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The jaguar in South America – status review and strategy

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Distribution and status of the jaguar in the Guiana shield

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

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

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

Methods

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

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

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

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

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

Region-wide distribution

We gathered 1,143 jaguar records from across the Guiana shield (Table 1, Fig. 1). The majority of these data (94%) were collected since 2000, with Venezuela contributing 83% of the pre-2000 data. Of the records collected

since 2000, 55% are classified C1 (mostly derived from camera-traps), 22% as C2 (mainly derived from interviews), and 23% as C3 (largely unverified direct observation and livestock attack testimonies; Table 1).

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

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

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

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

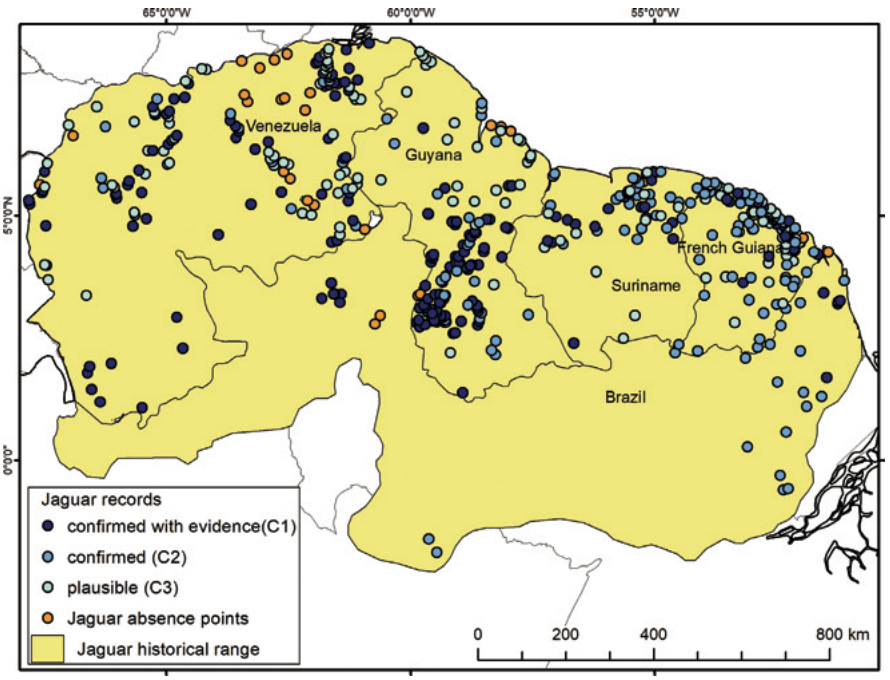

Fig. 1. Jaguar records and absence points used in the analysis of the current jaguar status against the historical range of the species in the Guiana Shield. Jaguar records are classified into three reliability categories: C1 – confirmed with hard evidence, C2 – confirmed by an expert but without hard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

