and humans			
4.1 Sustainable use of natural resources, jaguar-friendly agricultural production methods, and other forms of natural resources harvest are established to measurably begin ensuring a stable and abundant prey base in jaguar habitat by 2031.			
4.1.1 Develop standardised methods for data collection so that results can be integrated and compared with each other across the jag's range (interviews, camera trapping, disease, etc.)	Governments, NGOs, academia, research institutes	Number of jaguar habitats assessed	2026 (and ongoing)
4.1.2 Establish monitoring programmes for population trends of prey species (linked to Objective 3)		Number of monitoring programs established.	2027
4.1.3 Incorporate prey species into natural resource management frameworks (e.g. timber, Acaí, Brazil nuts, rubber, REDD+).	Private sector, producers, Governments, NGOs, academia, research institutes, local communities	Number of management frameworks, conservation agreements, and financial tools that include prey species as indicators.	2029
4.1.4 Develop and implement national or community-level management plans for wildlife species harvest in jaguar habitats	Government, NGOs, academia, research institutes, local communities	Number of management plans.	2029
4.1.5 Create and promote land-use practices compatible with the maintenance of abundant prey species	Governments, NGOs, academia, research institutes, private sector, engineering companies, construction companies, financial institutions	Number of systems developed	2029
4.1.6 Develop and implement innovative financial schemes towards maintaining prey species diversity and abundance	Financial companies, private sector, governments, development banks	Number of innovative schemes, amount of finances	2031

Activity	Actor	Indicator	Timeline
Habitat loss and degradation			
5. To minimise loss, degradation and fragmentation of jaguar habitat			
5.1 At least five multilateral lending institutions include specific criteria for conserving priority jaguar landscapes in their agricultural, natural resource extraction, and real estate (larger than 10 hectares), loan eligibility requirements by 2026 (see also Jaguar 2030 – Conservation Roadmap for the Americas)			
5.1.1 Develop guidelines for desired conservation outcomes and maps that identify priority jaguar areas in each country, at regional level	SAJCAT, facilitated by WG2; BINGOs (Big International NGOs), other NGOs, other specialists (multidisciplinary)	Criteria and maps available for South America through the Cat SG.	2025
5.1.2 Develop a communication and engagement strategy to approach the institutions	IUCN SSC CPSG, BINGOs	Communication and engagement strategy available	2025
5.1.3 Recruit and assist at least five major lending institutions in incorporating the criteria defined under A. 5.1.1 into their loan eligibility requirements	SAJCAT, IUCN, BINGOs, Lending Institutions	Number of institutions that have incorporated jaguar criteria into their requirements	2026
5.2 Regional and national land use plans incorporating priority jaguar landscapes and corridors are adopted by all South American range countries by 2031 (see also Jaguar 2030 – Conservation Roadmap for the Americas)			
5.2.1 Develop jaguar conservation criteria for land use and maps that identify priority jaguar landscapes at national level	SAJCAT; BINGOs, other NGOs, other specialists (multidisciplinary), Jaguar 2030 Roadmap Coordination Committee	Criteria and maps available for all countries	2025
5.2.2 Perform gap analysis of protected areas for jags throughout South America at national level	SAJCAT; Academia, National Governments, BINGOs, other NGOS	Gap analysis produced and published in scientific literature, including tiered recommendations for establishing new protected areas	2026
5.2.3 Develop a communication and engagement strategy to approach the national authorities to promote priority jaguar landscapes	SAJCAT, IUCN SSC CPSG, BINGOS	Communication and engagement strategies produced	2027
5.2.4 Utilising the published gap analysis produced in A. 5.2.2, and the strategy prepared in A. 5.2.3, meet before the end of 2027 with appropriate agencies in each range country to promote the creation of new Protected Areas where needed	SAJCAT, National Governments, IUCN Global programme on Protected Area, World Commission of Protected Areas	# new protected areas	2028
5.2.5 Utilising all the materials produced and relationships established in the activities under Results 5.1 and 5.2, recruit relevant stakeholders to support and participate with authorities in developing zoning and management plans that strengthen implementation of priority jaguar landscapes and corridors in all South American range countries	SAJCAT, IUCN, BINGOs, and other NGOs, Governments at different levels	# zoning and management plans that consider jaguar conservation	2030

