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Cover photo: Jaguar at the Estação Ecológica de Taiamã, Pantanal, Mato Grosso state (Photo Douglas B. Trent).

Foreword

Jaguar conservation in a country as expansive as Brazil is a significant challenge. There are three regional factors that require special consideration in jaguar conservation strategies in order to foster the greatest chance of achieving meaningful success for species survival.

First, the varied and frequently controversial interactions of jaguars with people across the country have led to distinct human perceptions and prejudices. For example, in some areas there are deep-seeded legends which have created a reputation of the jaguar as a deadly threat to people and livelihood whereby it should be shot on sight. In other regions, local people apply an almost spiritual cultural respect for the cat and strive for suitable ways to coexist with it. These powerful preconceptions suggest that there is a need to vary and adapt multiple management and conservation strategies depending on the regional opinions and experiences of local people toward the species.

Second, the jaguar is a nationally protected endangered species in Brazil, but it is virtually impossible to practice law enforcement over ranchers that retaliate against jaguars suspected of predating cattle. The vastness of jaguar range in the Amazon, Cerrado and Pantanal regions, where privately owned properties average around 15,000 hectares, prohibits any practical law enforcement approaches. Most real or alleged jaguar-human conflicts are solved by vigilante killings that go unreported. With about 85% of Brazil's wilderness in private lands, conservationists will need to employ creative tools such as compensation schemes for cattle losses, or government incentives for maintaining habitat suitable for jaguars, to sustain healthy jaguar populations on these important lands.

Third, although there is still an abundance of habitat favorable to jaguars in the Amazon, and on a smaller scale in some portions of the Pantanal, Brazil is witnessing an explosion of anthropogenic activities such as agriculture and cattle ranching which are drastically reducing jaguar populations in key habitats such as the Cerrado, Caatinga and the Atlantic Forest, the latter of which is on the verge of extinction already. These compromised areas still hold remnant populations of jaguars that will be essential for the long-term survival of the cat, and therefore they must not only be preserved, but they must be connected with real conservation corridors protected from non-compatible uses and unsustainable development.

Despite the many challenges to the survival of the jaguar in Brazil, it is home to half of the species' current global distribution. If jaguars are to thrive in the wild they will depend heavily on this nation. With this in mind, long-term comprehensive conservation strategies must be planned and practiced rapidly in Brazil. Without dramatic and sustained conservation efforts for jaguars throughout Brazil, this cat will eventually suffer the same level of endangerment as other large cats such as cheetahs, tigers and snow leopards.

The challenge before the conservation community is to balance all perceptions and attitudes towards the jaguar, and create an equilibrium that can enable the species to thrive on private and public lands, using metapopulation planning with conservation corridors to ensure the future of the jaguar in Brazil.

This special issue of CatNews will explore how researchers and conservationists in Brazil are working to meet the three primary challenges to regional jaguar conservation. I hope the articles in this issue can be an enhancement to your own conservation efforts, but more importantly, that you will be inspired to become part of the team of global researchers, specialists, conservationists, professionals, and volunteers devoted to protecting this magnificent animal.

Leandro Silveira, Ph.D
President Jaguar Conservation Fund / Instituto Onça-Pintada

Jaguar Distribution in Brazil: Past, Present and Future

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Historically, jaguars lived from southern Argentina to the southwestern United States, but due to anthropogenic pressure, their range has been reduced to less than 46% of its original size. As almost half of this area is within Brazilian territory, the country is key to future jaguar conservation. Knowledge of geographic distribution has been recognized as an important issue to support conservation plans, and recently, climatic change has been shown to influence species distribution. This study estimated potential jaguar distribution using ecological niche modeling. We accumulated 1,049 jaguar occurrence points and used climate and topographic data as predictive variables. We employed the Mahalanobis Distance Method to produce a historical and future distribution map, considering values for current and future climate, respectively. To estimate current jaguar distribution, we restricted the historical distribution according to the jaguar's preferred habitat classes. While range of distribution changed little from current to future climate, the extent of more suitable areas was reduced. Areas with high predicted future suitability are currently under habitat conversion. Comparison of these maps enables the identification of important areas for jaguar conservation in Brazil.

On a global scale, the biggest threats to biodiversity result from human occupation of natural landscapes (Ehrlich 1997). The conversion of natural habitat and its fragmentation are direct consequences of this trend (Wilcox & Murphy 1985). Recently, global climate change has been cited as responsible for relevant alterations of species' geographic distributions (Burns *et al*. 2003). The species' response to past and current climate modifications suggests that human climate change can act as a significant cause for extinction in the near future (Thomas *et al*. 2004).

The jaguar *Panthera onca* is the largest feline of the Americas, with a historical distribution ranging from southern Argentina to the southwestern United States (Seymour 1989). However, under hunting pressure and natural habitat conversion (Fig. 1), the jaguar's geographical distribution has reduced significantly. It is considered regionally extinct in El Salvador and Uruguay (IUCN 2007), and is presently estimated to occupy less than 46% of its original range (Sanderson *et al*. 2002a). Approximately 50% of the remaining distribution area is within Brazilian territory, making this country extremely important to guarantee long term jaguar conservation. Habitat variables, mostly related to vegetation cover, are important to determine jaguar distribution and possibly local abundance. Therefore, there is an increased concern about the loss of their habitats both due to direct human conversion and the possible alteration due to long-term climatic change.

At the present time, one of the main goals of conservation is to quickly and inexpensively identify the most important areas for biodiversity conservation. But species distribution data at precise scales are scarce and expensive to obtain in sufficient quantities to implement this kind of analysis based on species occurrences only (Williams & Gaston 1994). Therefore, it is important to adopt different approaches. Range-wide conservation plans should rely on the knowledge of a species' past and present geographic distribution, as well as on distribution of the known impacts affecting its populations. This would enable a more precise assessment of its conservation status based on remaining habitat and estimated population size yielding better design of conservation efforts at a landscape scale (Sanderson *et al*. 2002a,b, Wikramanayake *et al*. 2002).

