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The jaguar in South America – status review and strategy

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Biology and ecology of the jaguar

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

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

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

Sexual behaviour resembles that of other felid species with an elevated number of copulations likely to induce multiple ovulations (Jorge-Neto et al. 2018). Gestation period lasts around 100 days (90–111 days) and the reproductive season is year-round. In some places, however, it has been reported that cubs are born mainly during the rainy season (Rabinowitz & Nottingham 1986, Crawshaw 1987), and in forested flooded savannas of the Llanos mainly during the dry season (Hoogesteijn & Mondolfi 1992). Litter size is one to four cubs, with two cubs being the most common (Jędrzejewski et al. 2017a). Females give birth in a protected place like a cave, burrow, under a fallen tree, or in dense vegetation. Cubs stay with the mother until they are approximately 1.5 to 2 years old and reach sexual maturity at about 20 months for females (Viau et al. 2020) and about 4 years for males (Mondolfi & Hooge-

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

steijn 1986). The lifespan of wild jaguars is difficult to estimate, but there are records of jaguars of over 15 years old (A. Paviolo et al., unpubl. data). In captivity, they can live up to 22 years (Seymour 1989, Nowak 1991). The main causes of human-induced jaguar mortality are hunting and retaliatory killing, but recently road kills have often been reported as well (Crawshaw Jr. 2002, Carvalho & Morato 2013, Jędrzejewski et al. 2017b). Of the natural causes, there are records of males killing other males and of infanticide (Soares et al. 2006, Azevedo et al. 2010, Tortato et al. 2016). There is limited information on population structure. In a study in Los Llanos adult males constituted 21%, reproductively active females 26%, nonreproductive females 11%, and cubs 42% (Jędrzejewski et al. 2017a). Jaguar reproductive behaviour, breeding parameters and demographic patterns require further studies.

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

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

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

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

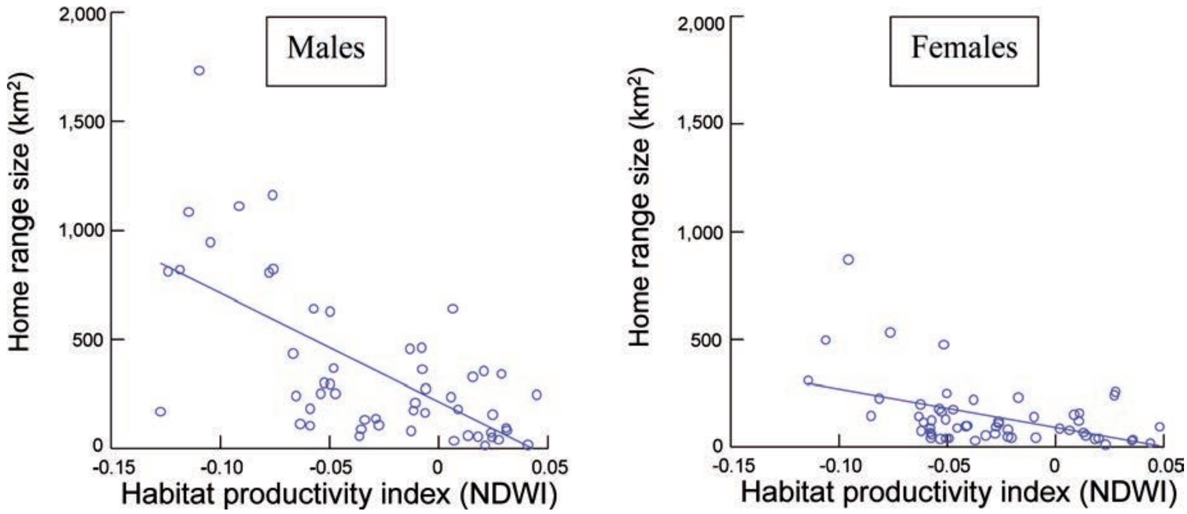

Fig. 3. Relationship between jaguar home range size and NDWI index. Jaguar home range sizes were calculated as minimum convex polygons (MCP 100%) based on radiotelemetry GPS data for 117 individual jaguars across jaguar range, published by Morato et al. 2018. NDWI (normalised difference water index,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

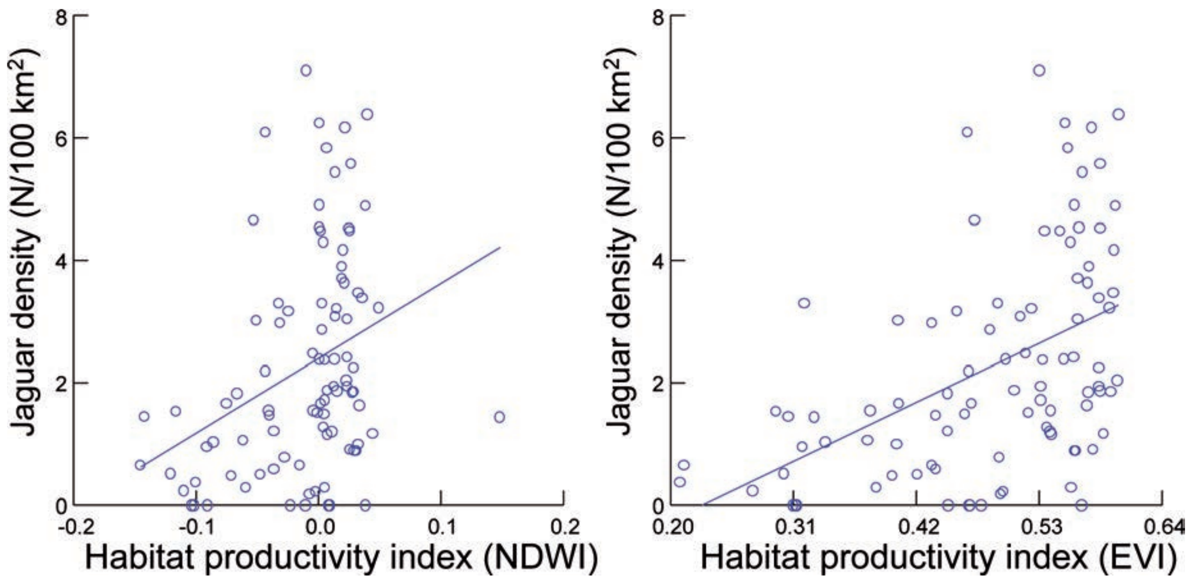

Fig. 4. Relationship between jaguar population density and indices of habitat primary productivity: NDWI and EVI. Jaguar population density data come from 117 camera trapping studies and were recalculated to the level of spatial capture-recapture models (Jędrzejewski et al. 2018). NDWI (normalised difference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

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

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

Prey preferences and feeding ecology

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

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

Infectious and non-infectious diseases

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

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

Zoos, captive breeding, artificial reproductive techniques, and reintroduction

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

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

Final considerations

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

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

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

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