JAGUAR CONSERVATION IN VENEZUELA AGAINST THE BACKDROP OF CURRENT KNOWLEDGE ON ITS BIOLOGY AND EVOLUTION

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SUMMARY

Current knowledge is reviewed on the jaguar Panthera onca *evolution, morphological, genetic and ecological variation, as a background for understanding conservation problems. Based on published sources and own data, the current situation of the jaguar in Venezuela is analyzed. Body size of today's jaguars is highly variable; the largest are found in the Brazilian Pantanal and Venezuelan Llanos (mean male body mass >100kg). The smallest jaguars live in Central America (~56kg). Skin coloration pattern is highly variable and may have a geographic correlation. The morphological variation correlates with its genetic variability, which in turn may reflect diversity of adaptations to different habitats and prey communities. Its diet is extremely diversified. The territorial size and density of jaguars varies amongst localities, probably reflecting variation in prey density and degree of human disturbance. Adaptation to kill large prey makes it a notorious livestock predator. Conflicts caused by jaguar predation on cattle are the main reason for killing them, although they are also hunted for skins, despite legal protection. Another threat is deforestation. Jaguar population in Venezuela has decreased substantially during the last 30-40 years, and is currently variable: in northern Venezuela isolated and declining small populations survive; south of the Orinoco, a vast population exists; in Los Llanos it was nearly eliminated ~40 years ago, but seems to have returned and re-colonized former territories. The most important measure for conservation of jaguars in Venezuela is to create more protected areas, to develop ecological corridors to protect connectivity and halt deforestation of critical regions. Hunting and killing could decrease through educational programs, involving local communities, compensations for losses from jaguar predation and incentivizing ecotourism.*

Summary of Current Knowledge on Jaguar Biology and Evolution

Evolution, morphological variation, genetics, and taxonomy of the jaguar

The jaguar *Panthera onca* evolved in Europe or Asia during the late Pliocene/early Pleistocene period, at least 1.8-2.0 million years ago (Kurten, 1965, 1973; Hemmer *et al*., 2001, 2010). Fossils of the European jaguar *P. onca gombaszoegensis* have been recorded from several localities of Eurasia, including Italy, Greece, Bulgaria, Hungary, Spain, France, Germany, Netherlands, Great Britain, Caucasus, lower Urals, and in Tajikistan (Sotnikova and Vislobokova, 1990; Koufos, 1992; Spassov, 1997; Turner and Anton, 1997; Kahlke, 2000; Hemmer *et al*., 2001, 2010; Baryshnikov, 2002, 2011; Palombo and Valli, 2003-2004; O'Regan and Turner, 2004; Foronova, 2005; Van Den Hoek Ostende and De Vos, 2006; Petronio *et al*.,

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2011). Based on the oldest jaguar fossils from North America, it colonized this continent via the Bering Strait during the middle Pleistocene, ~850,000 years ago (Simpson, 1941; Kurtén and Anderson, 1980; Seymour, 1989, 1993; Turner and Anton, 1997; Arroyo-Cabrales, 2002). Very soon, also in the middle Pleistocene, it passed from North to South America through the Panama (Darien) Isthmus (Webb, 1985, 2006; Marshall and Sempere, 1991; Arroyo-Cabrales, 2002). Rincón and Prevosti (2011) suggested that current dating may result from sampling bias, as there have been relatively few paleontological studies in northern South America. They hypothesized that in general the big cats came in a wave to South America much earlier, as the Isthmus of Panama was already functional in Late Pliocene, at least 2.7 million years ago (Webb, 2006; Rincón and Prevosti, 2011). However, most of jaguar fossils from South America are dated from middle or late Pleistocene (Marshall and Sempere, 1991; Arroyo-Cabrales, 2002; Prevosti and Vizcaíno, 2006; Tonni *et al*., 2009; Ghilardi *et al*., 2011). Repeated advances of ice sheets during glaciations caused the extinction of jaguars in Europe, Asia, and North America ~400,000 years ago. When the climate warmed up during the Holocene period, Central and North America were recolonized by jaguars (Turner and Anton, 1997). The current geographic range of the species covers from Mexico to northern Argentina (Sanderson *et al*., 2002a).

Morphological studies placed the jaguar close to the leopard *Panthera pardus*; however, recent molecular studies indicate that it is more closely related to the lion *P. leo* (Pocock 1939; Johnson *et al*., 2006; O'Brien *et al*., 2008; Werdelin *et al*., 2010) or the snow-leopard *P. uncia* (Yu and Zhang, 2005). It has been also suggested that the jaguar and the extinct American lion *Panthera atrox* (one of the biggest ever living cats) were the two closest related species. In this scenario, *P. o. gombaszoegensis*, after entering North America would had evolved into the modern jaguars and the extinct *P. atrox* (Christiansen and Harris, 2009). Nine subspecies of living jaguars were formerly distinguished, based on morphological features; more recently, based on a more thorough analysis and molecular studies, this division has been rejected and three distinct groups established (Pocock, 1939; Seymour, 1989; Larson, 1997; Wozencraft, 2005):

1) *Panthera onca hernandesii* (Western Mexico) + *P. o. centralis* (Central America -El Salvador to Colombia) + *P. o. arizonensis* (Southern Arizona to Sonora, Mexico) + *P. o. veraecrucis* (Central Texas to Southeastern Mexico) + *P. o. goldmani* (Yucatán Peninsula to Belize and Guatemala);

2) *P. onca onca* (Venezuela through the Amazon) + *P. o. peruviana* (Coastal Peru); and

3) *P. onca palustris* (Pantanal regions of Mato Grosso and Mato Grosso do Sur, Brazil) + *P. o. paraguensis* (along the Paraguay River into Paraguay and northeastern Argentina).

Additionally, five extinct subspecies have been proposed (Cabrera, 1934; Simpson, 1941; Hoffstetter, 1952; Seymour, 1993; Hemmer 2001, 2010): *P. o. mesembrina* (Pleistocene South American jaguar), *P. o. augusta* (Pleistocene North American jaguar), *P. o. gombaszoegensis* (Pleistocene Euroasian jaguar), *P. o. georgica* (early Pleistocene European-Caucasian jaguar, 1.8 mya), and *P. o. toscana* (most archaic, early Pleistocene European jaguar).

