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The jaguar in South America – status review and strategy





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Original contributions and short notes about wild cats are welcome

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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 km² 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-García 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 Iguazu 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).

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



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

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 (Brackowski 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-Urbe 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 anaesthetising 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 *Ozotoceros 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. Habersfeld, 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 km² 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, Guyana 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 Nations 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 km² 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 km²) 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 km²) 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 (Espinoza 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 km² of PAs and there are no officially approved ITs. There are 46 NPs and 36 other PAs. Caura NP is the largest (75,340 km²) 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 km² or 28% of the range. ITs cover an additional 190,700 km² 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-Percestequi & 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-Perceguy & Maffei 2016).

Brazil has over 1,330,000 km² of its jaguar range inside PAs and 995,000 km² 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 south-east 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 km², 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 km², while >4,200 km² 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 km² 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, Martínez 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-Urbe 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-Urbe 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 km².

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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