Activity	Actor	Indicator	Timeline
5.2.6 Others and actors engaged in A. 5.2.1–5.2.5, assist authorities in developing incentives and public policies that promote jaguar conservation and promote positive circumstances for coexistence with humans	SAJCAT, IUCN, BINGOS, and other NGOs, Governments at different levels, multidisciplinary specialists	# incentives promoting jaguar conservation, extent of area covered by jaguar conservation incentives, # countries that have public policies aligned with jaguar conservation	2031
5.3 Verifiable measures for efficient management of protected jaguar habitat are in use across all South American range countries by 2031.			
5.3.1 Develop standard indicators of and evaluate the management status of key protected areas, as identified in maps produced under A. 5.2.1, to identify successes, needs and gap.	SAJCAT facilitated by WG2, BINGOs, and other NGOs, National Governments, IUCN Global programme on Protected Area, World Commission of Protected Areas	# protected areas that have undergone assessment	2026
5.3.2 Utilising assessments conducted in Activity 5.3.1, acknowledge high-performing key protected areas, if possible, using recognised certification schemes (e.g. Green List, Conservation Assured / Jaguar Standards) and improve management of others using certification as incentive	National Governments, SAJCAT, BINGOs and other NGOs	# of protected areas that are under the Green List and/or other certification schemes	2028
5.3.3 In conjunction with R. 3.2, conduct long-term jaguar population monitoring in key protected areas	SAJCAT, Researchers across jaguar range with SAJCAT WG1 monitoring and reporting progress to the Cat SG, National Governments	# protected areas with long-term jaguar population monitoring jaguar population estimates	2029
5.4 In priority jaguar landscapes, production areas (agriculture, ranching, logging/forestry and mining) incorporate best practices compatible with jaguar presence/movement by 2031			
5.4.1 Develop best-practice guidelines for production activities compatible with jaguar presence/movement, specifically considering and including outputs from A. 5.1.1, 5.2.1, 5.2.5, and 5.2.6.	SAJCAT, other jaguar specialists, multidisciplinary specialists, government and other sectors (production and other)	Guidelines for different production activities designed	2026
5.4.2 Recruit stakeholders from all facets of Objective 5 to collaborate with authorities in all South American range countries to develop public policies that are aligned with priority jaguar landscapes, particularly including outputs from A. 5.3.1 and 5.4.1.	SAJCAT, National Governments, BINGOs	# countries with public policies aligned for jaguar conservation, changes in jaguar habitat extension	2029
5.4.3 . Include jaguar presence/abundance as a criterion to provide conservation-related certifications such as FSC, WHC, among others.	SAJCAT, Certification agencies, BINGOs	# international certifications that include jaguar abundance as a criterion	2031