The jaguar skull is robust and massive but relatively short, with wide zygomatic arches. The sagittal crest is well developed to support the powerful head muscles. Condylobasal length is usually 190-260mm, but in some may be longer than 275mm (Seymour, 1989; Hoogesteijn and Mondolfi, 1996). Powerful jaws, with very long and massive canines, endow it the strongest bite of all cats, capable of breaking the skull of a tapir or a turtle shell. Jaguars can kill a cow with a bite from ear to ear, piercing through the skull to the brain (Meachen-Samuels and Van Valkenburgh, 2009). They have sharp, strong, retractile claws, which they use to grasp and hold a prey. All these adaptations to kill large prey are better understood in the context of jaguar evolution. They evolved as predators in the mega-fauna communities of Pliocene/Pleistocene. In Europe, their fossils are found together with fossils of large herbivores: mammoths *Mammuthus trogontherii*; forest elephants *Elephas antiques*; large bovids such as bison *Bison schoetensacki*, *B. priscus*, *Bos* sp. and musk ox *Praeovibos priscus*; ancient wild boar *Sus scrofa priscus*; deer *Cervus* sp., *Dama* sp., *Megaloceros* sp.; wooly rhinos *Stephanorhinus* sp.; horses *Equus mosbachensis*; ancient moose *Alces latifrons*; and many others (Kahlke, 2000; Hemmer *et al*., 2001; Baryshnikov, 2002; Palombo and Valli, 2003-2004; Kahlke *et al*., 2011; Petronio *et al*., 2011). It is difficult to establish which of these herbivores were the jaguar's main prey, but the adaptations of ancient and living jaguars to kill large prey are obvious. In South America, after colonizing this continent in the middle Pleistocene up until ~10,000 years ago, jaguars coexisted with the local large herbivorous community composed of giant ground sloth *Megatherium*, forest elephants *Cuvieronius*, mastodonts *Stegomastodon*, camel-like *Macrauchenia*, huge armadillos *Glyptodon*, wild horses *Hippidion*, and *Toxodons*, animals similar to hippopotamus or rhinos (Lessa and Farina, 1996; Turner and Anton, 1997; Alroy, 2001; Cione *et al*., 2003; Soibelzon *et al*., 2008). Due to the extinction of South American mega-fauna 10,000-12,000 years ago, possibly because of climate change and also human hunting (Alroy, 2001), today jaguars are left with communities of much smaller prey.

The body size of jaguars is highly variable, both at the continental and local levels, and there is sexual dimorphism in body size, females being 10-20% smaller than males. Females from western Brazil and from Central America are the smallest, while jaguars from Paraguay and Pantanal are believed to be the largest (Seymour, 1989; Hoogesteijn and Mondolfi, 1996). Hoogesteijn and Mondolfi (1996) analyzed body mass and skull measures of several jaguars from the Venezuelan Llanos, the Brazilian Pantanal, the Amazon basin and Central America. The largest jaguars were from the Llanos (mean body mass for males of 104.5kg and for females of 66.9kg) and the Pantanal (99.5 and 76.7kg, respectively). Skull measures were slightly higher for Pantanal males and significantly higher for Pantanal females. The smallest jaguars were those from Central America (56.1 and 41.4kg in males and females, respectively) while those from the Amazon were intermediate (83.6kg for males, no data for females). Based on fossil morphometrics, it has been suggested that the late Pleistocene jaguars from North America (*P. o. augusta*) were 15-25% bigger than present jaguars, weighing up to 180kg. However, regression analyses of fossil measures, based on correlations between morphological measurements and body size of living jaguars, have shown that past jaguars were only slightly bigger than present ones, weighing ~120kg (Seymour, 1993).

The above-mentioned morphological variation must have a

genetic basis, but population genetic studies on extant jaguars are scarce (Eizirik *et al*., 2001, 2002; Ruíz-García *et al*., 2003, 2006, 2007; Haag *et al*., 2010). They include a large-scale screening of genetic variation based on a relatively small sample (n= 40) of jaguars taken from their entire range in Central and South America (Eizirik *et al*. 2001, 2002), and a more detailed analysis of the Colombian population (Ruíz-García *et al*., 2006, 2007). Both studies showed high microsatellite genetic diversity of jaguars (H= 0.739 and 0.846 in the in the first second study). In the sample of 40 individuals, Eizirik *et al*. (2001) identified 22 haplotypes of mitochondrial DNA and estimated that the haplotypes originated some 280,000-510,000 years ago. This suggests that the modern jaguar is a younger species than has been assumed based on paleontological studies. No signs of any past bottleneck have been detected, which might have been expected given both the history of their colonization of North and South America, and the recent human persecution of the species. Two partial barriers to gene flow were identified by Eizirik *et al*. (2001): the Amazon River and the Darien strait. Additionally, studies by Ruíz-García *et al*. (2006, 2007) revealed a significant heterogeneity between populations from two distinct regions in Colombia, in concordance with the occurrence of two subspecies distinguished earlier by taxonomists (*P. o. onca* and *P. o. centralis*).

Jaguar ecology

Jaguars inhabit a variety of environments, including various types of tropical and subtropical forests, marshlands, mangroves, savanna-forest mosaics and shrublands; they can live in lowlands and mountains, as well as in coastal areas. They show clear preference for wet habitats and waterbodies, and are often reported to swim (Sanderson *et al*., 2002a). Paleo-environmental reconstructions of habitats occupied by Pleistocene Eurasian jaguars also showed a wide habitat niche; they lived in a variety of deciduous woodlands, riparian forests, shrublands and dry meadow-steppes in both lowlands and mountain conditions (Hemmer *et al*., 2001).

Jaguars usually catch their prey by stalking or ambush. In a fast attack, a jaguar grasps a prey with its claws and bites the neck or head, or it just hits a prey with its paws. With bigger preys they may jump over them, biting the nape and dragging them down (Seymour, 1989; Meachen-Samuels and Van Valkenburgh, 2009). They often conceal bigger kills, are capable of dragging heavy carcasses for long distances, and can consume small prey at the site of killing.

About 85 species have been reported to be prey of jaguars (Seymour, 1989). The majority of studies document that the most important in terms of biomass consumed are: collared peccary *Tayassu tayacu*, white-lipped peccary *T. pecari*, brocket deer *Mazama* sp., white-tailed deer *Odocoileus virginianus*, cattle *Bos Taurus*, paca *Agouti paca*, agouti *Dasyprocta* sp., armadillo *Dasypus* sp., capybara *Hydrochoerus hydrochaeris*, caimans *Caiman yacare*, and coati *Nasua nasua*. In some studies red howler monkeys (*Alouatta seniculus*) also constituted an important source of food biomass. Less important in terms of biomass but frequently killed are hares *Sylvilagus brasiliensis*, opossums *Didelphis marsupialis*, medium size reptiles (especially turtles and iguanas), and large birds, such as curassows *Crax* sp. (Rabinowitz and Nottingham, 1986; Emmons, 1987; Chinchilla, 1997; Taber *et al*., 1997; Nuñez *et al*., 2000; Garla *et al*., 2001; Scognamillo *et al*., 2003; Nowak, 2005; Weckel*, et al*., 2006; Cascelli de Azevedo, 2008; Carrillo *et al*., 2009; Cavalcanti and Gese, 2009; Da Silveira *et al*., 2010; Foster*, et al*., 2010).