A common method long used to study species geographic distribution consists of projecting available presence records on a map and defining the area between them as a qualitative estimation of the species' range. However, this "dot map"–based estimation excessively simplifies biotic and abiotic distinctions of the covered area such as geographic variables, climatic differences and habitat types (Lim *et al*. 2002). More recently, Species Distribution Modeling (SDM) based on Geographical Information System (GIS) methods has been widely used as an alternative. This innovative method produces maps that indicate where species are likely to occur (Fuller *et al*. 2007, Pearson *et al*. 2007) by a measure related to the probability of occurrence. This modeling approach has been favored as large scale climatic and ecological datasets have become available. Consequently, the efficiency and options to model and map complex relationships between species and environment have increased (Rushton *et al*. 2004, Johnson & Gillingham 2005).

Fig. 1. Deforestation for extensive cattle ranching in the Brazilian Amazon biome (Photo Jaguar Conservation Fund/Instituto Onça-Pintada)).

The use of SDM to predict the potential distribution of a species based on its ecological requirements, extrapolating the data to unknown areas, can be useful for several objectives, including, among others, the prediction of effects of climatic change or estimating the real distribution of threatened and rare species (Peterson *et al*. 2002, Johnson & Gillingham 2005, Ortega-Huerta & Peterson 2005). However, as a species' distribution is also constrained by biotic interactions, anthropogenic effects, stochastic events and other factors that are not incorporated into the presence-only methods, results must be considered as potential distributions and not necessarily as realized ones (Hortal *et al*. 2008, Jiménez-Valverde *et al*. 2008). Further, extending a regression beyond the limits of the data from which it is derived bears uncertainty as it is impossible to know if the described relationship will persist in the same way (Kearney 2006).

Here, we estimate potential past, present and future jaguar distribution in Brazil using predictive modeling approaches. Considering the high dispersal abilities of this species (Quigley & Crawshaw 2002), small-scale conservation efforts that focus on narrowly defined areas may not be sufficient to guarantee its conservation (Sanderson *et al*. 2002a), and species distribution models may be an important tool to establish efficient conservation strategies for the jaguar.

Methods

Modeling methods

There is a wide array of SDM techniques and a number of reviews of their performance (e.g., Elith *et al*. 2006). It is recommended that biologists evaluate the performance of several methods to determine which one presents the best estimation for the species of interest (McNyset & Blackburn 2006, Stockman *et al*. 2006a,b). We chose modeling techniques based on the constraint of using presence-only data, as absence data are rarely available (collections typically have no information about failure to observe the species at any given location, and true absence can usually not be distinguished from failure of detection). Thus, we evaluated three modeling procedures: the Genetic Algorithm for Rule Set Production (GARP) (Stockwell & Peters 1999); the Maximum Entropy (Maxent) (Phillips *et al*. 2006) and the Mahalanobis Distance Method (Mahalanobis 1936). Available techniques to evaluate model performance based on the Receiver Operating Characteristics (ROC) curve (Manel *et al*. 2001) show very similar results for the three methods that varied from 0.910 to 0.952, and reveal a good predictive value. However, Mahalanobis Distance method (MD) was the most consistent predictor of jaguar distribution at the majority of areas where its presence is known, so we present results under this model only.

Mahalanobis Distance is a method that ranks potential sites by their Mahalanobis distance to a vector that expresses the mean environmental conditions of all the records in the environmental space. For each cell in the grid, the distance from this mean is projected and represents a quantitative variable that is expected to be monotonic inversely correlated to the cell habitat suitability for the species. It is possible to define a distance threshold based on the ROC procedure that is considered the boundary of the ecological niche (Farber & Kadmon 2003). This methodology provides a robust way of measuring how similar a set of conditions is to an optimum set, and can be useful for identifying which regions in a landscape are most similar to an optimum landscape (Jenness 2003). Besides, MD is based on both the mean and variance of the predictive variables, as well as the covariance matrix of them, and thus makes use of the covariance between the considered variables (Jenness 2003). Among the various methods designed to produce species range distribution based on a niche modeling approach, MD was considered one of the most efficient methods in recent reviews (Farber & Kadmon 2003, Nogués-Bravo *et al*. 2008).

Jaguar occurrence data

We compiled information (geographic coordinates) on known jaguar occurrence (from 1998 to 2008) from:
1) scientific books and papers;
2) online data bases: Global Biodiversity Information Facility – GBIF - http://www.gbif.org/; SpeciesLink - http://splink.cria.org.br; Museum of Vertebrate Zoology - http://www.mip.berkeley.edu/mvz/index.html);
3) field records from the NGO Jaguar Conservation Fund, which were obtained through camera trapping and interviews with locals; and
4) unpublished records from partner researchers that kindly authorized the use of this information.

We accumulated 1,053 occurrence points that were standardized to decimal degrees. A detailed list of references and locations is available from the main author upon request.

We used a cell precision of 0.0417 degrees (nearly 4 km precision in cells near the Equator Line). Under this constrain there were 795 spatially unique records to use in the modeling process.

Predictive variables

The predictive data for past and current distribution modeling consisted of six climatic variables (precipitation of warmest quarter, precipitation seasonality (coefficient of variation), annual precipitation, mean temperature of driest quarter, temperature seasonality (standard deviation *100) and annual mean temperature) derived from the WORDCLIM (http://www.worldclim.org/) and

Table 1. Land cover classes preferred by Jaguars, selected from a Vegetation Map of South America (Eva *et al.* 2002).

Land cover classes selected	
Closed evergreen tropical forest	Semi deciduous transition forest
Open evergreen tropical forest	Fresh water flooded forests
Bamboo dominated forest	Permanent swamp forests
Closed semi-humid forest	Grass savannah
Open semi-humid forest	Shrub savannah
Closed deciduous forest	Periodically flooded savannah
Open deciduous forest	Closed shrublands
Closed semi deciduous forest	Open shrublands
Open semi deciduous forest	Periodically flooded shrublands

two topographic variables (altitude and slope) derived from the Hydro-1K global digital elevation model (http://edcdaac.usgs.gov/gtopo30/hydro/). All variables were converted to a grid resolution of 0.0417 degrees. To model future jaguar distribution, the same variables were used considering the Community Climate System Model – CCSM 3 (Vertenstein et al. 2004). Composed of four separate models simultaneously simulating the earth's atmosphere, ocean, land surface and sea-ice, and one central coupler component, it allows evaluation of future climate states (Vertenstein *et al*. 2004).