Activity	Actor	Indicator	Timeline
5.5 Infrastructure in priority jaguar landscapes allows jaguar movement and can be demonstrated not to increase mortality of jags by 2029.			
5.5.1 Identify critical corridors for jaguar across their South American range, including data and analysis produced by A. 3.1.2, 3.1.3, 5.1.3 and 5.3.1, and additional published information as available	SAJCAT, other jaguar specialists, specialists in road ecology	Map of critical corridors	2026
5.5.2 Recruit all South American range countries to develop and adopt guidelines for infrastructure planning and design that facilitate jaguar movement and dispersal across its range, utilising outputs from A. 5.4.1 and 5.5.1	SAJCAT facilitated by WG2, other jaguar specialists, specialists in road ecology	Guidelines produced for each country	2027
5.5.3 Advocate and facilitate cross-agency implementation of guidelines for infrastructure planning and design that facilitate jaguar movement and dispersal in all South American range countries	National Governments (Transport and infrastructure Ministries), SAJCAT coordinated by WG2	Number of infrastructures built under guidelines recommendations	2028
5.6 All South American jaguar range countries implement fire risk maps, prevention and response protocols by 2031.			
5.6.1 Review and analyse the existing fire risk maps, prevention and response protocols, with particular reference to priority jaguar landscapes	SAJCAT range country representatives, coordinated by WG2	Results tabulated and posted to online jaguar conservation platform (1.3.1)	2025
5.6.2 Advocate for South American range country governments to develop and/or refine fire risk maps, prevention and response protocols.	Governments, NGOs	Fire risk maps, and prevention and response protocols available	2028
Regulations and law enforcement			
6. To improve regulation and law enforcement regarding jags, prey and habitat protection			
6.1 For all South American countries, national gaps in legislation that apply to jaguar protection are identified and addressed by relevant authorities before the end of 2026.			
6.1.1 Coordinated by Working Group 2, all SAJCAT national representatives provide documentation to identify national gaps in legislation that applies to jaguar, prey and habitat protection (linked to A. 2.3.1.)	SAJCAT coordinated by WG2, National Governments and legal consultants	Report on identified national gaps per range country is available.	2024
6.2 For all South American range countries, national shortfalls in resources for law enforcement related to jaguar conservation are eliminated by 2028			
6.2.1 Convene a workshop to develop and implement tools which national authorities in all South American jaguar range countries use to assess the shortfalls in wildlife and environmental law	National Governments, United Nations Office on Drugs and Crime, IUCN SSC SAJCAT, BINGOs and other NGOs	Workshop took place and tools to assess shortfalls have been developed and are implemented.	2025
6.2.2 Using outputs from A. 6.2.1, set baseline targets, propose desired annual percentage increases and begin working to secure funds for enhanced law enforcement (linked to A. 2.3.3.). Produce an annual progress report to be posted to the online jaguar conservation platform (A. 1.3.1)	National Governments, United Nations Office on Drugs and Crime, SAJCAT coordinated by WG2, BINGOs and other NGOs, multilateral institutions	Report on targets is available	2026 (ongoing)

Activity	Actor	Indicator	Timeline
6.2.3 Using outputs from activities in O. 5 and 6, identify and collaborate with stakeholders to assemble informational resource kits to support and facilitate training and provide resources needed to address the identified shortfalls (linked to A. 2.3.2.). Post resource kits to online jaguar conservation platform as well as arrange stakeholder meetings to engage authorities in each jaguar range country	National Governments, United Nations Office on Drugs and Crime, SAJCAT, BINGOs and other NGOs	Amount and quality of resources allocated to law enforcement at each country	2026 (ongoing)
7. To promote decision making and political will towards jaguar conservation			
7.1 Natural Resource Management NRM authorities and national decision-makers in all South American range countries can be demonstrably seen as allies for jaguar conservation by 2026			
7.1.1 Design a communication campaign to improve the understanding of jaguar conservation (linked to Activity 2.3.2), specifically including all topics, challenges and opportunities outlined in Objectives 1–6	SAJCAT coordinated by WG2, BINGOs and other NGOs	Report on communication campaign is available	2024
7.1.2 Compile an annual report of actions taken by NRM authorities and national decision-makers, and results obtained, under Objectives 1–5 to be included with materials supplied to stakeholders for all meetings and workshops associated with this plan. Post the annual reports on the online jaguar conservation platform (Activity 1.3.1), as well	SAJCAT-coordinated by WG2, national governments, BINGOs and other NGOs	# authorities acknowledging and participate in jaguar conservation in each country	2026 (ongoing)
Cooperation			
8. To unite forces for jaguar conservation			
8.1 Regional and national networks for research, monitoring, and management of jaguars and their habitats in South America are implemented by 2025.			
8.1.1 Form and maintain at least one national network per country and one continental South American network composed of governments, NGOs, research institutes and academia to establish and use strategic frameworks of communication and collaboration for jaguar conservation	SAJCAT facilitated by WG3, governments, NGOs, research institutes and academia	# networks per country and continent wide; # strategic frameworks; # network groups organised to conduct activities under O. 1–6	End of 2024
8.1.2 Strengthen and promote the role of networks at country, regional and continental levels of jaguar conservation	Governments, NGOs, research institutes and academia	Networks involved in jaguar conservation decision making; Comparison of the number of national and regional interventions (action plans, database, studies, management plans) proposed, specifically including Objectives 1–6, versus those undertaken	End of 2025 (ongoing)
8.2 Multilateral and bilateral cooperation among governments in South America to improve knowledge, enforcement and joint actions towards jaguar conservation are developed by 2026.			
8.2.1 In partnership with the Jaguar 2030 Roadmap, establish a multi-national stakeholder working group to develop a template and utilise components of this strategy to advocate for the development/updating of jaguar national action plans for all South American range countries	SAJCAT coordinated by WG3, Governments, universities and NGOs	Template completed; Number of meetings held with legislators and agencies in range countries; number of countries with updated action plans	Mid 2024

