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The jaguar in South America – status review and strategy

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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

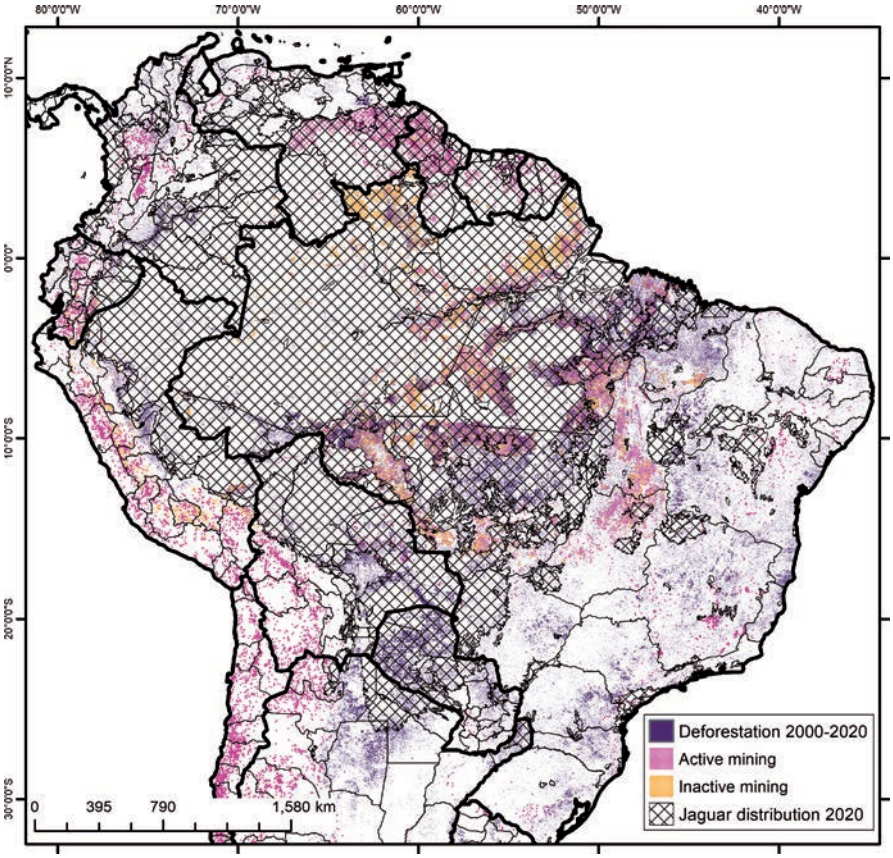

Fig. 1. Deforestation from 2000 to 2020 and areas with mining activities compared to the estimated jaguar distribution in South America in 2020. Mining areas are divided into active (with ongoing mining operations) and inactive (with concessions already granted or applied for). In the case of deforestation, 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 non-existent (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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