Jaguars seem to be opportunistic predators, able to hunt for a variety of prey species in proportions depending on local prey availability. However, closer studies showed that jaguars actively select some species from local communities and avoid others. The species most often reported as preferred and actively selected are collared and white lipped peccaries, brocket and white tail deer, giant ant eater *Myrmecophaga tridactyla*, capybara, and armadillo. Most avoided (taken less frequently than expected from their share in the communities) are all monkey species, tapirs *Tapirus terrestris*, cattle, caimans, coati, agouti, opossums, skunks *Conepatus* sp., small rodents, small and medium birds, and small reptiles (Garla *et al*., 2001; Nowak, 2005; Weckel *et al*., 2006; Cascelli de Azevedo, 2008; Cavalcanti and Gese, 2009). Both diet composition and selectivity of jaguars to various prey species are highly variable at different localities, and change with time in a given locality. For example, some studies document avoidance of peccary, although generally it is a preferred prey species (Weckel *et al*., 2006; Cavalcanti and Gese, 2009).

De Oliveira (2002) analyzed data on jaguar diet from 23 different studies. The mean standardized food niche breadth (Levins, 1968; Colwell and Futuyma, 1971) of jaguar was 0.43, very similar to that of puma (0.45). The mean jaguar prey mass was 31kg and that of its main prey was 41kg, values that were twice as big as for *Puma concolor*. However, the mean prey mass was highly variable between different study sites and ranged from 2.4 to 62.9kg (de Oliveira, 2002).

Cavalcanti and Gese (2010) estimated the jaguar kill rate based on data from 10 radiotracked specimens in Pantanal, Brazil. One animal killed on average a large or medium sized prey every 4 days, equivalent to 84 prey individuals killed per year. These included 25 caimans, 21 cattle, 20 peccary, 8 deer, 3 giant ant eaters, and 9 other medium/large prey. With such high kill rates, jaguar livestock predation can be high in some areas, depending on local jaguar densities. When hunting for cattle, jaguars kill mostly calves, but occasionally, some individuals (probably mostly males) may kill also adult cows and even adult bulls. They may kill also horses, donkeys, pigs, dogs and chickens (Hoogesteijn *et al*., 1993). In various studies, total reported cattle losses due to all natural mortality factors (droughts, diseases, flooding, and predation) were 2.1 to 4.2% of the population. About 10 to 30% of all natural mortalities were caused by jaguars. Annually, jaguars killed 0.1 to 1.1% of cattle. Calves may constitute 40-70% (in Mexico up to 100%) of all cattle hunted by jaguars. Jaguars eliminated 0.8-2.9% of all calves born/year (Crawshaw and Quigley, 2002; Cascelli de Azevedo and Murray, 2007a; Rosas-Rosas *et al*., 2008). Scognamillo *et al*. (2002, 2003) and Polisar *et al*. (2003) estimated a similar rate of jaguar predation on cattle at Hato Piñero. However, applying a kill rate from a radiotracking study by Cavalcanti and Gese (2010) to calculate losses in *hatos* (cattle ranches) with stable jaguar population leads to much higher estimates. For example, such calculation for Hato Piñero would result in 17% of calves and 2.8% of the total cattle population removed by jaguars per year. These figures show that jaguar predation can be an important problem for ranchers and should be seriously considered in conservation strategies. González-Fernández (1995) showed that most *hatos* in the Venezu-

elan Cojedes state have problems with jaguar and puma predation of livestock. Individual jaguars can show preference for killing livestock while others will do it rarely (Brock. 1963; Mondolfi and Hoogesteijn, 1986; Hoogesteijn *et al*., 1993). It has been also shown that jaguars killing cattle are often disabled individuals (injured, sick or old; Rabinowitz, 1986; Hoogesteijn *et al*., 1993, 2002, 2011). When these particular jaguars are shot or removed from an area, livestock losses cease even if there are other jaguars in the vicinity (Rabinowitz, 1986).

Jaguars very rarely kill humans, although accidental attacks may happen (Perry, 1970; Guggisberg, 1975; Neto *et al*., 2011). At Mission Tokuko, in the Sierra de Perijá, Zulia, Venezuela, a Franciscan father reported that he conducted two funerals of women killed and partially eaten by jaguars, at a Yukpa and Bari community at Saimadoyi.

Jaguars may live up to 23 years in captivity and up to 15 years in the wild (Hoogesteijn and Mondolfi, 1992; Nowell and Jackson, 1996). Females become sexually mature at 2 years old, males at 3 years (Mondolfi and Hoogesteijn, 1986; Seymour, 1989; Hoogesteijn and Mondolfi, 1992; Nowell and Jackson, 1996; Sunquist and Sunquist, 2002). When in estrous, females announce fertility by scent marking and increased vocalization. Gestation lasts ~3 months (Nowell and Jackson, 1996), and 1-4 cubs are born, usually two (Rabinowitz and Nottingham, 1986; Hoogesteijn and Mondolfi, 1992; Sunquist and Sunquist, 2002). The cubs are fully weaned at 3-6 months of age (Hunt, 1967; Sunquist and Sunquist, 2002). They start to follow the mother when they are 2-5 months old and they stay with her up to ~2 years old (Seymour, 1989; Hoogesteijn and Mondolfi, 1992; Nowell and Jackson, 1996).

Jaguars are territorial predators. Females maintain almost entirely exclusive territories from other females, while male territories may overlap widely. Male and female home ranges also overlap, with 1-3 female territories being partially within a male territory. Although generally males do not accompany females outside the mating period and do not take care of young, they may stay closer to females than expected from random distribution, and there are indications of social interactions between males and females throughout the year (Rabinowitz and Nottingham, 1986; Crawshaw and Quigley, 1991; Cascelli de Azevedo and Murray, 2007b; Cavalcanti and Gese, 2009). Jaguars mark their territories by spraying urine, leaving feces, scraping the ground and scratching trees, or with scent marking by rubbing their head, neck or whole body against the ground or trees (Perry, 1970; Wemmer and Scow, 1977; Seymour, 1989; authors unpublished data). Roaring is also a kind of territorial marking, playing a role in communication between males and females as well. Male jaguars often respond to roars of other males (Emmons, 1987). Their roaring resembles mews, grunts or short, loud cough, fast repeated 3-6 times. Both sexes are vocal, although males vocalize more frequently.