Activity	Actor	Indicator	Timeline
8.2.2 Engage all South American jaguar range country governments in multilateral and bilateral initiatives, specifically incorporating components of this strategy, toward improving knowledge and enforcement for jaguar conservation	Governments (national level), secretariat of MEA's (Multilateral Environmental Agreements)	Participations of the governments in cooperative ventures; # engagement events; Established channels and identified topics agreed upon to achieve cooperation; # agreements signed; Reported number of attended committee meetings and signed agreements	2025
8.2.3 SAJCAT national representatives develop, submit and follow up on proposals to Colombia, Guyana, Suriname and Venezuela to join the United Nations Convention on Migratory Species	Governments (national level)	Number of new members to CMS	Mid 2024
8.2.4 Include the Jaguar 2030 Roadmap in all advocacy materials, communications plans and informational outputs of this strategy with the goal of all South American range countries adopting it by the end of 2025	All participants in this strategy, Governments (national level)	Number of countries adopting Jaguar Roadmap 2030	2026
8.3 In all South American range countries, improved management of landscapes, law enforcement and joint actions for jaguar conservation via better intra-government cooperation and communication are developed by 2026 and fully implemented by 2031			
8.3.1 For each South American jaguar range country, through direct connection and activating networks established through A. 8.1.1, identify and engage government ministries, agencies, divisions and departments to include in discussions of landscapes, law enforcement and jaguar conservation issues for the purposes of implementing the activities in this strategy	SAJCAT-coordinated by WG3, national authorities, ministries, NGOs, academia	Evidence of meetings, documents, reports, visits demonstrating continuity in ongoing participation	End of 2025
8.3.1 Incorporate results of the discussions (A. 8.3.1) among different levels of government ministries and associated agencies into management practices, law enforcement and jaguar conservation actions with particular emphasis on documenting and achieving Objectives 4–6	SAJCAT, networks established in Activity 8.1.1	Results of discussions incorporated in into management practices; refined management practices based on discussions; SAJCAT assessments of Activities from Objectives 5, 6 and 7 demonstrate multi-agency participation	End of 2026
Awareness and education			
9. To make jaguars universally recognised as a positive symbol			
9.1 A continental scale education and awareness project under a common logo "All4Jaguars" ("Todos por los jaguars", "Allen voor de jaguar", "Tudo para jaguares)) is launched using nature conservation materials that follow local education standards and featuring jags and used in schools across all South American range countries by 2031			
9.1.1 Collect science education standard documents from each range country and identify their objectives and goals into which content on jaguar conservation can readily be included	AZA Jaguar SSP/ SAFE, NGOs, education institutions	Number of collected science education standard documents from each range country	End of 2024

