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Abstract: The IUCN Red List is widely used to guide conservation policy and practice. However, in most cases the evaluation of a species using IUCN Red List criteria takes into account only the global status of the species. Although subpopulations may be assessed using the IUCN categories and criteria, this rarely occurs, either because it is difficult to identify subpopulations or because of the effort involved. Using the jaguar Panthera onca as a model we illustrate that wide-ranging species that are assigned a particular category of threat based on the IUCN Red List criteria may display considerable heterogeneity within individual taxa in terms of the level of risk they face. Using the information available on the conservation status of the species, we evaluated the jaguar's current geographical range and its subpopulations. We identified the most threatened subpopulations, using the extent of occurrence, area of occupancy, population size and the level of threat to each subpopulation. The main outcome of this analysis was that although a large subpopulation persists in Amazonia, virtually all others are threatened because of their small size, isolation, deficient protection and the high human population density. Based on this approach, future conservation efforts can be prioritized for the most threatened subpopulations. Based on our findings we recommend that for future Red List assessments assessors consider the value of undertaking assessments at the subpopulation level. For the jaguar, sub-global assessments should be included on the Red List as a matter of urgency.

The jaguar's spots are darker than they appear: assessing the global conservation status of the jaguar *Panthera onca*

J. Antonio de la Torre, José F. González-Maya, Heliot Zarza
Gerardo Ceballos and Rodrigo A. Medellín

Abstract The IUCN Red List is widely used to guide conservation policy and practice. However, in most cases the evaluation of a species using IUCN Red List criteria takes into account only the global status of the species. Although subpopulations may be assessed using the IUCN categories and criteria, this rarely occurs, either because it is difficult to identify subpopulations or because of the effort involved. Using the jaguar *Panthera onca* as a model we illustrate that wide-ranging species that are assigned a particular category of threat based on the IUCN Red List criteria may display considerable heterogeneity within individual taxa in terms of the level of risk they face. Using the information available on the conservation status of the species, we evaluated the jaguar's current geographical range and its subpopulations. We identified the most threatened subpopulations, using the extent of occurrence, area of occupancy, population size and the level of threat to each subpopulation. The main outcome of this analysis was that although a large subpopulation persists in Amazonia, virtually all others are threatened because of their small size, isolation, deficient protection and the high human population density. Based on this approach, future conservation efforts can be prioritized for the most threatened subpopulations. Based on our findings we recommend that for future Red List assessments assessors consider the value of undertaking assessments at the subpopulation level. For the jaguar, subglobal assessments should be included on the Red List as a matter of urgency.

Keywords Assessment, conservation, IUCN, jaguar, *Panthera onca*, subpopulations, threats, threatened species

Introduction

Assessment of extinction risk is one of the most informative tools available to guide conservation policy and practice (Mace et al., 2008). However, the specific facts and processes that lead to listing, assessing or delisting species are rarely available other than the schematic listings within the IUCN Red List or other national protocols. The IUCN Red List uses three categories of threat (Critically Endangered, Endangered and Vulnerable), which are assigned on the basis of quantitative criteria to reflect varying degrees of threats of extinction. Taxa that do not qualify as threatened but may be close to qualifying are categorized as Near Threatened, as are taxa that are likely to meet criteria for a threatened category if ongoing conservation action abates or ceases (IUCN, 2012).

In most cases, species evaluations are undertaken only at the global level. Although IUCN Red List assessments may be undertaken at the subpopulation level, following the proper categories and criteria (IUCN Standards and Petitions Subcommittee, 2016), these are often not implemented, usually because it is difficult to identify subpopulations or because of the effort involved. This is problematic, especially for species with a wide distribution range, because the categorization does not necessarily reflect the status of the species throughout its range (Wallace et al., 2010). There are many species that have lost most of their habitat within their geographical range but do not qualify within these risk categories because they still maintain a wide range or a single large population. This is the case for the jaguar *Panthera onca*, the largest felid on the American continent.

Historically, the jaguar ranged across c. 19,000,000 km² from south-western USA to central Argentina (Seymour, 1989). However, since 1900 its range has decreased to c. 9,000,000 km² and it is now found only from northern Mexico to northern Argentina, although it occasionally disperses to the extreme south-western USA (Medellín et al., 2002, 2016; Sanderson et al., 2002). Previous efforts to evaluate the jaguar's conservation status at regional and continental scales have concluded that the species is declining throughout much of its range (Swank & Teer, 1989; Sanderson et al., 2002; Zeller, 2007; Medellín et al., 2016). However, the jaguar is categorized as Near Threatened on the IUCN Red List, the second lowest risk category, being close to qualifying for the Vulnerable category under criteria

J. Antonio de la Torre, José F. González-Maya*, Gerardo Ceballos and Rodrigo A. Medellín (Corresponding author) Instituto de Ecología, Universidad Nacional Autónoma de México, Ciudad Universitaria, 04318, México D.F., México. E-mail medellin@iecologia.unam.mx

Heliot Zarza Departamento de Ciencias Ambientales, Universidad Autónoma Metropolitana Unidad Lerma, CP 52005 Lerma de Villada, México

*Also at: Proyecto de Conservación de Aguas y Tierras, Bogotá, Colombia

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A2cd or A3cda. The main reason the jaguar is not assigned a higher risk category, such as Vulnerable or Endangered, is its wide geographical range, along with the fact that it still maintains a large subpopulation in the Amazon basin (Caso et al., 2008).

Assessment of subpopulations can help to draw attention to conservation priorities that may otherwise be obscured. We thus undertook such an assessment of the jaguar, and we present a methodology for identifying subpopulations within the species' range, and assessing each subpopulation against the IUCN Red List categories and criteria. We used available information on the jaguar's range and estimates of density to assess the species' conservation status throughout its range. Additionally, we developed a threat evaluation system to assess the level of threat for each subpopulation and to allocate conservation priorities. Our aims were (1) to estimate the current geographical range of the species and its subpopulations, (2) to estimate the size of the global population and subpopulations of jaguars, and (3) to identify the most threatened subpopulations throughout the jaguar's range. We illustrate that for wide-ranging species assigned to a particular category of threat on the IUCN Red List there may be considerable heterogeneity within the extinction risk for the taxon, and that assessments, especially for species with a wide distribution range, should be based on the level of threat for all subpopulations throughout the species' range. We hope this information will encourage assessors to consider the value of undertaking assessments at the subpopulation level.

Methods

Geographical range

To determine the jaguar's current range we compiled the most recent information on its distribution from all available sources. We included information from the Jaguar Conservation Units (Sanderson et al., 2002; Zeller, 2007; Rabinowitz & Zeller, 2010), and published population maps for the range countries (Cavalcanti et al., 2012; Beisiegel et al., 2012; de Oliveira et al., 2012; de Paula et al., 2012; Moraes, 2012; Carrillo-Percastegui & Maffei, 2016; Chávez et al., 2016; de Azevedo et al., 2016; de Thoisy, 2016; Díaz-Santos et al., 2016; Espinosa et al., 2016; Figueroa et al., 2016; García-Anleu et al., 2016; González-Maya et al., 2016; Hoogesteijn et al., 2016; Maffei et al., 2016; Mora et al., 2016; Moreno et al., 2016; Payán Garrido et al., 2016). We mapped polygons to define jaguar subpopulations at the continental scale, delineated based on the information available for jaguar distribution in each country. Because the information was obtained from various sources, we recognized that criteria for defining subpopulation polygons in each country were dissimilar. For instance, subpopulations in Mexico and Brazil were delineated with detailed maps, using expert knowledge. In other cases we supplemented the Jaguar Conservation Unit information with published maps of the jaguar's range in each of its range countries. Using all this information we generated detailed geographical information system layers that represented the subpopulation polygons on a map. Although most of this information has not been published in peer-reviewed journals, it represents the latest knowledge of the species' range based on assessments by experts working in the jaguar range countries.