To obtain a reliable prediction of the current jaguar distribution, we restricted our past distribution model to areas of currently remaining natural vegetation classes preferred by jaguars, derived from a vegetation map of South America from 2000 (Eva *et al*. 2002), as vegetation types are not directly modeled under our approach. This was not possible for future predictions as information on natural vegetation changes is not available.

Results

Modeling results for past jaguar distribution were similar to historical maps from the literature (Seymour 1989), showing its distribution throughout most of Brazil, with the majority of the country's area being highly suitable for the jaguar, except most of the Pampas biome (Fig. 2).

A model restricted to the species' preferred habitat (Fig. 3) to estimate current distribution shows areas that currently have the climatic conditions for potential occurrence of the jaguar and still present native vegetation cover, considering information from 2000 (Eva *et al*. 2002). It shows large suitable vegetation blocks in the Amazon and Pantanal biomes, some parts of the central Cerrado (especially the Cerrado-Amazon ecotone) and the Caatinga biome. For the Atlantic Forest biome, however, the potential for jaguar occurrence is predicted only in extremely fragmented and isolated areas.

The results based on climate change models shows that the main areas for jaguar persistence with suitable conditions for its occurrence in the future will be concentrated in the Amazon, Cerrado and Atlantic Forest biomes (Fig. 4).

Comparing historical and future distributions (Fig. 2 and 4), the overall area of distribution is not expected to change based on climate changes, but a decrease in the most suitable areas is obvious. This prediction seems to be more serious if comparing with current distribution (Fig. 3) as many areas predicted to be suitable in the future actually suffer from deforestation.

Discussion

Studies on conservation biology have confirmed the importance of increasing the scale of conservation planning, especially adopting methodologies that emphasize entities other than populations or the species as a target for conservation effort. Thus, species distribution models are increasingly being used to inform conservation strategies, providing insights into the broad-scale environmental niche of a species and its potential distribution (Soberón & Peterson 2005, Araújo & Guisan 2006, Soberón 2007).

The apparent success of the MD method in describing jaguar distribution in Brazil may be due to the broad environmental and geographic range of the jaguar occurrence dataset and the use of predictor variables that closely reflect known limits to its environmental distribution. Some other studies have concluded that MD is an efficient technique for SDM (Farber & Kadmon 2003, Hellgren *et al*. 2007, Tsoar *et al*. 2007).

The use of a vegetation map to restrict potential distribution makes the estimation more consistent, and our results can be considered a reliable map

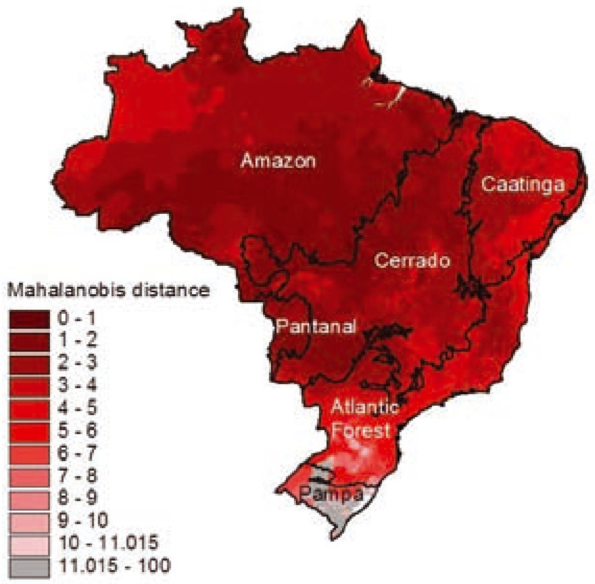

Fig. 2. Map of historical jaguar distribution in Brazil based on habitat modeling using Mahalanobis Distance. Progressively lower MD values (darker red) indicate progressively higher habitat suitability for the jaguars, while higher MD scores (grey) indicate unsuitable areas.

Fig. 3. Current jaguar distribution (shown in red), as predicted by the Mahalanobis Distance Method constrained by remaining native vegetation cover in Brazil.

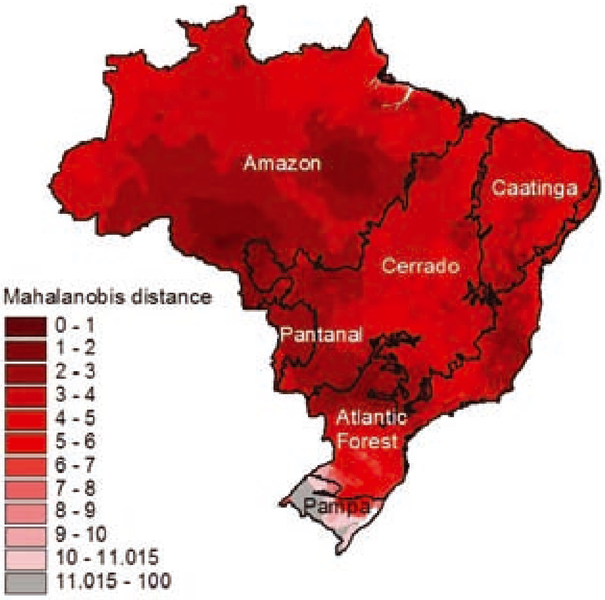

Fig. 4. Map of future jaguar distribution in Brazil based on habitat modeling using Mahalanobis Distance considering climate change. Progressively lower MD values (darker red) indicate progressively higher habitat suitability for the jaguars, while higher MD scores (grey) indicate unsuitable areas.

of current jaguar distribution in Brazil. The areas indicated in this map must be considered as primary targets for jaguar conservation, especially if we consider the future distribution map, which shows that some areas predicted as highly suitable in the future are presently suffering severe human impact by deforestation.