Activity	Actor	Indicator	Timeline
9.1.2 . Conduct an inventory of existing jaguar conservation educational content from zoos, NGOs and government agencies across South American range countries, AZA, EAZA and ALPZA	AZA Jaguar SSP/ SAFE, NGOs, education institutions	Number of collected existing jaguar conservation materials from AZA Jaguar SSP/ SAFE zoos, AZAB, Suriname Ministry of Education, WCS, WWF, NGOs and govt.	End of 2025
9.1.3 Construct a conceptual framework for jaguar conservation education and merge and/or produce additional content for different grade levels as necessary based on the identified gaps and convergence between existing materials and education standards collected in Activities 9.1.1 and 9.1.2 and referring to Objectives 1–5	AZA Jaguar SSP/ SAFE, NGOs, education institutions	Gaps identified, number of adapted or produced materials and information	Mid 2026
9.1.4 Materials approval/distribution by range country educators and/or government agencies in all South American jaguar range countries	AZA Jaguar SSP/ SAFE, NGOs, education institutions	Connections between SSP/SAFE zoo educators and volunteer teacher coordinators established in each country, and jaguar conservation activities/materials being used in 10 schools in each South American range country (some attention must be paid to urban vs rural schools)	2028
9.2 The jaguar is shown to be one of the most loved South American wildlife species by 2033.			
9.2.1 Carry out public service announcements about the value of protecting jaguars at least one by television/radio station in each country	SAJCAT-coordinated by WG4, Somebody with a TV Network connection, WildAid	Ratings data	2026
9.2.2 . Launch an “Yo <3 Jaguares” (Dutch (Ik <3 Jaguars), English (I <3 Jaguars) and Portuguese (Eu <3 Jaguares) social media campaign that receives 500,000 likes by mid-2024	Local NGO Facebook campaigns, with guidance and contributions from SAJCAT coordinated by WG4	Half a million likes	2025 (onwards)
9.2.3 Celebrate official jaguar day in all South American range countries	SAJCAT coordinated by WG4, local and international NGOs, range country wildlife agencies	Events/activities occurring in all range countries	At least half in 2027, 100% beginning in 2033
9.2.4 . Conduct before/after polls in 2023 and 2032 to establish the change in popularity over the decade	Diego Zoo Wildlife Alliance Conservation Science Community Engagement team and others	Published results	2024 and 2033
9.3 Presence of jaguars is utilised by all South American range country environment and agriculture agencies as a positive indicator of ecosystem health by 2031 (linked to Results 2.2, 2.6, 3.1, and 5.1–5.5, Activity 7.1.1).			
9.3.1 Identify methodology for environmental impact mitigation in each country	Each country participant of this workshop (SAJCAT)-coordinated by WG4	List compiled of regulations about environmental impact assessments/mitigation for all range countries	End of 2025

Activity	Actor	Indicator	Timeline
9.3.2 For each South American range country, compile and summarise scientific literature describing the jag's role in relevant ecosystems.	All workshop participants	Summary prepared	End of 2025
9.3.2 Using outputs of Result 9.1 and 9.2, and from Activity 9.3.1 and 9.3.2, prepare materials and language for inclusion in advocacy and networking activities in Objective 2–7, demonstrating that the presence of jaguar is a positive indicator of ecosystem health. Seek to incorporate the language into environmental impact regulations in all South American range countries	Workshop participants, coordinated by WG4, NGOs and government agencies	Materials incorporated into activities under O. 2–7, changes in the national environmental regulations of all range countries in favour of jags.	Beginning of 2027 (ongoing)

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Appendix I - Glossary

Term	Explanation
BINGO	Jargon term for Big International Non-Governmental Organisation. In the context of this plan, a BINGO is arbitrarily identified as an NGO with a total annual operating budget in excess of USD $100,000,000.
Cat SG	IUCN Species Survival Commission Cat Specialist Group. See http://www.catsg.org/
CPSG	IUCN Species Survival Commission Conservation Planning Specialist Group. See https://cpsg.org/
Green List	IUCN Green List of Protected and Conserved Areas. See www.https://www.iucn.org/theme/protected-areas/our-work/iucn-green-list-protected-and-conserved-areas
IUCN	International Union for the Conservation of Nature. See https://www.iucn.org/
JCU	Jaguar Conservation Unit, as defined in Zeller & Rabinowitz (2013). Using Geo-graphic Information Systems for Range-Wide Species Conservation Planning. Geographic Information Systems.
NGO	Non-governmental Organisation. NGOs are often presumed to have not-for-profit tax status and to focus on non-commercial missions and objectives. In the context of this plan, NGOs will usually have clearly defined conservation, education philanthropic and/or scientific missions
NRM	Natural Resource Management
SAJCAT	South American Jaguar Conservation Action Team

Appendix II - List of participants

SAJCAT: South American Jaguar Conservation Action Team. This list identifies all participants in the initial planning workshop, which took place at the San Diego Zoo Wildlife Alliance (formerly San Diego Zoo Global) Beckman Center for Conservation Research, November 18–22, 2019, and their contribution to the Working Groups (WG). Participants are listed based on their respective WG and then alphabetically based on their last name.

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