Various studies documented a high variation in jaguar home range size across South and Central America. The smallest territories were found in Belize and Costa Rica: 11-12km^2 for females and 33km^2 for males (Rabinowitz and Nottingham, 1986; Carrillo *et al*., 2000). Small territories (36-45km^2 for females and 37-67km^2 for males) were also documented in Calakmul, Mexico (Ceballos *et al*., 2001) and in some areas of Pantanal, Brazil (Soisalo and Cavalcanti, 2006; Cascelli de Azevedo and Murray, 2007b). The biggest average home range size was also documented in the Pantanal: 163 and 157km^2, respectively (Crawshaw and Quigley, 1991). Radiotracking of jaguars in Hato Piñero (Venezuela) revealed fairly large home ranges of 83 and 100km^2, for females and males, respectively (Scognamillo *et al*., 2002, 2003; Polisar*, et al*., 2003).

Similar variation has been observed for jaguar densities. The highest densities, 7-10 individuals/100km^2, were found for tropical rain forests in Belize, Costa Rica, Calakmul (Mexico) and a mosaic of wetlands, forests and grasslands in Pantanal, Brazil. The lowest densities, 2-3 individuals/100km^2, were recorded for dry scrublands in Caatinga and dry savanna in Cerrado-Pantanal, Brazil, agricultural lands in Belize, and a mosaic of dry forests, wetlands and open pastures in Hato Piñero, Venezuela (Ceballos *et al*., 2001; Scognamillo *et al*., 2002; Polisar *et al*., 2003; Scognamillo *et al*., 2003; Silver *et al*., 2004; Harmsen, 2006; Cascelli de Azevedo and Murray, 2007b; Salom-Pérez *et al*., 2007; Foster *et al*., 2010; Nájera, 2010). Densities <1.0 or as low as 0.3 individuals/100km^2 were documented for very dry or human altered habitats in Brazil, Argentina and Uruguay (Paviolo *et al*., 2008; Sollmann *et al*., 2010). Habitat and prey productivity, degree of habitat alteration and intensity of hunting by humans are the most likely factors responsible for this variation in home range size and density.

State of Knowledge, Current Situation and Conservation Problems

This section is based partially on a literature review and partially on observations and data gathered during trips to 10 different areas, in order to prepare and conduct a project on jaguar ecology and its morphological and genetic variation in Venezuela. The visited localities were: 1) Los Llanos in Cojedes state (Hato Piñero, El Baúl area), 2) Amazonas (Puerto Ayacucho, Yutaje, San Juan de Manapiare), 3) Serranía de Imataca (El Palmar), 4) Delta Amacuro, 5) Sucre-Monagas (Paría, Guariquen, Río San Juan), 6) Río Caura (lower and middle Caura), 7) Sierra de Perijá (in the mountains and at a mosaic of forests and agricultural areas near Machiques), 8) forests on both sides of Río Boconó, Trujillo state in Los Andes, 9) forest west of Betijoque in western Trujillo, and 10) Rancho Grande in Henri Pitter National Park, in the Cordillera de la Costa. During these trips censuses were conducted by recording tracks on sand or mud, and camera trapping (14-30 automatic cameras set in the places selected as possible jaguar passes for periods of 2-5 weeks). Local people were interviewed about the presence and conservation problems of jaguars. Additionally, information was collected through personal contacts from some other parts of Venezuela.

In Venezuela, the jaguar is commonly known as 'el tigre'. However, each aboriginal nation has usually its own name for this predator: Guarani use 'yaguá', Piaroa 'buo jäwi', Jodi 'jkyo yëwi', Bari 'sebraaba', Pemon 'tümennen' or 'wayamoikö¡, Yekuana 'mádo', Yanomami 'ironasi', and Warao 'toobe'. The names usually refer to the power or fierceness of the jaguar.

The jaguar population in Venezuela is diversified regionally in terms of both morphological features (i.e. body mass and skin coloration patterns), and ecological parameters (i.e. food habits and population densities). As mentioned above, reports on body mass of jaguars hunted during the past 50 years in different parts of Venezuela indicate high morphological variation within an area that was believed to be inhabited by a single subspecies (*P. o. onca*; Hoogesteijn and Mondolfi, 1996;

Figure 1. Jaguar skins from Sierra de Imataca ('serrano' or 'menudo' coloration pattern, left) and from Los Llanos ('mariposa' pattern, right)

authors' unpublished data). While jaguars in some parts of the country, such as Amazonas or the basin of the Caura River, seem to be rather small, with the usual male weight not exceeding 80kg, several reports from regions such as Los Llanos describe the hunting of extremely large jaguars (Hoogesteijn and Mondolfi, 1996; authors' unpublished data). According to reports of workers at Hato Piñero, one jaguar male killed there weighed 159kg and another, recently killed in the vicinity, weighed 130kg. Accordingly to a worker at Hato Socorro, a jaguar killed on the border of Cojedes and Portuguesa states weighed 180kg. Large jaguars are also believed to live in the area of Lake Maracaibo. Although these reports cannot be verified, it seems that in parts of Venezuela where jaguars prey on cattle, their body mass is generally higher. Also, the skin coloration pattern is diversified and seems to have some regional variation (Figure 1 and authors' unpublished data). The skin coloration patterns are recognized in the popular knowledge throughout the country. Jaguars with rosette-type spots are commonly called 'mariposa' (butterfly), those with smaller spots (sometimes black dots) are called 'menudo' in the plains, and 'serrano' in the mountains and hills in the north and east of Venezuela (Figure 1). Some jaguars are black (melanistic), and seem to be more common in eastern and south-eastern regions (Sierra de Imataca and along the border with Guyana) than in the central and western parts of the country. These observations on morphological diversity and distinctiveness of jaguars in various parts of Venezuela may have important consequences for the approach to species conservation. Recent studies have shown that both morphological and genetic variation in large carnivores may have a spatial patterning. The populations of some species are composed of sub-units distinguished by differences in genetic composition reflecting different adaptations to local habitats, climate, and food resources. Also, gene flows are often directional, with restricted or even no genetic exchange between nearby sub-populations, even in the absence of obvious geographic barriers between them. Such cryptic population divisions have been revealed for Canadian lynx (Rueness *et al.*, 2003) and wolves (Pilot *et al.*, 2006; Musiani *et al.*, 2007). The mechanisms responsible for the differentiation of populations into separate genetic sub-groups may involve aminoacid alterations in nuclear and mitochondrial DNA encoding proteins responsible for cellular respiration, as well as a high rate of adaptive mutations in mitochondrial DNA. The lack of compatible nuclear and mitochondrial DNA (as in the case of two breeding individuals coming from ecologically different regions) can lead to reproductive barriers and cryptic population divisions, consistent with the habitat structure, climate and food distribution (Blier *et al.*, 2001; Gershoni *et al.*, 2009; Lane, 2009). Thus, the many haplotypes of mitochondrial DNA found in South American jaguars by Eizirik *et al.* (2001, 2002) and the high genetic variation in nuclear DNA microsatellites shown by Ruíz García *et al.* (2006) may reflect not only neutral genetic drift, but perhaps evolutionary adaptation to diversified habitats and prey resources in South America. Jaguars that appear the same or very similar may in fact bear different sets of genes which allow them to live in different environmental conditions. If this were true, it would have significant consequences for conservation strategies and action plans for jaguars and possibly other species. To preserve the genetic diversity and adaptive potential, it would be necessary to protect not only the jaguar as a species, but also all the genetic variability in the different subpopulations inhabiting different habitats and different parts of Venezuela. Action plans and conservation strategies that ignore the possible genetic variation and spatial genetic structure of the species may have a limited impact on species preservation.