We defined the polygons using the IUCN definition: geographically or otherwise distinct groups in the global population between which there is little demographic or genetic exchange (typically one successful migrant individual or gamete per year or less); a subpopulation may or may not be restricted to a region (IUCN, 2012; IUCN Standards and Petitions Subcommittee, 2016). As the taxonomic and genetic research indicated little difference among jaguar subpopulations (Larson, 1997; Eizirik et al., 2001; Ruiz-Garcia et al., 2006) we defined the subpopulation polygons as discrete units following these criteria: (1) we considered only polygons $> 2,000$ km², with the aim of including in the analysis only regions where resident subpopulations occurred; i.e. we considered only sites that could potentially contain a subpopulation of at least 5 resident jaguars, considering the lower density estimate throughout the species' distribution range (0.25 jaguars per 100 km²; Paviolo et al., 2008); and (2) we identified geographical, natural and anthropogenic barriers between the polygons, such as mountain ranges that potentially divide the polygons (the upper elevation limit of the species is 3,000 m; Caso et al., 2008), and urban areas and large areas modified by human activities. We considered subpopulations to be independent if the distance of habitat that was modified by human activities between a polygon and its nearest neighbouring polygon was > 50 km. For this we used the GlobCover land-use classification (Arino et al., 2012). We reclassified the Natural and Semi-natural Terrestrial Vegetation layers as 'natural vegetation' and the Cultivated and Terrestrial and Management layers as 'intervened', according to the GlobCover land-use classification (Arino et al., 2012). We assumed the polygons included both the Jaguar Conservation Units and the corridors under the scheme proposed by Rabinowitz & Zeller (2010).

Using the subpopulation polygons we delineated an approximation of the jaguar's current range at the continental scale. We estimated the extent of jaguar occurrence using the minimum convex polygon that enclosed the range of each subpopulation (IUCN Standards and Petitions Subcommittee, 2016; Joppa et al., 2016). Top-level predators such as jaguars are particularly threatened in regions of high human population density by direct persecution and habitat loss (Woodroffe, 2000; Cardillo et al., 2004), and jaguar extinction can be predicted according to certain thresholds of human population density (Woodroffe, 2000). Given these two factors, we estimated the jaguar's area of occupancy for each polygon, using a grid of the human population density in the Americas for the year 2000 at a resolution of 30 arc-seconds (c. 1 km; Center for International Earth Science Information Network et al., 2011). We defined two scenarios of area of occupancy because threshold values of human population density that predict the extinction of jaguars are 12–24 people per km^2 (mean 17 people per km^2; Woodroffe, 2000). Our lower and upper estimates were defined by obtaining the natural vegetation layers for each polygon (Arino et al., 2012) and excluding the sites where human density was > 12 and > 24 people per km^2, respectively. We calculated our lower and upper estimates of area of occupancy at the reference scale of 4 km^2 (2×2 km grid size), as suggested in the IUCN Red List Guidelines (IUCN Standards and Petitions Subcommittee, 2016).

To estimate the jaguar's range loss we contrasted our estimates of range and area of occupancy with the historical distribution of the species, based on the maps of Patterson et al. (2007). All geographical analyses were performed using *ArcGIS 10.2* (ESRI, Redlands, USA).

Subpopulations

For each subpopulation polygon we estimated the total area covered, and we listed the biomes and ecoregions found within the polygon (Olson et al., 2001). We compiled all published estimates of jaguar density based on camera traps, including those published in indexed journals, book chapters and technical reports. In total we included 78 density estimates from 31 studies from Mexico to Argentina, published during 2004–2014. As the majority of camera trap studies of the jaguar do not meet the requirements necessary to produce unbiased density estimates, and probably overestimate densities (Tobler & Powell, 2013), we conservatively corrected the estimate for each study using the inferior interval of the density estimate (subtracting the standard error from the density estimate reported). Each study was categorized according to the biome and ecoregion using the coordinates reported in the sources (Table 1). For the polygons for which there were no available density estimates or estimates for a particular type of biome, we used the most conservative density estimate reported for the nearest polygon.

We defined a subpopulation as the estimated number of individuals in each polygon, and used the term population to refer to the sum of all subpopulations across the range (IUCN, 2012; IUCN Standards and Petitions Subcommittee, 2016). We estimated the subpopulation size for each polygon by extrapolating the density estimates to our layers of area of occupancy. For each polygon we performed two estimates of jaguar population size, based on our upper and lower area of occupancy scenarios. For these estimates we assumed that jaguar density declined linearly as the human population density increased (Woodroffe, 2000). This implies that jaguar densities across the polygons were estimated for each cell in the area of occupancy maps using the linear regression formula $y = xm + b$, where y is the estimated jaguar density adjusted according to the human population density, x is the human population density (Center for International Earth Science Information Network et al., 2011), m is the constant rate at which jaguar densities decline as the human population density increases, and b is the jaguar density defined for each biome in each polygon (Table 1). We used the Raster Calculator tool in *ArcGIS 10.2* to estimate the jaguar density adjusted according to the human population density for each grid cell in the area of occupancy maps. Using the jaguar density values of each grid cell we estimated the number of jaguars for the biome or biomes contained in each polygon.

Importantly, jaguar density varies according to habitat type, prey availability, degree of fragmentation, season, and human disturbance. Also, density estimates based on camera trapping could be skewed, depending on how the methodology was used by various researchers throughout the range of the species (Tobler & Powell, 2013). For these reasons our estimates of subpopulation sizes should be interpreted with caution because we are extrapolating from the available information to vast areas. However, our approach was robust because we extrapolated jaguar densities only for sites where the human population density was not > 12 (lower estimate) or > 24 people per km^2 (upper estimate), and assumed that jaguar densities were not homogeneous across the biomes (i.e. jaguar densities were adjusted according to the human population density across the polygon).

Assessment under the IUCN threat categories

Based on the extent of occurrence, area of occupancy and estimated population size, we assessed the conservation status of each subpopulation using the IUCN criteria (IUCN Standards and Petitions Subcommittee, 2016). We used this evaluation to illustrate the risk of extinction of each subpopulation independent of the conservation status of the other subpopulations. To conduct the assessments we evaluated each subpopulation against the five criteria: (A) declining population, (B) geographical range size, (C) small population size, (D) very restricted distribution, and (E) quantitative analysis of extinction risk (IUCN, 2012). Each subpopulation was categorized as Least Concern, Near Threatened, Vulnerable, Endangered or Critically Endangered.

As there is little information available about the recent decline of jaguars within the polygons, to apply Criterion A we estimated the species' area of occupancy in the recent past. For this we used the University of Maryland Land Cover Classification, developed from a collection of satellite

TABLE 1 Densities (per 100 km^2) of the jaguar *Panthera onca* in various biomes, used to extrapolate the population size of each subpopulation (Fig. 1).