Recently, modeling has been used to estimate distributions of species under future climatic scenarios, as the climatic global changes are apparently responsible for significant alterations in species' geographic distributions (Burns *et al*. 2003, Thomas *et al*. 2004, Broenniman et al. 2006). Nevertheless, these analyses are based on complex climatic change scenarios and should consider variation in land use, which may change as a response to climate change. Especially for jaguars, which present a broad bioclimatic envelope, the potential negative effects of climatic changes might not be too dramatic generally. The potential overall jaguar distribution in Brazil does not seem to change when present or future climate variables are examined, but a considerable difference is observed in the most suitable areas. However, incorporating changes in land use might provide different results.

Considering that under current theoretical niche models, smaller Mahalanobis distances mean habitats with near optimum conditions, and assuming a direct relation between optimal conditions and jaguar abundance, the most important prediction of our models is the decrease of overall jaguar abundances under a climatic change scenario. Even if the potential distribution does not change, a decrease in local abundance in peripheral areas may lead to increased local extinction. The worst prediction for jaguar conservation is that those areas with good habitat suitability in the future (mainly Amazon and Cerrado areas) are located in the 'arc of deforestation' (Nogueira *et al*. 2008; Fig. 5), currently under strong pressure of habitat conversion to soybean and sugarcane plantations. The interaction of current deforestation and the potential future decrease in jaguar abundance may restrict the opportunities for jaguar conservation actions and call for urgent measures to maintain viable jaguar populations in these areas. Considering that this is the most important threat for jaguar, monitoring of these changes is needed to guarantee its conservation.

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Fig. 5. Areal view of a region in the state of Mato Grosso, located within the so-called Arc of Deforestation, one of the main areas that retain high potential suitability for jaguars when modeling the species' distribution under future climate changes, but currently threatened by extensive habitat conversion. Photo by Jaguar Conservation Fund/Instituto Onça-Pintada.

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Comparative Ecology of Jaguars in Brazil

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Historically, jaguars lived from southern Argentina to the southwestern United States, but due to anthropogenic pressure, their range has been reduced to less than 46% of its original size. As almost half of this area is within Brazilian territory, the country is key to future jaguar conservation. Knowledge of geographic distribution has been recognized as an important issue to support conservation plans, and recently, climatic change has been shown to influence species distribution. This study estimated potential jaguar distribution using ecological niche modeling. We accumulated 1,049 jaguar occurrence points and used climate and topographic data as predictive variables. We employed the Mahalanobis Distance Method to produce a historical and future distribution map, considering values for current and future climate, respectively. To estimate current jaguar distribution, we restricted the historical distribution according to the jaguar's preferred habitat classes. While range of distribution changed little from current to future climate, the extent of more suitable areas was reduced. Areas with high predicted future suitability are currently under habitat conversion. Comparison of these maps enables the identification of important areas for jaguar conservation in Brazil.

Contributing almost 50% to the jaguar's current distribution, Brazil presents the largest variety of habitats with jaguar occurrence. Of the country's six biomes, the species can still be found in five: The Amazon rainforest, the semiarid Caatinga, the Cerrado grasslands, the Pantanal floodplain, and the coastal Atlantic Forest. With their differences in habitat and prey base, jaguar ecology should differ widely among these biomes. Since the first studies of jaguars in the wild in the Brazilian Pantanal (Schaller & Vasconcelos 1977, Schaller & Crawshaw 1980), there has been a considerable increase in the amount of research in different aspects of jaguar ecology. With the intention of revealing ecological differences, we used the existing literature to compare jaguar diet, home range, density, habitat use, and activity pattern between biomes.

Diet

The jaguar is considered opportunistic in its feeding habits (Seymour 1989), with more than 85 prey species described so far (Sunquist & Sunquist 2002). Throughout its range, the species primarily feeds on medium to large prey species (López González & Miller 2002). Table 1 shows the results from 15 different jaguar diet studies from Brazil.

In the Atlantic Forest, white-collared peccaries (Guix 1997, Leite & Galvão 2002, Azevedo 2008), deer (Leite & Galvão 2002, Azevedo 2008), armadillos (Facure & Giaretta 1996) and white-lipped peccaries (Guix 1997, Garla *et al*. 2001) were the most frequently consumed species. With the exception of one study (Facure & Giaretta 1996) showing an important presence of the giant anteater, this and other large species such as tapirs and capybaras are almost absent in the jaguar's diet in this biome. With its highly fragmented landscape under strong human pressure, cattle can become the single most important prey in terms of frequency of occurrence (almost 40%, Guix 1997) or biomass consumed (26%, Azevedo 2008).

Likewise, in the Pantanal, where jaguars coexist with domestic cattle, this can become an important part of the jaguar's diet (Almeida 1984, Crawshaw & Quigley 2002, Dalponte 2002), constituting up to 48% of the consumed items (Crawshaw & Quigley 2002). Jaguars in the Pantanal also prey abundantly on wild species. In general, the capybara (Fig. 1) seems to be the most frequently consumed large prey species (Dalponte 2002, Azevedo & Murray 2007), followed by deer (Dalponte 2002, Azevedo & Murray 2002) and white-lipped peccary (Crawshaw & Quigley 2002; Fig. 2), while coati is the most frequently consumed medium prey (Dalponte 2002). Although probably more abundant than any of the mammalian prey species, caimans (*Caiman yacare*) are not consumed more frequently (e.g. Azevedo & Murray 2007).

In the Amazon, studies in two distinct areas show considerable differences in jaguar diet, probably due the distribution and abundance of prey species. In the seasonally flooded Várzea marshlands,

Fig. 1. Capybaras represent an important prey species for jaguars in the Pantanal (Photo L. Leuzinger).

jaguar prey consists of a small number of arboreal species, like sloths, and species associated with water, like caimans *Caiman crocodilus* and *Melanosuchus niger*, and their eggs (Ramalho 2006). On the other hand, in areas with influence from the neighboring Cerrado biome, jaguars prey on a large number of species, with tapirs, peccaries and cattle making up the largest part of consumed biomass (Nuno 2007).