Originally, jaguars probably inhabited most of the territory of what today is inland Venezuela, excluding perhaps the highest regions of Andes and driest areas of the country. With increasing human population, the range inhabited by jaguars decreased. However, some authors have reported that jaguars were widespread across most of Venezuela at least until 1950 (Zárraga, 1992). In response to the fashion for furs of spotted cats in North America and Europe from the 1960s to the early 1980s, intensive jaguar hunting occurred all over South America (Gieteling, 1972; Fitzgerald, 1989; Ruíz–García *et al.*, 2003; Payán and Trujillo, 2006). Increased killing of jaguars during that period, which also happened within large cattle ranches, was probably also stimulated by parallel predator control programs that were promoted and introduced to hunting management in North America, Europe and the Soviet Union in the 1950s to 1960s (Jędrzejewska *et al.*, 1996; Jędrzejewski *et al.*, 1996; Fritts *et al.*, 2003). As a result, jaguar populations declined substantially all over Venezuela and became extinct in some regions (Zárraga, 1992; Linares, 1998; Hoogesteijn *et al.*, 2002; Ojasti and Lacabana,

2008). For example, about 30-40 years ago many jaguars were killed in Trujillo state in Los Andes and at the foothills of Sierra de Perijá, near Machiques, and today they are absent in these areas. The introduction of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 1975 started the gradual reduction of international fur trading, which reduced the markets for jaguar skins and therefore decreased jaguar hunting (Jackson, 1992; Nowell and Jackson, 1996). In Venezuela, the jaguar became a protected species in 1996; its hunting was forbidden and was declared a species threatened by extinction in north of the Meta-Orinoco rivers (Venezuela, 1996 a, b; Ojasti and Lacabana, 2008).

More detailed studies are needed to verify the current status and recent changes in distribution of the jaguar population in Venezuela. However, some conclusions can be drawn based on published sources (Bisbal, 1989; Hoogesteijn and Mondolfi, 1990, 1991; Medina Padilla *et al.*, 1992; Linares, 1998; Ojasti and Lacabana, 2008), the data obtained from camera trapping, tracking and interviews, and jaguar specimens found in museum collections (Sistema de Información de Museos y Colecciones de Zoología, SIMCOZ, www.simcoz.org.ve). Additional data on recent records of jaguar populations were provided by Ernesto Boede and Rafael Hoogesteijn (Figure 2). Compared to the jaguar distribution shown by Linares (1998), the more recent map presented in The Red Book of Venezuelan Fauna (Rodríguez and Rojas-Suárez, 2008) indicates a substantial decline of jaguar populations throughout the northern part of the country (Ojasti and Lacabana, 2008). According to this book, a contiguous jaguar range stretches from southern Apure and Bolivar states south of Orinoco to Amazonas State. In the north-eastern part of Venezuela, jaguars can be found in the Delta de Orinoco and along the coast in Monagas and Sucre up to the Peninsula de Paria. In the west, jaguars are present in Perijá up to Maracaibo Lake, and along the eastern and part of the western slopes of Andes, with an extension as far as Yaracuy and Falcon states. Small isolated populations are present in Serranía de Turimiquire on the border of Sucre and Monagas, in Falcon, in Miranda in the Guatopo National Park and the area of Río El Guapo, in Cojedes, and in Falcón and Zulia (Figure 2). During the trips to the 10 different regions of Venezuela listed above, the presence of jaguar populations was confirmed in Amazonas, Río Caura, Imataca, Delta Amacuro, Río San Juan, Cojedes, and Perijá (Figure 2). Based on our data, the situation of the jaguar in Los Andes and in the northern parts of the country might be even worse than described in The Red Book of Venezuelan Fauna. There have been only single, unconfirmed recent observations of jaguar tracks in Trujillo, in the area of Río Boconó and the forests west of Betijoque, in the western part of this Andean state, although ~30 years ago jaguars were common and often hunted there. Also, no strong evidence was found of current jaguar presence in the eastern part of Serranía de Turimiquire, in the north-east of Venezuela, nor in central part of Cordillera de la Costa (Figure 2). The presence of jaguars in the area of Guatopo N.P was confirmed (Emiliana Isasi, personal communication). In contrast to the northern part of the country, in Los Llanos (central Venezuela) the situation seems to have improved and jaguars have returned to areas of Apure, Cojedes, and Guárico (and possibly also to Barinas), where they have not been noted for the past 40-50 years (Figure 2).