No.	Jaguar subpopulation	Biome[1] MBF	DBF	GSS	FGS	MGS	TCF	D	M	References
1	Mexican Pacific	1.8	1.5				0.65	0.65	0.65	Núñez-Pérez (2011); de la Torre & Medellín (2011); Gutiérrez-González et al. (2012)
2	Sierra de Tamaulipas	0.75					0.75	0.65		Gutiérrez-González et al., (2012); Chávez et al. (2016)
3	Gulf of Mexico	1.8	1.5						0.65	de la Torre & Medellín (2011); Chávez et al. (2016)
4	Selva Maya	1.8	1.5				0.65		0.65	Núñez-Pérez (2011); de la Torre & Medellín (2011); Chávez et al. (2016)
5	Maya Mountains	5.75					4	0.65	0.65	Silver et al. (2004)
6	Honduras Caribbean	1.55					1		1	Mora et al. (2016)
7	Honduran Mosquitia	1.55	1				1		1	Mora et al. (2016)
8	Indio-Maíz Tortuguero	1.5					1		1	Díaz-Santos et al. (2016)
9	Talamanca	1.34								González-Maya et al. (2016)
10	Osa Peninsula	4							0.65	Salom-Pérez et al. (2007)
11	Central Panama	2							0.65	Moreno et al. (2016)
12	Biogeographic Choco	1.5	1.5			0.65			0.65	Moreno et al. (2016)
13	Paramillo-San Lucas	1.5	1.5							
14	Sierra Nevada de Santa Marta	1.5	1			0.65		0.65	0.65	
15	Serrania de Perija-Catatumbo	1.5	1.5			0.65		0.65		
16	Santa Helena-Guayas	1.5	1.5			0.65		0.65		
17	Amazonia[2]	1	1	1	1	0.65		0.65	0.65	Maffei et al. (2004); Soisalo & Cavalcanti (2006); de Oliveira et al. (2012); Tobler et al. (2013)
18	Maranhão-Babaçu	0.67								Moraes (2012)
19	Nascentes Parnaíba	0.67	0.67	0.67						
20	Boquerião da Onça		0.5	0.5				0.5		De Paula et al. (2012)
21	Serra da Capivara							0.2		De Paula et al. (2012)
22	Chapada Diamantina		0.3	0.3				0.3		De Paula et al. (2012)
23	Araguaia	0.67		0.67						Moraes (2012)
24	Goiás & Tocantins	0.67		0.67						Moraes (2012)
25	Sertão Veredas Peruaçu	0.67	0.67	0.67				0.67		de Oliveira et al. (2012)
26	Mato Grosso	1	1	1						de Oliveira et al. (2012)
27	Chapada dos Guimarães		0.69	0.69						Moraes (2012)
28	Emas			0.69						Sollmann et al. (2011)
29	Espinhaço de Minas	0.69		0.69						Moraes (2012)
30	Sooretama	0.33							0.33	Paviolo et al. (2008)
31	Mantiqueira-Rio Doce	0.33								Paviolo et al. (2008)
32	Pontal do Paranapanema	0.33		0.33						Paviolo et al. (2008)
33	Serra do Mar	0.33		0.33					0.33	Paviolo et al. (2008)
34	Iguaçu	0.33		0.33						Paviolo et al. (2008)

[1] MBF, Moist Broadleaf Forest; DBF, Dry Broadleaf Forest; GSS, Grasslands, Savannahs, Scrublands; FGS, Flooded Grasslands and Savannahs; MGS, Montane Grassland and Scrublands; TCF, Tropical Coniferous Forest; D, Deserts; M, Mangroves.

[2] For the Amazonia subpopulation polygon we used the most conservative density estimate of 1 jaguar per 100 km^2 (de Oliveira et al., 2012) for most of the biomes because most of this vast area has never been surveyed for jaguars, and thus there is considerable uncertainty in the extrapolation for this area. However, density estimates for the Moist Broadleaf Forest biome are 1–4.4 jaguars per 100 km^2 (de Oliveira et al., 2012; Tobler et al., 2013), for the Dry Broadleaf Forest biome 2.27–5.37 jaguars per 100 km^2 (Maffei et al., 2004), and for the Flooded Grasslands and Savannahs biome 6.6 jaguars per 100 km^2 (Soisalo & Cavalcanti, 2006).

TABLE 2 Demographic parameters used in our base model in *VORTEX* to evaluate jaguar subpopulations under criterion E of the IUCN Red List.

Parameters	Values in the base model
Inbreeding depression	3.4 lethal equivalents per individual, & 1.57 recessive lethal alleles
Extinction definition	No individuals of one or both sexes
Reproduction system	Polygynous
First age of reproduction	3 years for females & 4 years for males
Maximum breeding age	10 years
Sex ratio at birth	0.5
Adult males in the breeding pool	90%
% of adult females breeding	Reproduction is density dependent, according to the formula $((50 \times [1 - ((N/K)^2)]) + (30 \times [(N/K)^2])) \times (N/(0.50 + N))$
Number of offspring per female per brood	1–4 litters; 5% of females produce litter of 1 cub, 40% produce litter of 2, 30% produce litter of 3 and 25% produce litter of 4
Mortality of females	34% aged 0–1 years, 17% aged 1–2, 19% aged 2–3, and 20% adults
Mortality of males	34% aged 0–1 years, 17% aged 1–2, 35% aged 2–3, 30% aged 3–4, and 30% adults

images acquired during 1981–1994 (Hansen et al., 1998, 2000), and a grid of the human population density in the American continent for the year 1990 at a resolution of 30 arc-seconds (Center for International Earth Science Information Network et al., 2011). In a similar way we defined two scenarios for our estimation of area of occupancy in the recent past. Our lower and upper estimates were defined by obtaining the natural vegetation layers in each polygon from the University of Maryland Land Cover Classification and excluding the sites where human density was > 12 and > 24 people per km^2, respectively, in 1990. We rescaled the maps of area of occupancy in the recent past at the reference scale of 4 km^2, and we estimated the percentage of range reduction for each polygon based on the estimates of the area of occupancy at present and in the recent past (IUCN Standards and Petitions Subcommittee, 2016). We set the generation time at 7 years, based on approximate age of maturity (3 years for females and 4 years for males) plus half the length of the reproductive lifespan (6 years; Eizirik et al., 2002; Quigley & Crawshaw, 2002), and thus past and future declines were estimated for a maximum period of 21 years.

Criterion B was applied using our estimates of the extent of occurrence and area of occupancy of jaguars in each polygon. Criteria C and D were applied using the mean of our estimates of population size in each polygon and using the patterns of jaguar occurrence within the polygon according to our estimate of the area of occupancy. Criteria C and D were applied using the number of mature individuals, defined as the number of individuals known, estimated or inferred to be capable of reproduction (IUCN Standards and Petitions Subcommittee, 2016). Given that most studies of jaguar density report data on adult individuals only, we assume that our estimations of jaguar subpopulation size include only mature individuals.

Criterion E was applied using a population viability analysis in *VORTEX v. 10.0.8* (Lacy & Pollak, 2015). To assess the subpopulations under this criterion we estimated the probability of extinction of each subpopulation based on their estimated population size and for time intervals of 21 years (three generations), 35 years (five generations) and 100 years. As most of the demographic parameters for jaguars are unknown, our generic model was based on the parameters used by Eizirik et al. (2002) to model the viability of jaguar populations (Table 2). We did not include catastrophes in our model, and we used 500 iterations in each subpopulation model.