Large prey species seem to become even more important in the Cerrado, where jaguar diet consisted exclusively of the six larger prey species found locally; white-lipped peccaries and giant anteaters constitute 49% to the consumed biomass (Silveira 2004). While the open Cerrado habitat favors the abundance of these large grassland species, their complete dominance of the jaguar's diet may be peculiar to the study site, a protected area surrounded by large-scale crop plantations, which knowingly serve as an abundant food source for local herbivores.

Finally, the only study case in the Caatinga, a vast xeric biome characterized by frequent periods of long, severe droughts, found that jaguars are opportunistically preying on available large-sized species such as giant anteaters, as well as smaller prey like the abundant armadillos (Olmos 1993).

Judging from frequency of occurrence in scats and from mean prey weight (Table 1), in both the Amazon and Atlantic Forest, smaller prey species seem to be more important than in the Pantanal and Cerrado biomes, characterized by open habitat. The frequency of medium and small prey items in the Caatinga demonstrates adaptation to an environment where large mammals are scarce. The variation in frequency of certain prey species within biomes reflects differences in diet on a smaller scale, again indicating the jaguar's opportunistic feeding behavior – in the Amazon, the species has even been reported to prey on freshwater dolphin (*Inia geoffrey*; Silveira *et al.* 2004).

Home Range

Home ranges and spacing patterns of solitary carnivores are influenced by the availability, distribution and seasonality of favorable habitat, food, and reproductive resources, as well as inter and intraspecific interactions (Sandell 1989). Jaguar home range size and spacing has been studied in the Pantanal, Cerrado and Atlantic Forest, and Table 2 shows the result of the different home range size and overlap estimates among these studies.

Due to the large variation of home range size within biomes and even within study sites, combined with the different estimators used, it is hard to affirm that differences are ecologically based rather than methodological artifacts. However, there is a demonstrated tendency for home ranges in the Pantanal to be smaller than those in the Atlantic Forest or Cerrado.

While open habitat is generally associated with larger home ranges (reviewed by Silveira 2004), the comparatively smaller home ranges observed in the Pantanal may correspond mostly to a more abundant and uniformly distributed prey base (Azevedo & Murray 2007), as the Pantanal is known for its rich and abundant fauna (Swartz 2000). The observed degree of intrasexual overlap of approximately 50% indicates

Table 1. Frequency of occurrence (%) of prey species in jaguar scats from different diet studies in Brazil; value represents mean frequency for the particular species of all studies in the respective biomes, values in brackets give minimum and maximum reported values; mean prey weight (MPV) is the mean from all studies providing this value. (N.A. = Not available)

BIOME References	**Atlantic Forest** (1-6)	**Pantanal** (7-11)	**Amazon** (12,13)	**Cerrado** (14)	**Caatinga** (15)
Small prey (< 2kg)					
Mammals	2.5 (3.9 – 11.3)	0.4 (0.0 -1.9)	7.8 (0.0 – 15.6)	0.0	0.0
Reptiles	1.3 (1.4 – 6.6)	0.0	6.9 (6.3 – 7.5)	0.0	0.0
Others	5.6 (1.4 – 14.3)	2.8 (0.0 – 7.2)	3.0 (0.0 – 6.0)	0.0	14.3
Medium prey (2-10 kg)					
Monkeys (general)	0.4 (0.9 – 1.4)	0.0	11.3 (10.0 – 12.5)	0.0	0.0
Coati (*Nasua nasua*)	7.2 (5.7 – 27.4)	8.6 (4.8 – 38.4)	0.0	0.0	0.0
Crab-eating raccoon (*Procyon cancrivorus*)	1.8 (2.0 – 8.6)	0.8 (0.0 – 4.8)	1.6 (0.0 – 3.1)	0.0	0.0
Armadillos (*Dasypus* sp and others)	9.1 (8.5 – 22.0)	0.0	1.6 (0.0 – 3.1)	0.0	14.3
Sloth (*Bradypus variegatus*)	0.4 (0.0 – 2.1)	0.0	20.5 (0.0 – 41.0)	0.0	0.0
Others	11.6 (0.0 – 33.4)	4.6 (0.0 – 8.0)	12.5 (0.0 – 25.0)	4.0	0.0
Large prey (>10 kg)					
Tapir (*Tapirus terrestris*)	2.2 (0.0 – 12.5)	0.4 (0.0 – 2.0)	3.2 (0.0 – 6.3)	4.0	0.0
Capybara (*Hydrochaeris hydrochaeris*)	1.6 (1.4 – 7.9)	47.5 (14.0 – 100.0)	0.0	0.0	0.0
White-lipped peccary (*Tayassu pecari*)	7.6 (0.0 – 17.9)	7.2 (0.0 – 22.0)	3.1 (0.0 – 6.3)	35.0	0.0
White-collared peccary (*Tayassu tajacu*)	23.2 (7.8 – 37.5)	2.9 (0.0 – 9.0)	3.1 (0.0 – 6.3)	0.0	14.3
Giant anteater (*Myrmecophaga tridactyla*)	9.5 (0.0 – 57.1)	0.9 (0.0 – 2.4)	1.6 (0.0 – 3.1)	30.0	57.1
Rhea (*Rhea americana*)	0.0	0.2 (0.0 – 0.8)	0.0	13.0	0.0
Deers (*Mazama* sp. and others)	8.8 (2.8 – 23.7)	8.3 (0.0 – 26.4)	0.0	13.0	0.0
Caiman (general)	0.0	7.2 (0.0 – 23.0)	22.8 (3.1 – 42.5)	0.0	0.0
Livestock	13.8 (0.0 -37.5)	20.2 (0.0 – 48.0)	4.4 (2.5 – 6.3)	0.0	0.0
Others	0.0	0.8 (0.0 - 4.0)	8.5 (0.0 -17.0)	0.0	0.0
MWP (kg)	**11.8**	**14.0**	**5.4**	**84.7**	**N.A.**

References: 1) Crawshaw 1995; 2) Facure & Giaretta 1996; 3) Guix 1997; 4) Garla *et al.* 2001; 5) Leite & Galvão 2002; 6) Azevedo 2008; 7) Crawshaw & Quigley 2002; (8, 9 and 10) Dalponte 2002; 11) Azevedo & Murray 2007; 12) Ramalho 2006; 13) Nuno 2007; 14) Silveira 2004; 15) Olmos 1993.