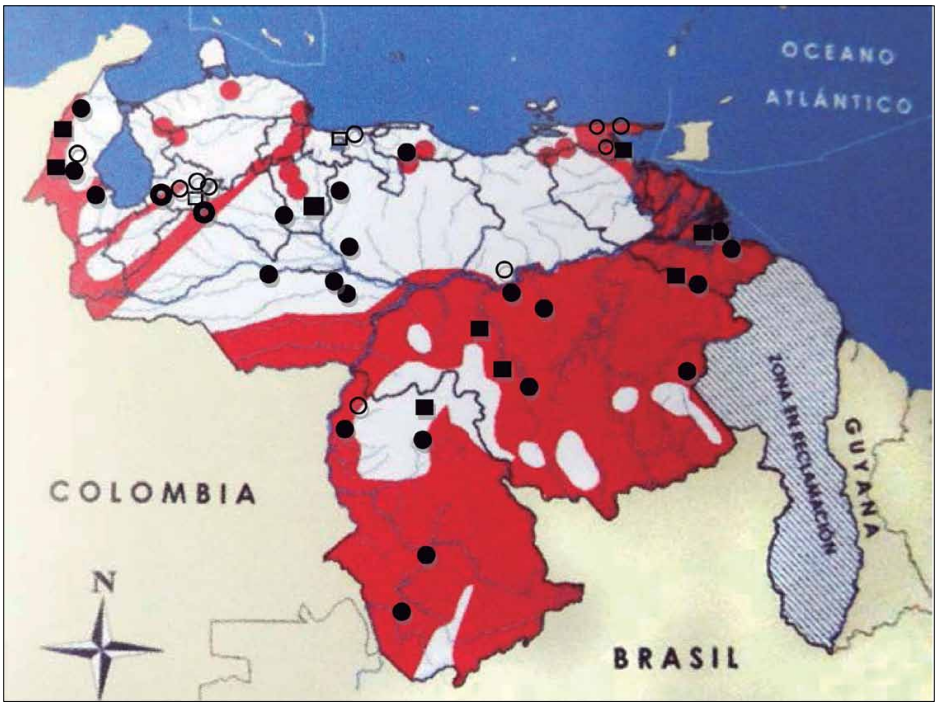

Figure 2. Jaguar distribution according to the *Libro Rojo de la Fauna de Venezuela* (Rodríguez and Rojas-Suárez, 2008, red color) and results of our surveys conducted with the aids of tracking, camera trapping, and interviews with local people. Also included is one data point in Apure from the SIMCOZ database, 2007 (www.simcoz.org.ve). Two data points in Apure, two in Amazonas, one in Guárico, and one in Zulia were provided by Ernesto Boede and Rafael Hoogesteijn.
Filled rectangles: records of jaguars obtained by the authors through camera trapping or track counting; empty rectangles: locations where camera-trapping and tracking were conducted but no evidence of jaguar presence was found; filled circles: jaguar presence confirmed from interviews with local people (confirmed visual observations or hunting) and information obtained from other researchers; half-filled circles: sporadic or unconfirmed jaguar observations, based on interviews with local people; empty circles: no recent records of jaguars, based on interviews with local people.

Altrichter *et al.* (2006) showed in Argentina that the time elapsed since the last sighting of a jaguar in any locality correlates with the age of local human settlements. This means that the growth of the human population in any area is unavoidably associated with jaguar decline and its eventual local extinction. Two factors are associated with the growth of the human populations that have a direct impact on jaguar survival: habitat alterations (principally deforestation) and direct killing (hunting and persecution). Habitat alteration and fragmentation have been postulated to be the most important factor responsible for jaguar decline and local extinctions throughout South and Central America (Nowell and Jackson, 1996; Sanderson *et al.*, 2002b). Usually, deforestation is connected with spreading human settlements and the development of agricultural activity. In many parts of Venezuela, there has been an acceleration of deforestation

Figure 3. Jaguar killed in Bolivar state in 2010. Photo taken by a tourist.

due to cutting and burning tropical forests and converting them to pastures or crop cultivation, which threatens large areas of jaguar habitats. One example is the Sierra de Imataca, where, according to reports of local conservationists, the continuous forest has been shrinking at an average of 1-2km/year. In the last 15 years the forest border moved 30km away from El Palmar (Padilla, 2003). Another example is from the eastern foothills of Los Andes, where primeval forests such as the famous Selva de Ticoporo, have disappeared almost completely over the past 30 years.

Not only habitat alterations, but also habitat fragmentation constitutes a serious threat for the future of jaguars (Sanderson *et al*., 2002a; Ojasti and Lacabana, 2008; Rabinowitz and Zeller, 2010). In northern Venezuela, the rapid expansion of areas with construction, industrial development and transportation infrastructure create barriers to animal movements, and especially for animal dispersal. There are plans, some of which are being implemented, for building railways and highways in northern and central parts of Venezuela, as well as along the Orinoco River. Dispersal of jaguars and other large mammals may be additionally restricted by large open pastures, fences, large water reservoirs, and intensively managed agricultural areas. A combination of all above mentioned factors in some areas becomes especially dangerous. Animal population fragmentation and isolation result in the cause for loss of genetic diversity, due to genetic drift, and speed up population decline (Jedrzejewski *et al*., 2008, 2009; Colchero *et al*., 2010; Haag *et al*., 2010). Small, isolated jaguar populations, such as those in the northern part of the country, are very vulnerable and may soon disappear.

Despite the fact that the jaguar has been a protected species in Venezuela since 1996 and is considered vulnerable by the scientific community (Ojasti and Lacabana, 2008) direct killing remains commonplace and is another important threat to jaguar populations (Figure 3; compare Hoogesteijn *et al*. 1993, 2002, 2011). Jaguars are killed for variety of reasons. The most common cause and the one that has the biggest impact on jaguar population in Venezuela is persecution by ranchers and farmers due to livestock depredation (Hoogesteijn*, et al*., 1993, 2002; González Fernández, 1995; Polisar *et al*.. 2003; Scognamillo *et al*., 2003). As mentioned above, jaguars may indeed become a problem for cattle breeding in some situations. However, the study of human-jaguar relationships in Pantanal, Brazil, documented that ranchers blame jaguars for many more losses than they actually cause; ranchers see jaguars as the main reason for economic loss, even if other factors such as drought, disease, flooding and starvation cause a much higher mortality of calves and adult cattle (Hoogesteijn *et al*.. 1993; Chávez and Gese, 2005; Chávez *et al*.. 2005; Zimmermann *et al*., 2005; Sarancho *et al*., 2006; Cavalcanti*, et al*., 2010). The negative perception in the population, principally associated with livestock depredation, may lead to killing jaguars even inside national parks (Conforti and Cascelli de Azevedo, 2003; Carvalho and Pezzuti, 2010). It is very common throughout Venezuela, but especially in Los Llanos, that ranchers who lost even one calf from jaguar predation organize a deliberate hunt for that jaguar, following various modalities: mobilizing workers from the ranch ('baquianos') to track and kill the jaguar, usually with the help of dogs, hiring a specialized jaguar hunter to do the job, or trying to poison the jaguar or kill it with some kind of traps, such as self-firing guns. On the foothills of Sierra de Perijá near Machiques, ranchers reported that it usually takes them one to two weeks to kill a jaguar after they discover a first calf killed or even the first tracks of a jaguar that has settled inside their 'fundo' or farm.

Private land owners also kill jaguars simply out of fear, even though jaguars very rarely kill people. An encounter with a jaguar makes people so scared that they try to kill it, as they kill snakes, to protect themselves and feel more secure. However, a fairly common accident is when a man riding a horse breaks his neck due to the sudden reaction of the horse or the man upon encountering a jaguar. In such cases the jaguars are tracked and killed, even if they never displayed any aggressiveness towards humans.