Level of threat for jaguar subpopulations

To assess the level of threat for each subpopulation we developed a threat evaluation system, which was applied independently to each polygon. This system was based on five criteria: extent of habitat, degree of human disturbance, viability of the populations, isolation from the other subpopulations, and level of protection. Extent of habitat was based on the percentage of natural habitat contained in each polygon, calculated based on the remaining areas with natural vegetation in each polygon (Arino et al., 2012). As the hunting pressure on large carnivores and their prey species is likely to be higher in areas of high human population density (Woodroffe, 2000; Dupain et al., 2012; Espinosa et al., 2014; Fa et al., 2015; Ziegler et al., 2016), we measured the degree of human disturbance using a human population density grid (Center for International Earth Science Information Network et al., 2011) and by calculating the mean human density in each polygon. To estimate the viability of the populations, we used our estimates of population size for each polygon and the criteria defined by Eizirik et al. (2002). Subpopulations with < 300 individuals were considered to be non-viable, subpopulations with 300–650 individuals were considered to be viable in the medium term (100 years, with 99% probability), and those with > 650

Table 3 IUCN Red List criteria used to evaluate the level of threat in each jaguar subpopulation polygon.

		Threshold*		
Criterion	Unit	Maximum (4)	Medium (3)	Low (2)
A. Habitat availability	% of natural habitats within the polygon	< 50	≥ 50 & < 75	≥ 75
B. Degree of human perturbation	Mean human population density within the polygon	≥ 500	≥ 100 & < 500	< 100
C. Viability of the population	Population size	< 300	≥ 300 & ≤ 650	> 650
D. Isolation	Mean minimum distance to the nearest four polygons (km)	> 200	> 100 & ≤ 199	≥ 50 & ≤ 100
E. Protection	% of area protected within the polygon	< 25	≥ 25 & ≤ 50	> 50

*We defined three thresholds for the five criteria according to the level of threat (see text for details). The higher the total score assigned to a subpopulation, the greater the level of threat.

individuals were considered to be viable in the long term (200 years, with 99% probability; Eizirik et al., 2002). Degree of isolation was defined using the minimum distances to the four nearest polygons, and distances were estimated using the Proximity tools of *ArcGIS 10.2*. The level of protection of each subpopulation was determined by the percentage of protected area within the species' range in each polygon; this percentage was estimated using the World Database on Protected Areas (UNEP-WCMC & IUCN, 2015). We overlaid our estimation of the species' range on the terrestrial protected areas of the American continent and estimated the percentage protected in each polygon. We included in this analysis the protected areas recognized by national governments, areas designated under regional and international conventions, privately protected areas, and territories conserved by indigenous people and communities, all of which met the IUCN and Convention on Biological Diversity definitions of protected areas (UNEP-WCMC & IUCN, 2015).

We scored the level of threat for each subpopulation according to each of the five criteria. The highest level of threat for each criterion was assigned a score of 4, a medium level of threat was assigned a score of 3, and the lowest level was assigned a score of 2; therefore, each population could get a maximum score of 20 and a minimum score of 10 (Table 3). Subpopulations with a final score of ≥ 17 (equivalent to having more than three criteria with the highest threat score) were defined as having a high level of threat, those with a final score of 13–16 (equivalent to having more than one criterion with the highest threat score) were defined as having a medium level of threat, and those with a final score of ≤ 12 (equivalent to having only one criterion with the maximum score) were defined as having a low level of threat.

Results

Current geographical range and level of protection According to our estimates the jaguar's geographical range is c. 8,420,000 km^2 (Table 4). Jaguars are still found in 18 countries across the continent, from northern Mexico to northern Argentina; they have disappeared from El Salvador and Uruguay and are practically extinct in the USA (Fig. 1). Using the area covered by the subpopulation polygons we estimate that the jaguar's geographical range has contracted by 48% in the last century. However, using our estimation of the area of occupancy, the situation is even worse; the area of occupancy is c. 7,400,000 km^2 and jaguar range may have decreased by 55% in the last century. Circa 38.4% of the species' geographical range is protected. Brazil has the largest proportion of area protected (66% of the jaguar's range), followed by Venezuela (8%), Peru (8%), Bolivia (5%) and Colombia (3%). We identified 34 subpopulation polygons of 2,241–6,691,521 km^2. One subpopulation, in Amazonia, covers 79% of the species' global range (Table 4). This means that jaguars have declined by c. 82% throughout their range outside Amazonia.

Population size We estimated the global population of jaguars to be c. 64,000 individuals (Fig. 2; Table 4). The largest subpopulation, in Amazonia, comprises c. 57,000 individuals; the mean estimated population of the remaining 33 subpopulations is 209 ± SD 293. The Amazonian subpopulation represents c. 89.2% of the total jaguar population, leaving only 10.8% in the rest of the range.

Assessment of subpopulations using IUCN criteria Based on our assessment of the subpopulations using IUCN criteria, jaguars are threatened virtually everywhere except in Amazonia (Fig. 3; Table 5). According to our assessment, and using the precautionary principle, 25 subpopulations should be categorized as Critically Endangered, and eight as Endangered. Only the Amazonian subpopulation maintains the status of Least Concern. Most subpopulations qualified for one of the threat categories under at least three criteria (C, D and E).

TABLE 4 Jaguar subpopulations (Fig. 1), with the area of the subpopulation polygon, the extent of occurrence (EOO) in each polygon, lower and upper estimates of the area of occupancy (AOO) in each polygon, and lower and upper estimates of the subpopulation size (no. of mature individuals).

No.	Jaguar subpopulation	Area of subpopulation polygon (km^2)	EOO, km^2 (Minimum Convex Polygon)	Lower estimate of AOO (km^2)	Upper estimate of AOO (km^2)	Lower estimate of jaguar subpopulation size[1]	Upper estimate of jaguar subpopulation size[2]
1	Mexican Pacific	195,848	1,274,871	117,964	151,000	852	1,179
2	Sierra de Tamaulipas	54,447	94,043	36,860	43,048	149	218
3	Gulf of Mexico	9,059	13,804	3,436	7,016	26	52
4	Selva Maya	88,923	182,895	80,016	83,308	764	1,079
5	Maya Mountains	17,856	28,246	7,248	9,556	217	332
6	Honduras Caribbean	6,333	9,999	1,532	2,284	9	16
7	Honduran Mosquitia	26,502	39,294	19,124	23,764	188	231
8	Indio-Maíz Tortuguero	26,766	43,303	13,132	18,332	101	152
9	Talamanca	15,141	17,887	7,712	11,484	25	69
10	Osa Peninsula	2,241	3,305	0	1,788	0	21
11	Central Panama	5,129	7,809	2,532	2,932	26	35
12	Biogeographic Choco	159,175	278,753	89,164	105,244	697	1,035
13	Paramillo-San Lucas	38,186	38,342	19,728	32,732	70	214
14	Sierra Nevada de Santa Marta	8,662	8,765	0	3,832	0	25
15	Serrania de Perija-Catatumbo	43,367	52,370	21,552	29,340	106	198
16	Santa Helena-Guayas	10,592	10,866	1,324	4,240	5	13
17	Amazonia	6,691,521	9,874,482	6,244,810	6,289,556	56,223	58,183
18	Maranhão-Babaçu	22,414	22,522	7,140	19,652	10	45
19	Nascentes Parnaíba	148,027	162,275	118,360	118,360	491	491
20	Boquerião da Onça	12,327	15,239	10,564	10,600	10	13
21	Serra da Capivara	81,466	103,542	52,704	57,080	132	169
22	Chapada Diamantina	25,110	30,076	14,496	16,188	21	24
23	Araguaia	122,212	143,080	103,832	103,832	531	566
24	Goiás & Tocantins	124,726	141,670	88,976	90,444	315	349
25	Sertão Veredas Peruaçu	138,305	162,923	72,528	76,396	202	239
26	Mato Grosso	112,103	146,001	91,696	91,696	762	782
27	Chapada dos Guimarães	44,246	48,245	24,512	24,536	72	80
28	Emas	15,169	15,182	9,212	9,212	30	31
29	Espinhaço de Minas	29,599	32,261	17,684	21,592	59	81
30	Sooretama	4,974	5,006	232	1,796	0	1
31	Mantiqueira-Rio Doce	5,249	5,285	1,204	1,804	2	3
32	Pontal do Paranapanema	34,888	44,925	13,636	16,444	12	16
33	Serra do Mar	56,400	116,227	16,012	26,968	23	45
34	Iguaçu	46,011	56,705	15,100	24,080	26	43