Table 2. Jaguar home range size (min - max) and overlap (F = overlap between females, M = overlap between males) estimates from the Pantanal, Cerrado, and Atlantic Forest, and means calculated for each biome, with sample (N).

Habitat	Home Range (km^2)	Mean Home Range (km^2)		Degree of overlap	Reference
		Males (N)	Females (N)		
Pantanal (A)	25 – 90	90 (1)	32.3 (3)		Schaller & Crawshaw 1980
Pantanal (A)	97.1 – 168.4	152.4 (1)	139.6 (4)	42% F	Crawshaw & Quigley 1991
Pantanal (B)	52 – 176	116.5 (4)	58.5 (2)		Soisalo & Cavalcanti 2006
Pantanal (D)		67.4 (3)	32.2 (5)	49.7% M, 52.9% F	Azevedo & Murray 2007
Pantanal (B)	1.41 – 122.2	79.6 (3)	49.4 (8)	44% F	JCF (unpub. data)
Mean Pantanal		101.2	62.4	49.7% M, 46.3% F	
Cerrado (C)	228 – 265	265 (2)	228 (1)	81.8% M[A]	Silveira 2004
Atlantic Forest (A)	8.8 – 138	88.7 (4)	39.4 (2)		Crawshaw 1995
Atlantic Forest (A)	43.8 – 177.7	102 (2)	87.3 (5)	6% M, 18% F	Cullen *et al*. 2005
Atlantic Forest (E)*	87 – 173	147 (1)	130 (2)	15% F	Cullen 2006*
Mean AF		112.6	85.6	6% M, 16.5% F	

A) Minimum Convex Polygon (MCP) at 100% of locations, B) Minimum Convex Polygon (MCP) at 95% of locations; C) Minimum Convex Polygon (MCP) at 80% of locations; D) Fixed Kernel at 95% of locations; E) Fixed Kernel at 85% of locations. * To avoid autocorrelation with the study presented in Cullen *et al*. 2005, we used only data from another area which was not included in the previous work.

the presence of regions of exclusivity in jaguars' home ranges (Azevedo & Murray 2007), which is expected in solitary carnivores when food resources are abundant and uniformly distributed and the cost of defense of such a core area is lower than the benefit of an exclusive use of the resource present in it (Sandell 1989).

Home range estimates for the Cerrado are on average 2.6 (males) to 3.6 (females) times larger than in the Pantanal (Table 2). While several large prey species are common in the Cerrado study site at Emas National Park (ENP), their abundance is considerably lower than in the Pantanal (Silveira 2004). Also, the habitats preferentially used by jaguars are restricted, and in ENP males have been observed to occasionally travel more than 40 km from regular home ranges, probably to find mates (Silveira 2004). Several individual jaguars made use of the same preferred habitat patches, a pattern expected when resources are aggregated (Sandell 1989). This could explain the high degree of range overlap observed (Table 2). Emas National Park, as most areas of suitable jaguar habitat in the Cerrado, is largely isolated by farmland, forcing resident jaguars to live under an ecological stress (Soares *et al*. 2006) that could be affecting their spacing patterns (Silveira 2004).

In the Atlantic Forest - the most degraded and fragmented biome of Brazil - jaguar spacing patterns seem to be influenced by human activities (Crawshaw 1995; Cullen 2006). Jaguars generally establish core areas of their home ranges within the limits of protected areas or in remaining patches of native habitat. The larger home ranges come from a study site influenced the nearby Cerrado, whose semi-deciduous, dry vegetation is characterized by a low carrying capacity for herbivores and consequently for carnivores. Home range estimates from areas with more typical Atlantic Forest vegetation are unambiguously smaller (Crawshaw 1995).

Throughout Brazil, female jaguars' home ranges are consistently smaller than males', reflecting the species' polygamous breeding system. While home range size for a female is determined by her and her offspring's metabolic demands, male ranges are determined by the distribution of females (Fig. 2) generally overlap ranges of various females (Sandell 1989).

Abundance

Abundance of large terrestrial mammals like the jaguar seems to be regulated most often by their food supply (Sinclair 1989). Because abundance has to refer to area to be comparable among studies, density is often used as a surrogate value. Table 3 shows jaguar density estimates for the different Brazilian biomes, based on radio-telemetry and camera trapping studies. Whenever more than one estimate per study was given, we used the value considered the best by the authors.

Consistent with smaller home ranges, the highest jaguar densities are supported in the Pantanal (Schaller & Crawshaw 1980, Crawshaw & Quig-

Table 3. Jaguar density estimates based on radio-telemetry data and camera-trapping in different biomes of Brazil.

Biome	Methodology	Density ± SE (ind./100 km^2)	Reference
Atlantic Forest	Telemetry	3.70	Crawshaw 1995
Atlantic Forest	Telemetry	2.33	Cullen *et al*. 2005
Atlantic Forest	Camera-traps	2.22 ± 1.33	Cullen *et al*. 2005
Mean AF		2.75	
Pantanal	Telemetry	2.90	Schaller & Crawshaw 1980
Pantanal	Telemetry	4.00	Crawshaw & Quigley 1991
Pantanal	Telemetry/ camera-traps	6.7 ± 1.06	Soisalo & Cavalcanti 2006
Mean Pantanal		4.53	
Amazon	Camera-traps	2.58 ±1.04	JCF (unpub. data)
Cerrado	Camera-traps	2.00	Silveira 2004
Caatinga	Camera-traps	2.67 ± 1.06	JCF (unpubl. data)

Fig. 2. Male (right) and female (left) jaguar during mating season on a river bank in the Pantanal (Photo M. Andrews).

ley 1991, Soisalo & Cavalcanti 2006). The seasonal flooding regime concentrates prey species, and consequently predators, in patches of suitable habitat (Crawshaw & Quigley 1991). In addition to the rich natural fauna (Schwartz 2000), cattle present an abundant food source for jaguars (Crawshaw & Quigley 2002). The combination of habitat dynamics, prey availability and cattle density may be responsible for the comparatively high jaguar densities (Soisalo & Cavalcanti 2006).