Jaguars are also commonly killed in Venezuela by 'professional' hunters who earn money from selling the skins and other parts of the jaguar body (Hoogesteijn *et al*.. 1993, 2002; authors data; see Figure 3). As reported by hunters, trading with jaguar skins is still very common, and in several cities located close to large forest expanses there are people in the business of buying jaguar skins from hunters. Prices have substantially increased recently due to a revival of the fashion for decorating houses with jaguar skins. Some 3-4 years ago the skin value was less than 500BsF (80USD), and usually only 200-300BsF (30-50USD). Today a hunter can get 3000-5000BsF (400-600USD) for a skin, plus what he can get for canine teeth (~200BsF each) or

for the whole skull. Jaguar fat is a desired product, as many believe it to be a remedy for arthritis. Additionally, the whole jaguar carcass, particularly bones, can often be sold for the production of Chinese medicines. Jaguar hunting is especially common in areas with high densities of them, such as in the Sierra de Imataca, Río Caura and other parts of Bolívar state, but it occurs all over Venezuela, wherever they are still found. Recent killing of jaguars was invariably documented in the ten areas of Venezuela visited, upon interviewing hunters, ranchers and other local people in regions where jaguars are present. Killing jaguars to sell skins and other products, and the commercial trade of these products was confirmed in five regions (Imataca, Caura, Delta, Amazonas, and Perijá). Although hunting is usually performed by specialized hunters, almost any hunter who spots a jaguar will shoot it, a practice known as 'opportunistic killing' (Swank and Teer, 1989, 1992). An exception are hunters from some indigenous communities of Venezuela, who will not kill jaguars because of their traditional belief that it may result in something bad happening to them or their family. Sport hunting of jaguars is also still practiced in Venezuela, and individuals are known to regularly visit the Sierra de Imataca, Río Caura and other regions to pursue this hobby, as stated by local interviewees. A variety of ways to hunt jaguars exist (Medina, 1964; Zárraga, 1992) but probably it is most efficiently done with dogs. Some hunters have special dogs trained to track jaguars, to find, follow and chase them up a tree, whereupon the hunter has a relatively easy target to shoot. In general, hunters in Venezuela usually keep many dogs that are used for hunting a variety of game animals, principally peccary and white-tailed deer, and also jaguars.

Another very important, although indirect, limiting factor for jaguars populations is the reduction in the densities of large and medium size animals, the potential jaguar prey, as the result of intensive hunting (Hoogesteijn *et al*., 2002; Cascelli de Azevedo and Conforti, 2008; Loveridge *et al*., 2010). Novack *et al*. (2005) have shown that hunting has had a specially high impact on populations of peccary, the most important jaguar prey. In many rural areas of Venezuela most men are hunters. Although the efficiency of hunting is generally very high, in some parts it is increased due to the common practice use of dogs. In Sierra de Imataca and in Los Andes the authors observed that groups of dogs are also often released and allowed to hunt by themselves. The large effects of the hunting on animal populations are obvious by mere visual comparison of the protected areas, where hunting is absent or limited and animal densities are usually high, with non-protected areas where hunting is intense and animal densities are usually low. For example, in Hato Piñero there is no hunting, animal densities are high, while in other 'hatos' in the region of El Baul, in Cojedes, there is intensive hunting and animal densities are low. The result of a reduction of wild prey densities is an increase in jaguar predation on cattle, which magnifies conflicts with ranchers (Hoogesteijn *et al*., 2002; Polisar *et al*., 2003; Loveridge *et al*., 2010).

Proposals for Conservation and Needs for Further Research

Over the past 20 years, several actions and solutions have been proposed to make jaguar conservation more effective in Central and South America, including Venezuela (Quigley and Crawshaw, 1992; Rabinowitz, 1992; Taber *et al*., 1997; Sanderson *et al*., 2002a; Sollmann*, et al*., 2008; Cavalcanti *et al*., 2010; Loveridge *et al*., 2010). The creation of protected areas, such as national parks, has been a basic approach in jaguar conservation, although its efficacy depends primarily on the size of the protected area (Sollmann *et al*., 2008; Isasi-Catalá, 2010a). As mentioned above, individual jaguars may have large territories and an area sufficient for maintaining a population of jaguars must be quite extensive. In Venezuela, several national parks play an important role in protecting habitats suitable for jaguars. However, many areas that are very important for jaguar conservation are not adequately protected: there are either no protected areas, the protected areas are too small, or the category of protection is too low. It seems obvious that forest reserves do not guarantee enough protection for areas as valuable as Sierra de Imataca or Río Caura. The creation of national parks should be urgently considered for several parts of Bolivar state, especially in the Sierra de Imataca and in the basins of the principal rivers, such as Orinoco, Cuchivero, Caura, Aro and Paragua. Protecting the jaguar populations in the delta and mangrove ecosystems requires a substantial enlargement of the Delta de Orinoco and Turuepano national parks, and the creation of new national parks in Delta Amacuro, Monagas, and Sucre. Similarly, some national parks in Los Andes should be enlarged and others must be established to halt the rapid deforestation and habitat alterations.

There is also the need to consider creating new, large national parks in Cojedes, Portuguesa and Barinas, and it is especially important to enlarge the national parks in areas inhabited by small, isolated, and genetically distinct subpopulations of jaguars. However, the protected areas will have little effect on jaguar conservation if they remain or become isolated from each other. Efficient protection requires that they be joined into one functional geographic network, enabling animal dispersal and gene exchange. For this reason, the design and implementation of a national system of ecological corridors, connecting protected areas and other jaguar habitats is essential, with legal measures to protect ecological connectivity (Sanderson *et al*., 2002a, b; Dutton *et al*., 2008; Olmos Yat Sing and Gonzalez-Fernandez, 2008; Rabinowitz and Zeller, 2010). Maintaining ecological connectivity and preventing deforestation along these corridors is the most important goal. In order to reduce the impact of human constructed barriers, it is crucial that there be a legal requirement that all plans for investment in construction or infrastructure include an ecological evaluation of their effect on animal movement and gene flow, and they should include proposals for mitigation measures, such as special animal passes (Jedrzejewski *et al*., 2009; Jędrzejewski and Ławreszuk, 2009).

Efficient jaguar protection needs support and involvement of local rural communities (Cavalcanti *et al*., 2010; Loveridge *et al*., 2010), and this entails the development of adequate education programs. Active education would increase local knowledge of jaguar ecology, produce an awareness of conservation problems, reduce fear of jaguars and, hopefuly, change the general attitude of rural communities towards these animals. In consequence, it could lower the rate of jaguar killing (Conforti and Cascelli de Azevedo, 2003; Cavalcanti *et al*., 2010; Isasi-Catalá, 2010b; Loveridge *et al*., 2010). Education programs targeted to local communities living around national parks inhabited by jaguars are especially important (Conforti and Cascelli de Azevedo, 2003; Carvalho and Pezzuti, 2010). Also, increased cooperation between national parks and local authorities, particularly in obtaining funds for pro-conservation activities and the promotion of ecotourism, could benefit jaguar conservation.