[1] Critical human density = 12 persons km^{-2}
[2] Critical human density = 24 persons km^{-2}

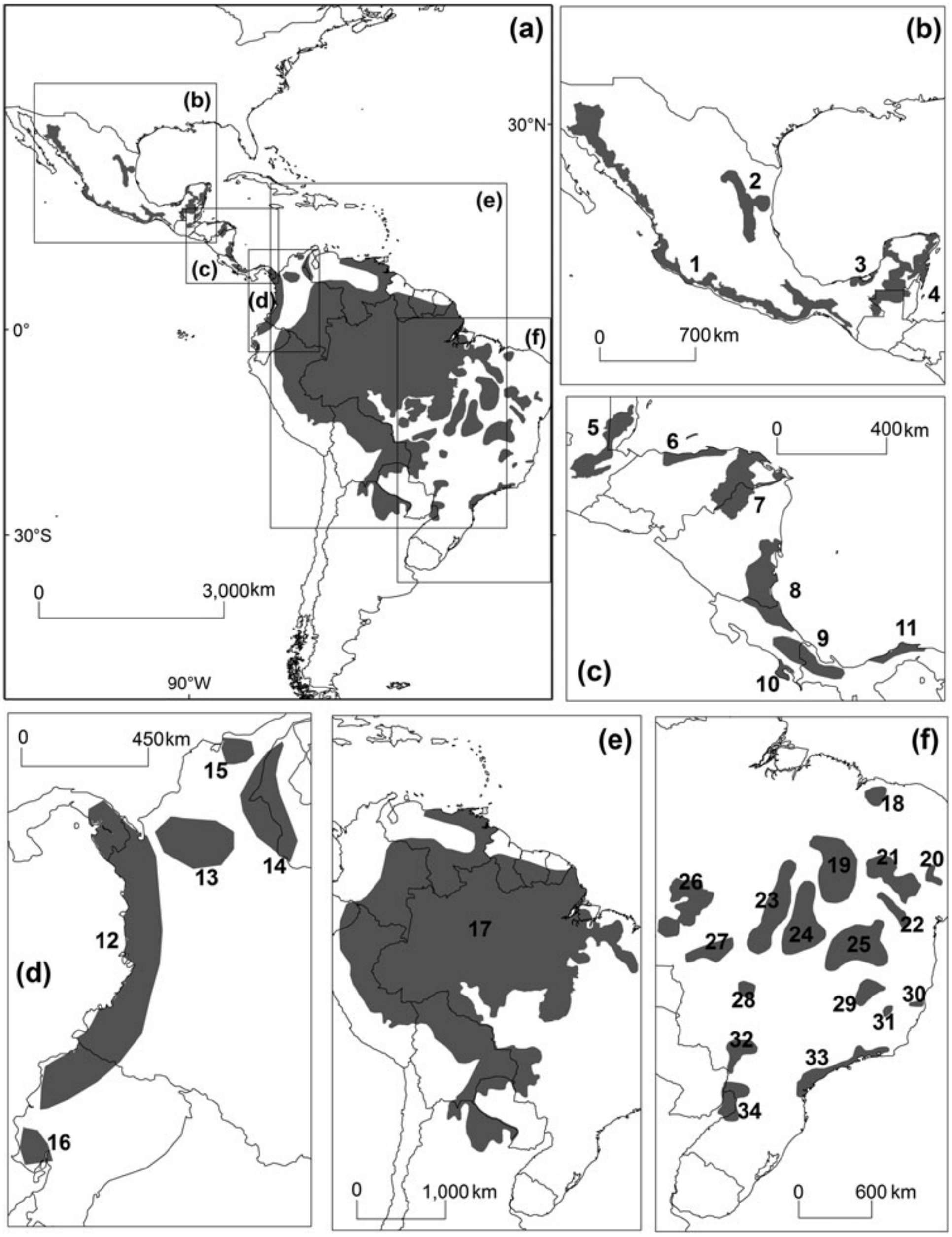

Fig. 1 (a) Locations (grey shaded areas) of the 34 known jaguar *Panthera onca* subpopulations identified (Table 4); (b) 1, Mexican Pacific; 2, Sierra de Tamaulipas; 3, Gulf of Mexico; 4, Selva Maya; (c) 5, Maya Mountains; 6, Honduras Caribbean; 7, Honduran Mosquitia; 8, Indio Maíz-Tortuguero; 9, Talamanca; 10, Osa Peninsula; 11, Central Panama; (d) 12, Biogeographic Choco; 13, Paramillo-San Lucas; 14, Sierra Nevada de Santa Marta; 15, Serrania de Perija-Catatumbo; 16, Santa Elena Guayas; (e) 17, Amazonia; (f) 18, Maranhão-Babaçu; 19, Nascentes Parnaíba; 20, Boquerião da Onça; 21, Serra da Capivara; 22, Chapada Diamantina; 23, Araguaia; 24, Goiás and Tocantins; 25, Sertão Veredas Peruaçu; 26, Mato Grosso; 27, Chapada dos Guimarães; 28, Emas; 29, Espinhaço de Minas; 30, Sooretama; 31, Mantiqueira-Rio Doce; 32, Pontal do Paranapanema; 33, Serra do Mar; 34, Iguaçu.

Level of threat to subpopulations According to our evaluation most of the subpopulations faced a high level of threat (Fig. 3; Table 6). We identified 17 subpopulations with scores that exceeded the threshold for a high level of threat, and 14 exceeded the threshold for a medium level of threat. Only the Amazonia, Araguaia and Selva Maya subpopulations scored as having a low level of threat. Most of the subpopulations with the highest levels of threat were in the southern portion of the species' range in Brazil and Argentina (n = 11). Additionally, three subpopulations in northern South America had high levels of threat: in Santa Helena-Guayas in Ecuador, and in Paramillo San Lucas and Sierra Nevada de Santa Marta in Colombia. In Central America the subpopulations with the highest levels of threat were in Central Panama and the Honduras Caribbean. In Mexico the subpopulation with the highest level of threat was the Sierra de Tamaulipas (Table 6).