The lower densities registered for the Atlantic Forest could be attributed to a combination of factors: hunting of jaguars (Crawshaw 1995), competition with humans for food resources (Crawshaw 1995; Leite & Galvão 2002) and the lower carrying capacities of some deciduous and semideciduous habitats present in this biome (Cullen *et al*. 2005, Cullen 2006).

In the Cerrado, the predominantly dry and open vegetation does not present prime jaguar habitat. Again, a less abundant mammal fauna than in the Pantanal (Silveira 2004), also dominated by open vegetation, could reduce carrying capacities for a top predator like the jaguar.

Results from the Brazilian Amazon come from a transitional area between savannas of the Cerrado and Amazonian forests (JCF, unpublished data). Density estimates from the Bolivian Amazon are similar (2.8/100km², Silver et al. 2004). However, core areas of the Amazon could have higher jaguar densities, considering that the ecotonal study area is under influence of the Cerrado, where jaguar densities are lower.

Finally, the first results from the semi-arid Caatinga biome are higher than expected based on the biome's habitat characteristics and reports of low medium to large sized prey abundance (Oliveira *et al*. 2003). Jaguars were endangered, or at least scarce, in the study area (Serra da Capivara National Park) throughout the previous decade (SMAPR 1994, Wolff 2001). The comparatively actual high jaguar abundance could be explained by an increase of medium and large prey due to an increased patrolling policy in the area, where poaching is common practice (Silveira et al., unpublished data), as well as due to a park-wide system of artificial water holes. This is not the reality in other parts of the Caatinga (T. de Oliveira, pers. comm).

Activity Patterns

Felid activity patterns can be influenced by physical, social, climate and habitat conditions (e.g. Bailey 1993), and for some species including the jaguar, they have been found to coincide with activity of their main prey species (Emmons 1987, Schaller & Crawshaw 1980, Crawshaw & Quigley 1991, Weckel *et al.* 2006). Figure 3, based on results from camera trapping studies, shows predominantly a crepuscular-nocturnal activity pattern for the jaguar throughout all biomes where detailed data is available.

In the Atlantic Forest, the species is more active at night than during the day, an activity pattern also exhibited by some of the main prey species (Crawshaw 1995). Considerable daytime activity has also been shown for jaguars in the Amazon and Pantanal (Figure 5, Schaller & Crawshaw 1980, Crawshaw & Quigley 1991). In the former case, daytime activity could be favored by the dense forest habitat (Silveira 2004). Nocturnal habits of the jaguar in the Cerrado have been confirmed by radio-telemetry studies (Silveira 2004) and repeated camera trapping (JCF, unpubl. data). In this biome, peccaries – one of the main prey species in the study area - showed peaks of activity between 05:01 to 11:59hrs and 19:01 to 04:59hrs (Jácomo 2004), the latter coinciding with the peak of activity for jaguars. Apart from prey activity patterns, extreme climatic conditions like daytime heat in the semi-arid Caatinga may play a role in confining jaguars to a mostly crepuscular-nocturnal activity pattern (Astete 2008).

Habitat Use

Distributed from the south of the United States to the north of Argentina, jaguars are found in many distinct habitat types (Sanderson *et al*., 2002). Studies on jaguar habitat use in Brazil indicate that although they show a trend to use habitats close to water and with denser vegetation cover, the species uses a large variety of habitat forms:

In the Atlantic Forest, the original vegetation is characterized primarily by ombrofilous and semideciduous forests, but anthropogenic activities have reduced forest cover to 22% of its original extent (MMA 2007a). Here, jaguars were found to strongly select the sparsely available primary and secondary forests and to use dense and open marshlands twice as much as its availability (Cullen *et al*. 2005, Cullen 2006). Jaguars also showed avoidance of human-dominated areas such as agriculture and pasture (Cullen 2006). Dense marshes and forest patches possibly enhance the ability of jaguars to hunt; preference for riparian areas makes them important potential dispersal paths for jaguars (Cullen 2006).

The Pantanal combines influences from neighboring biomes characterized by open (Cerrado, Bolivian Chaco) and closed (Atlantic and Amazon Forest) vegetation with vast open floodplains and marshes (MMA 2007b). In this mosaic landscape, jaguar seem to prefer forested habitats, using gallery forest and forest patches more frequently than expected based on their availability (Schaller & Crawshaw 1980, Crawshaw & Quigley 1991). Even in this water dominated landscape, jaguars are found closer to permanent watercourses than expected by chance (Crawshaw & Quigley 1991).

A similar trend can be observed in the seasonally-flooded Amazon lowlands, where different shrubby and forest habitats occur according to duration and level of flooding. There, jaguars used shrubby low marshlands (*chavascal*) more frequently than other higher and more forested habitat types available, probably because the main prey species are mostly found in this habitat (Ramalho 2006).

The remaining native Cerrado vegetation is dominated by savannah shrub fields, interspersed with areas of forest and open grassland vegetation (MMA 2007c). In the Cerrado, where jaguars have been studied only in one protected area and its surroundings, they showed a preference for arboreal savannah habitat, followed by forest and open grassland (Silveira 2004). Although jaguars have not been recorded in agricultural areas, evidence of the species has been found on cattle pastures (Silveira 2004) and open habitat bordering agricultural matrix (Vynne *et al.* 2007).

Finally, in the Caatinga, characterized primarily by semi-arid steppe-like savannah vegetation forms (MMA 2007d), the only preliminary information comes from a protected area. There, more jaguar records than expected, based on sampling unit distribution, were obtained in extremely dense shrubby Caatinga vegetation, whereas less than expected were obtained in the more open Caatinga. Relative jaguar abundance (photographic rate) showed no correlations with distance to the closest water source (Astete 2008), which is probably due to the Parks' extensive water management system, artificially increasing abundance of this otherwise scarce resource.