Venezuela

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

The three Guianas

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

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

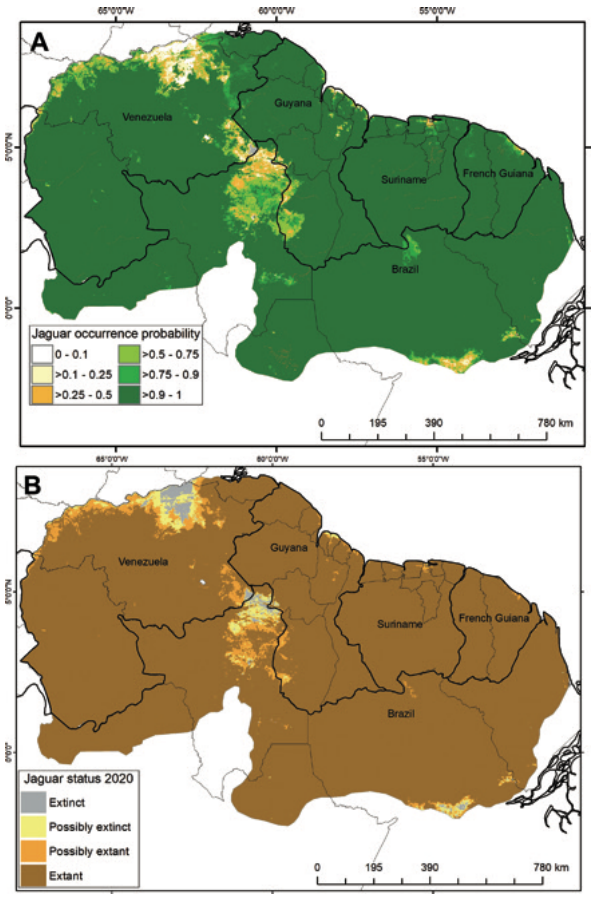

Fig. 2. A. Probability of jaguar occurrence (indicating also habitat suitability for jaguars) estimated with the logistic regression model of jaguar presence and absence; B. Jaguar status in Guiana Shield classified into four IUCN categories: Extinct, Possibly Extinct, Possibly Extant and Extant; assessment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

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

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

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

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

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

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

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

Brazil

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

Habitat

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

Diet and prey availability

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

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

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

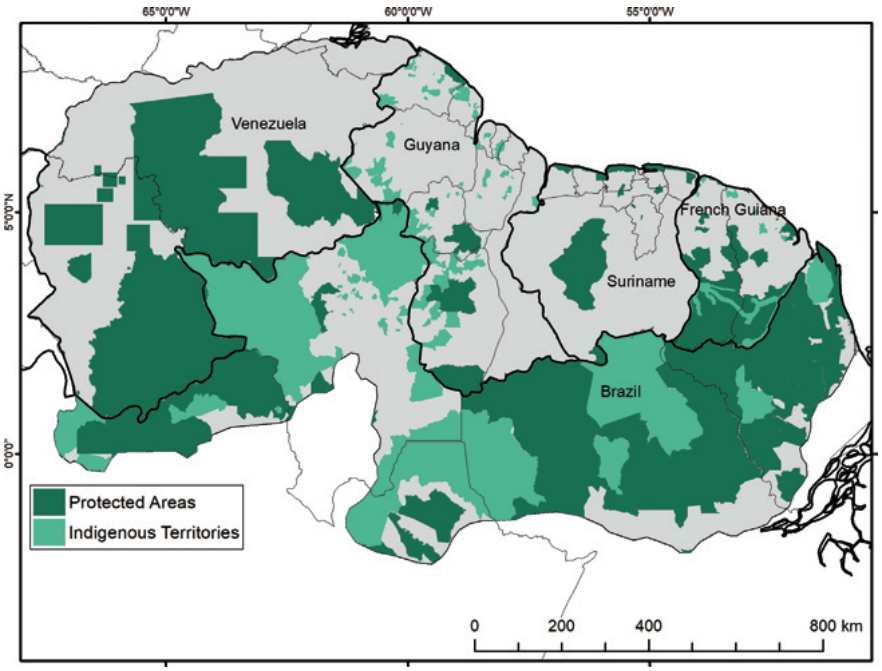

Fig. 3. Protected areas and indigenous territories of the Guiana Shield. Protected areas included National Parks, Nature Parks, Biological Reserves, Biosphere Reserves, National Natural Reserves, National Monuments and Ramsar sites.

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

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

Threats

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

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

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

Importantly, mining does not only cause forest and soil loss, but the use of toxins (i.e. mercury) and erosion can also cause large-scale water contamination (Ouboter et al. 2012, Legg et al. 2015). Extractive industries

also create a network of roads through otherwise forested interiors to transport materials that increase access and hunting pressure on jaguars and their prey (Wilkie et al. 2011, Hallett et al. 2019).

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

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

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

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

Conservation

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

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

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

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

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

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

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

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

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

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

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

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

Conclusion

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

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