Discussion

Our results support and provide greater robustness to prior assessments of range loss and population decline of jaguars at the continental scale (Sanderson et al., 2002; Zeller, 2007). Jaguars have been extirpated from more than half of their original range in the last 100 years, and the most recent assessments of the regional and continental conservation

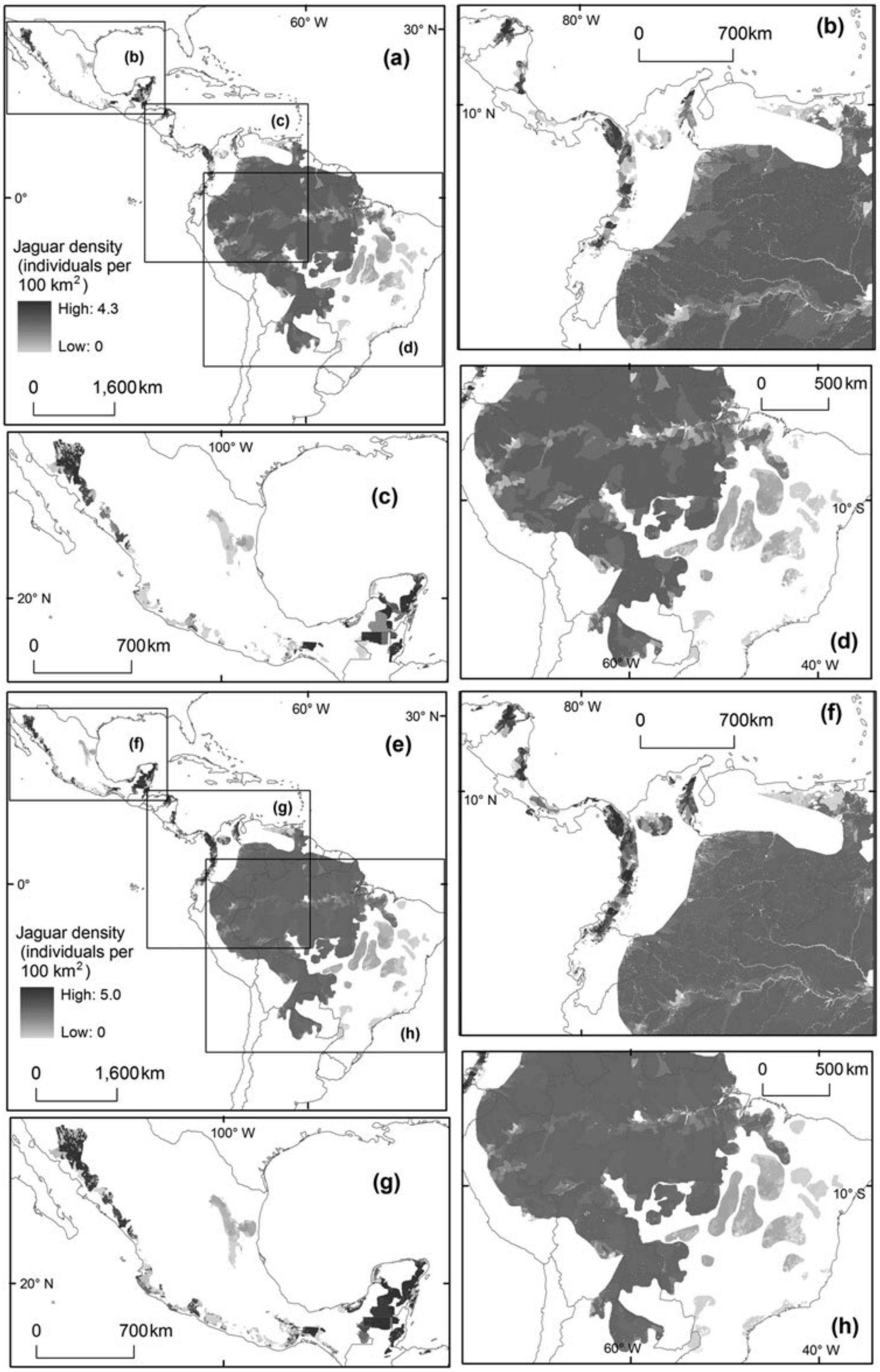

FIG. 2 Jaguar densities across the species' range according to our lower (a, b, c & d) and upper (e, f, g & h) estimates of subpopulation sizes. Density estimates were extrapolated only for sites where the human population density was ≤ 12 people km^{-2} (for our lower estimate) or ≤ 24 people km^{-2} (for our upper estimate), and jaguar densities were adjusted according to the human population density.

status of the species have concluded that the jaguar continues to decline in much of its current range (Swank & Teer, 1989; Medellín et al., 2002, 2016; Sanderson et al., 2002; Zeller, 2007; Caso et al., 2008). Our use of subpopulation polygons to estimate range loss is similar to the approach of Sanderson et al. (2002; 54% range loss). However, we included areas in the current range of the species where its occurrence was previously unknown (Sanderson et al., 2002; Zeller, 2007), and for the first time we assessed the species' status across its historical range, c. 16,300,000 km^2 (Patterson et al., 2007). Our estimates of the decline in the jaguar's range and population are therefore more accurate than previous approaches because our analysis was based on the most recent information on jaguar