The conflict between livestock owners and jaguar predation is

one of the most important problems to be solved. In order to reduce the probability of jaguar attacks on cattle, special management solutions and mitigation measures have been proposed, including locating calving grounds far from forests, using electric fences, and mixing cattle with buffalo (Hoogesteijn *et al*., 1992, 1993, 2002; Scognamillo *et al*., 2002; Polisar *et al*., 2003; Hoogesteijn and Hoogesteijn, 2008). It is necessary to prepare and disseminate educational materials with adequate instructions for ranchers. However, the most effective solution would be to introduce special financial instruments, similar to those functioning in the European Union and other countries, that include compensation for livestock loses and monetary rewards for ranchers who demonstrate pro-conservation management of their ranches and healthy jaguar and other wildlife populations on their land (Mishra, 1997; Ciucci and Boitani, 1998; Mech, 2003; Dutton *et al*., 2008; Zabel and Holm-Muller, 2008, Cavalcanti *et al*., 2010). An additional approach is to involve owners of large cattle ranches in conservation activities, with ecotourism as an additional source of income (Hoogesteijn *et al*., 1993, 2002; Hoogesteijn and Chapman, 1997; Rosas-Rosas and Valdez, 2010). In Venezuela, programs of this nature have been recently proposed for the areas of El Baúl and Hato Piñero by Olmos Yat Sing and Gonzalez-Fernandez (2008).

In order to provide an adequate knowledge base for the implementation of all the proposed conservation activities there should be a broad research program combining a variety of approaches and techniques, as has been proposed (Medina Padilla *et al*., 1992).

In summary, an adequate strategy and action plan for jaguar conservation in Venezuela should include the following points:

1-Creation of a network of new national parks and enlargement of several existing parks.

2-Application of laws to stop deforestation.

3-Establishment of a network of protected ecological corridors that would join all jaguar populations and all protected habitat areas.

4-Elaboration of laws to protect ecological connectivity, and the requirement that environmental impact assessments accompany all large scale investments.

5-Institution of a compensation system for livestock loses by ranchers from jaguar depredation; in parallel, educational materials on minimizing livestock losses from predation should be prepared and disseminated to ranchers.

6-Elaboration and implementation of conservation programs directed at ranchers and ranch owners that should include monetary incentives or other rewards for farms where the presence of jaguars is maintained.

7-Development of educational programs in collaboration with the national park services, to include school curricula and television programs. These efforts should be directed to increase awareness of nature and jaguar conservation problems in the country.

8-Promotion of ecotourism.

9-Control at locations where there is active trading of jaguar skins.

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LA CONSERVACIÓN DEL JAGUAR EN VENEZUELA FRENTE AL CONOCIMIENTO ACTUAL SOBRE SU BIOLOGÍA Y EVOLUCIÓN

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RESUMEN

El conocimiento actual sobre la evolución y las variaciones morfológicas, genéticas y ecológicas del jaguar Panthera onca *son revisados como trasfondo para comprender problemas de conservación. Con base en publicaciones y datos propios, se analiza la situación actual del jaguar en Venezuela. El tamaño corporal del jaguar actual es muy variable; los más grandes se han encontrado en el Pantanal, Brasil, y Los Llanos venezolanos (masa corporal promedio macho >100kg). Los más pequeños viven en América Central (~56kg). El patrón de coloración de la piel es altamente variable y podría tener correlación geográfica. La variación morfológica es confirmada por su variabilidad genética, que a su vez podría reflejar la diversidad de adaptaciones a hábitats y comunidades de presas. Su dieta es muy diversificada. El territorio y la densidad de los jaguares varían entre localidades, reflejando posiblemente diferencias de presas y grado de disturbio antropogénico. Su adaptación a matar presas grandes lo hacen un importante predador de ganado y los conflictos causados por ello son la principal causa de su matanza, además de caza para pieles a pesar de la protección legal. Otra amenaza es la deforestación. La población de jaguares en Venezuela ha decrecido sustancialmente en los últimos 30-40 años y es actualmente variable: en la zona norte sobreviven poblaciones aisladas pequeñas; al sur del Orinoco existe una población importante; en Los Llanos casi se eliminó hace ~40 años pero parece haber retornado y recolonizado antiguos territorios. La medida más importante de conservación del jaguar en Venezuela es crear más áreas protegidas, desarrollar corredores ecológicos para proteger la conectividad, y detener la deforestación de regiones críticas. Caza y matanza disminuirían con programas educativos involucrando comunidades locales, compensación por pérdidas por prelación, e incentivando el ecoturismo.*

A CONSERVAÇÃO DO JAGUAR NA VENEZUELA PERANTE O CONHECIMENTO ATUAL SOBRE SUA BIOLOGIA E EVOLUÇÃO

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RESUMO

O conhecimento atual sobre a evolução e as variações morfológicas, genéticas e ecológicas do jaguar Panthera onca *são revisados como plano de fundo para compreender problemas de conservação. Baseado em publicações e dados próprios, se analisa a situação atual do jaguar na Venezuela. O tamanho corporal do jaguar atual é muito variável; os maiores têm sido encontrados no Pantanal, Brasil, e nos Llanos venezuelanos (massa corporal média macho >100kg). Os menores vivem na América Central (~56kg). O padrão de coloração da pele é altamente variável e poderia ter correlação geográfica. A variação morfológica é confirmada por sua variabilidade genética, que por sua vez reflete diversidade de adaptações a hábitats e comunidades de presas. Sua dieta é muito diversificada. O território e a densidade dos jaguares variam entre localidades, refletindo possivelmente diferenças de presas e grau de distúrbio antropogênico. Sua adaptação a matar presas grandes faz dele um importante predador de gado e os conflitos causados por isto são a principal causa de sua matança, além de caça para peles apesar da proteção legal. Outra ameaça é a deflorestação. A população de jaguares na Venezuela tem decrescido substancialmente nos últimos 30-40 anos e é atualmente variável: sobrevivem na área norte pequenas populações isoladas; ao sul do rio Orinoco existe uma população importante; nos Llanos foi quase eliminada há ~40 anos mas parece haver retornado e recolonizado antigos territórios. A medida mais importante de conservação do jaguar na Venezuela é criar mais áreas protegidas, desenvolver corredores ecológicos para proteger a conectividade, e deter a deflorestação de regiões críticas. A caça e a matança diminuiriam com programas educativos envolvendo comunidades locais, compensação de perdas por prelação, e incentivando o ecoturismo.*