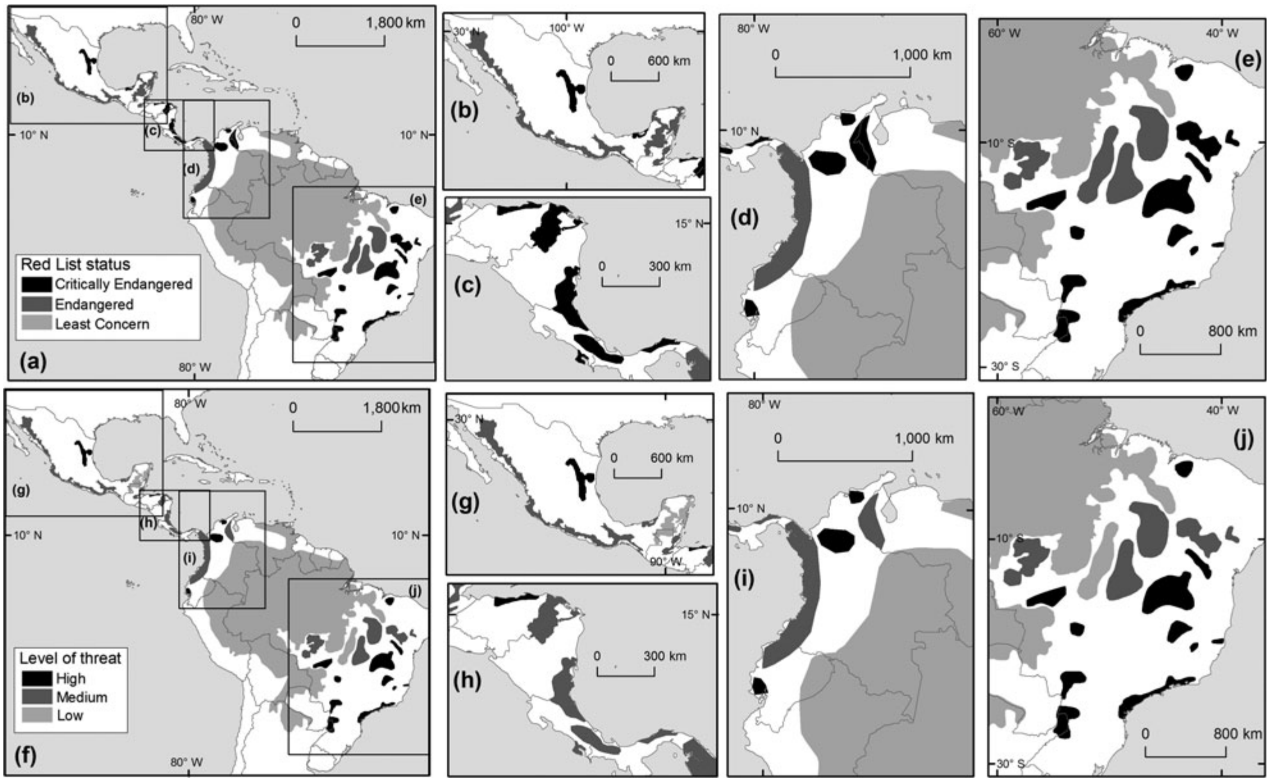

FIG. 3 Conservation status of jaguar subpopulations according to the IUCN Red List criteria (Table 5) (a) throughout the species' range, (b) in Mexico, (c) in Central America, (d) in northern South America, and (e) in southern Amazonia; and level of vulnerability of the subpopulations according to the levels of threat (Table 6) (f) throughout the species' range, (g) in Mexico, (h) in Central America, (i) in northern South America, and (j) in southern Amazonia.

distribution and on a more precise historical range of the species. Our estimate of the jaguar's global area of occupancy yields a worse scenario than previous assessments had projected; according to our analyses jaguars have already disappeared from c. 55% of their historical range and the majority of subpopulations are Endangered or Critically Endangered.

Our global estimate of the jaguar population could be questioned as it is based on the extrapolation of localized density estimates to extensive areas, ignoring local conditions such as fragmentation, prey availability and varying levels of threat. However, our approach and estimate are realistic and conservative because we extrapolated jaguar densities only for sites where human population density did not exceed the threshold at which jaguar extirpation was predicted (Woodroffe, 2000), and because we assumed that jaguar density decreased with increasing human population density. Furthermore, there are other estimates of local population sizes that suggest that our approach is reasonable (Tobler et al., 2013; Chávez et al., 2016; de Thoisy, 2016; Di Bitetti et al., 2016; Díaz-Santos et al., 2016; Espinosa et al., 2016; Figueroa et al., 2016; García-Anleu et al., 2016).

Amazonia is the only remaining stronghold for the species, and several studies have highlighted the importance of this region for jaguar conservation (Sanderson et al., 2002; Sollmann et al., 2008; de Oliveira et al., 2012; Tobler et al., 2013). Even this subpopulation is likely to be affected in the coming decades by deforestation and other threats because the region is rapidly being transformed by human activity (Rosa et al., 2012, 2013; Coe et al., 2013; Morton et al., 2013). Ochoa-Quintero et al. (2015) predicted that by 2030 only 22% of the landscapes in the Amazon will be able to sustain at least 75% of the focal species of mammals and birds, including the jaguar, as a result of habitat fragmentation.

Assessments of the conservation status of a species should not be based on, or affected significantly by, the existence of a single large subpopulation. Rather, conservation plans should be based on an integrated assessment of the species over its entire range (Ceballos & Ehrlich, 2002; Wallace et al., 2010). Data based on only one subpopulation is likely to result in a biased assessment and the risk that all other subpopulations will become extinct. As most of the jaguar subpopulations are threatened and subspecific categorization has been rejected, we propose that jaguar conservation assessments should include not only one global category but should consider subpopulations/sub-global assessments. Data on only the range size of this species has biased the assessment, and conservation resources have not been allocated specifically for threatened subpopulations, given the species' global Near Threatened, rather than threatened, status. In addition,

TABLE 5 Categorization of each jaguar subpopulation (Fig. 1) based on evaluation against each of the IUCN Red List criteria, and the category assigned under the most precautionary principle.

		IUCN criteria					
No.	Jaguar subpopulation	A. Population size reduction	B. Geographical range	C. Small population size & decline	D. Very small or restricted population	E. Quantitative analysis	IUCN Red List category* assigned
1	Mexican Pacific			EN C2a(i)	VU D1		EN
2	Sierra de Tamaulipas			CR C2a(ii)	EN D	VU E	CR
3	Gulf of Mexico	VU A2a+4c	VU B1ab(i)	CR C2a(ii)	CR D	EN E; CR E	CR
4	Selva Maya			EN C2a(ii)	VU D1	VU E	EN
5	Maya Mountains	VU A4c		CR C2a(ii); EN C2a(ii)	EN D1;VU D1	VU E	EN
6	Honduras Caribbean	VU A2a+4c	VU B1ab(i) +2ab(ii)	CR C2a(i)	CR D	CR E	CR
7	Honduran Mosquitia	VU A4c		CR C2a(ii)	EN D	VU E	CR
8	Indio-Maíz Tortuguero			CR C2a(ii)	EN D	VU E	CR
9	Talamanca		VU B1ab(i)	CR C2a(ii)	CR D; EN D1	EN E; CR E	CR
10	Osa Peninsula	VU A4c	EN B1ab(i); VU B2ab(ii)	CR C2a(ii)	CR D	CR E	CR
11	Central Panama		VU B1ab(i)	CR C2a(ii)	CR D	EN E; CR E	CR
12	Biogeographic Choco			EN C2a(ii)	VU D1	VU E	EN
13	Paramillo-San Lucas			CR C2a(ii)	EN D	VU E; EN E	CR
14	Sierra Nevada de Santa Marta		VU B1ab(i)	CR C2a(ii)	CR D	CR E	CR
15	Serrania de Perija-Catatumbo	VU A4c		CR C2a(ii)	EN D	VU E	CR
16	Santa Helena-Guayas	VU A4c	VU B1ab(i)	CR C2a(i)	CR D	CR E	CR
17	Amazonia						LC
18	Maranhão-Babaçu	VU A4c		CR C2a(ii)	CR D	EN E; CR E	CR
19	Nascentes Parnaíba			EN C2a(ii)	VU D1	VU E	EN
20	Boquerião da Onça		VU B1ab(i)	CR C2a(ii)	CR D	CR E	CR
21	Serra da Capivara	VU A4c		CR C2a(i)	EN D	VU E	CR
22	Chapada Diamantina			CR C2a(i)	CR D	CR E	CR
23	Araguaia			EN C2a(ii)	VU D1	VU E	EN
24	Goiás & Tocantins	VU A4c		EN C2a(i)	VU D1	VU E	EN
25	Sertão Veredas Peruaçu	VU A2a+4c		CR C2a(i)	EN D	VU E	CR
26	Mato Grosso			EN C2a(i)	VU D1	VU E	EN
27	Chapada dos Guimarães	VU A2a+4c		CR C2a(i)	EN D	EN E	CR
28	Emas	VU A4c	VU B1ab(i)	CR C2a(i)	CR D	EN E	CR
29	Espinhaço de Minas			CR C2a(i)	EN D	EN E	CR
30	Sooretama	VU A2a+4c	VU B1ab(i) +2ab(ii)	CR C2a(i)	CR D	CR E	CR
31	Mantiqueira-Rio Doce	VU A4c	VU B1ab(i) +2ab(ii)	CR C2a(i)	CR D	CR E	CR
32	Pontal do Paranapanema	VU A4c		CR C2a(i)	CR D	CR E	CR
33	Serra do Mar			CR C2a(i)	CR D	EN E; CR E	CR
34	Iguaçu	VU A4c		CR C2a(i)	CR D	EN E; CR E	CR

*VU, Vulnerable; EN, Endangered; CR, Critically Endangered

TABLE 6 The 34 jaguar subpopulations (Fig. 1), with values for each of the five criteria used to evaluate the level of threat to each subpopulation.

No.	Jaguar subpopulation	% natural cover	Human population density (km^{-2})	Mean no. of jaguars	Mean distance to four nearest subpopulation polygons (km)	% protected	Total score	Level of threat
1	Mexican Pacific	86.08	488.3	1,016	161.00	8.87	14	Medium
2	Sierra de Tamaulipas	93.75	1033.1	184	858.00	16.73	18	High
3	Gulf of Mexico	79.25	263.6	39	301.00	66.47	15	Medium
4	Selva Maya	95.32	216.8	922	131.00	50.67	12	Low
5	Maya Mountains	90.10	884.5	275	183.83	49.74	16	Medium
6	Honduras Caribbean	45.78	1096.1	13	240.00	29.59	19	High
7	Honduran Mosquitia	85.90	116.6	210	284.00	87.46	15	Medium
8	Indio-Maíz Tortuguero	74.69	408.5	127	160.00	63.79	14	Medium
9	Talamanca	81.24	572.0	47	99.00	48.16	15	Medium
10	Osa Peninsula	69.94	307.7	11	206.00	63.53	16	Medium
11	Central Panama	73.03	1687.5	31	186.00	57.96	16	Medium
12	Biogeographic Choco	74.17	928.4	866	86.00	11.62	15	Medium
13	Paramillo-San Lucas	72.06	521.0	142	138.00	9.16	18	High
14	Sierra Nevada de Santa Marta	75.61	1451.2	13	228.00	38.87	17	High
15	Serrania de Perija-Catatumbo	65.51	1151.8	152	100.00	25.28	16	Medium
16	Santa Helena-Guayas	51.66	4544.6	9	534.00	2.10	19	High
17	Amazonia	93.02	83.6	57,203	51.00	42.75	11	Low
18	Maranhão-Babaçu	70.72	392.0	28	366.00	20.95	18	High
19	Nascentes Parnaíba	61.13	53.1	491	59.00	19.58	14	Medium
20	Boquerião da Onça	68.81	155.6	12	63.00	5.88	18	Medium
21	Serra da Capivara	60.66	106.8	151	294.00	20.30	16	Medium
22	Chapada Diamantina	54.70	195.3	23	141.00	17.05	17	High
23	Araguaia	76.93	27.8	549	69.00	35.33	12	Low
24	Goiás & Tocantins	55.54	132.5	332	89.00	10.01	15	Medium
25	Sertão Veredas Peruaçu	35.87	151.0	221	101.63	12.96	18	High
26	Mato Grosso	78.57	29.6	772	329.00	13.94	14	Medium
27	Chapada dos Guimarães	42.51	380.7	76	166.00	10.90	18	High
28	Emas	42.39	58.9	31	235.00	10.79	18	High
29	Espinhaço de Minas	58.70	209.1	70	225.00	7.49	18	High
30	Sooretama	44.41	744.9	1	297.53	15.10	20	High
31	Mantiqueira-Rio Doce	51.64	2024.6	3	225.11	7.90	19	High
32	Pontal do Paranapanema	25.26	220.5	14	298.00	29.24	18	High
33	Serra do Mar	77.36	5757.6	34	307.24	44.02	17	High
34	Iguaçu	59.12	771.1	35	338.00	14.37	19	High

decline is accelerating in most subpopulations, and the causes of decline are still present, and therefore it is likely the jaguar will become more threatened in most of its range. The main threats to the species throughout its range are hunting, depletion of prey, and habitat loss and fragmentation (Sanderson et al., 2002; Caso et al., 2008; Haag et al., 2010).

Based on our evaluation of threats, conservation efforts for the most threatened subpopulations should be prioritized. Identification and implementation of corridors to maintain connectivity should be a priority in the polygons that have the highest degree of isolation and the lowest population sizes (Rabinowitz & Zeller, 2010); for example, subpopulations in the Atlantic Forest in Brazil and Argentina are threatened not only by their isolation and low numbers but also by low genetic diversity, lack of gene flow, and small effective population sizes (Haag et al., 2010). Another priority is to plan reserves throughout the jaguar's range to ensure the long-term connectivity and conservation of most subpopulations. In most of the subpopulation polygons $<$ 25% of the area is protected. Vast areas of high-quality habitat are required to ensure the viability of a jaguar population over the long term (Quigley & Crawshaw, 1992; Ceballos et al., 2002; Sanderson et al., 2002); however, few regions where the species currently ranges maintain protected areas that are large enough to ensure the protection of at least 300 jaguars, to guarantee population viability over the next 100 years (Eizirik et al., 2002). Furthermore, many protected areas throughout the species' range have limited or no real protection. The jaguar is considered to be an umbrella, charismatic, and symbol or flag species in many conservation programmes throughout Latin America (Medellín et al., 2002, 2016; Sanderson et al., 2002; Rabinowitz & Zeller, 2010), and ensuring the protection of areas large enough to maintain viable populations of jaguars offers a unique opportunity to ensure protection of the biodiversity with which jaguars coexist (Thornton et al., 2016). In areas that are threatened by high human densities and risk of habitat loss, sustainable development policies should be implemented to ensure the conservation of jaguar habitat and the well-being of human communities that coexist with this felid.

Our analysis is the first to provide a global population estimate for the jaguar. It also establishes a basis for determining geographical conservation priorities for this iconic umbrella species based on the vulnerability of its individual populations. More detailed information is needed about the areas occupied by the species across its range. Additional density estimates for more biomes and ecoregions would also help to improve the definition of subpopulations, and more accurate estimates of the distances that jaguars can travel between fragmented landscapes would indicate where conservation efforts should be allocated. The sub-global assessments should be included under the IUCN Red List as a matter of urgency; we believe that consideration of our analysis, and further research, would result in a robust regional conservation strategy that could be designed and implemented by local conservation leaders across the species' range.

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Author contributions

JAT and RAM conceptualized and designed the study. JAT compiled the information on the jaguar subpopulations, conducted the assessment using the IUCN Red List guidelines, and drafted the article. RAM and JFGM also wrote sections of the article. JFGM and HZ compiled the information on jaguar distribution and analysed the spatial information. RAM and GC reviewed the data, reviewed the article critically and directed the revisions.

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Biographical sketches

J. Antonio de la Torre is interested in carnivore ecology, behaviour and conservation; he has studied jaguars in southern Mexico for the past 10 years. José F. Gonzalez-Maya is interested in functional ecology and the conservation of mammals, with a particular focus on Colombia and Costa Rica. Heliot Zarza works on research projects involving spatial analysis and conservation of carnivores. Gerardo Ceballos and Rodrigo A. Medellín have studied the ecology and conservation of mammals in Mexico for more than 30 years. All the authors have guided the conservation and management plans for jaguars in Mexico and other countries.

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