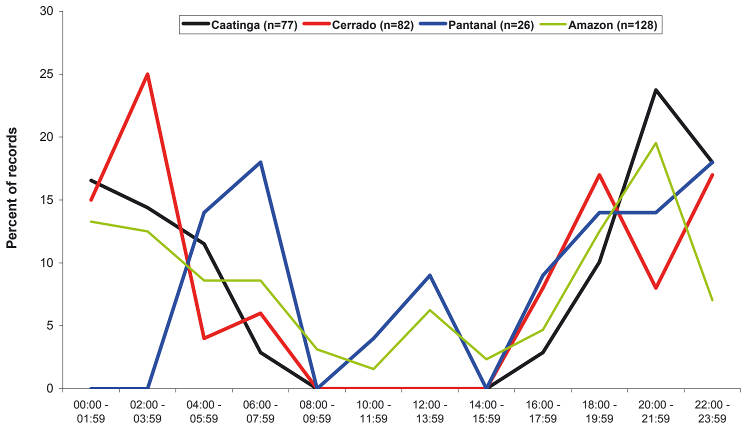

Fig. 3. Jaguar activity pattern expressed as percentage of jaguar records obtained with camera traps in the Amazon, Cerrado, Caatinga and Pantanal (Silveira 2004; Astete 2008; JCF, unpubl. data).

Conclusions

Jaguar studies in Brazil are progressively including most aspects of the basic ecology of the species across the biomes where the species occurs. The most common research topic is diet, while jaguar population dynamics remain virtually unstudied. Most studies are concentrated in the Atlantic Forest and the Pantanal, whereas there is still a lack of information in the Amazon, Cerrado and Caatinga. Nevertheless, available knowledge shows jaguars in Brazil to be well adapted to a variety of distinct ecological settings. However, the species' adaptability is limited by its demand for large areas of adequate habitat and a stable prey base. Jaguar ecology in landscapes under human influence are particularly important to better understand these limitations as they provide insight into the species' adaptability, as well as baseline information for landscape scale jaguar conservation efforts.

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Jaguar Conservation in Brazil: The Role of Protected Areas

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Brazil holds 50% of the jaguar's current range, much of it centring in the Amazon basin, which has long been considered the species' stronghold. Jaguars also range across four other biomes of Brazil (Cerrado, Caatinga, Pantanal and Atlantic Forest). We estimated jaguar population size for reserves and indigenous lands > 100km² using biome-specific density estimates. These results informed a population viability analysis (PVA) to assess the potential of the protected areas system for jaguar conservation in the five biomes. Mean protected area and jaguar population size varied significantly among biomes: the Atlantic Forest biome had the smallest and the Amazon forest biome the largest mean area and mean population sizes (431 km² and 10 individuals, and 10,993 km² and 311 individuals, respectively). Based on the PVA, jaguar populations >85 individuals were viable for > 200 years. These populations accounted for 90% of all protected jaguars, but are mostly restricted to the Amazon biome. In the other biomes, ≥ 50 % of populations were viable for up to 10 years only. Only in the Amazon are protected areas alone large enough to have the potential for long-term jaguar conservation. In other more fragmented biomes, landscape-scale conservation will be essential to sustain jaguar populations over the long term.

As the largest predator in the tropical Americas, the jaguar *Panthera onca* faces threats typical for large carnivores worldwide: Habitat loss and persecution. Large-scale habitat conversion (Fig. 1) collapses the range and fragments the landscape, constraining jaguar populations to protected areas. Where cattle ranching overlaps with jaguar range (Fig. 2), hunting as retaliation for domestic livestock predation can drive the species to local extinction (IUCN/SSC Cat Specialist Group 1996). As a result, the jaguar's entire range has been reduced by more than 50% since 1900 (Sanderson *et al.* 2002), and the species is thought to be extirpated in two of the 21 countries in which it originally occurred (Cat Specialist Group 2002). Listed as *Near Threatened* on the IUCN Red List (Cat Specialist Group 2002), the species' major stronghold is the 6,915,000-km² Amazon basin, although significant populations are also thought to exist in the Paraguayan Chaco and the Pantanal wetlands shared by Brazil and Paraguay (Sanderson *et al.* 2002).

According to a recent range-wide assessment, 50% of the jaguar's distribution lies within Brazil (Sanderson *et al.* 2002). Brazil gains even more importance for the species' range-wide conservation because half of the Amazon basin is located in Brazil and provides the large un-fragmented block of habitat essential for the survival of this area-sensitive top predator. In addition to the Amazon forest, jaguars occur in four other Brazilian biomes: the savannah-like Cerrado, the semi-arid Caatinga, the coastal Atlantic Forest, and the Pantanal wetlands. Ecological conditions, as well as the socio-economical situation of the human population vary widely among these biomes, so the jaguar's conservation status is likely to vary accordingly. Nationally, the species is listed as threatened (IBAMA 2003). The protection of threatened species such as the jaguar on a regional and national level is an explicit objective of the Brazilian National System of Conservation Units (Sistema Nacional de Unidades de Conservação – SNUC, IBAMA 2000). In an ever changing and developing human landscape, protected areas are one of the most important tools for conservation in any biome and should be cornerstones for regional conservation planning (Noss *et al.* 1996, Margules & Pressey 2000, Rylands & Brandon 2005).

The purpose of this study was to classify the potential of the Brazilian protected areas for the jaguar's long-term survival in the five biomes, utilizing estimates of jaguar population size in protected areas in a Population Viability Analysis (PVA). Comparing results between biomes, we give the first systematic assessment of differences in jaguar protection status within major regions of Brazil.

Fig. 1. Large-scale agriculture in central Brazil is one of the main activities responsible for the fragmentation of jaguar populations (Photo Jaguar Conservation Fund/Instituto Onça-Pintada).

Fig. 2. Extensive cattle ranching requires deforestation and induces jaguars to prey on the domestic livestock. Hunting in retaliation to cattle predation poses a major threat to jaguar populations on ranchland. Photo by Jaguar Conservation Fund/Instituto Onça-Pintada.

Material and Methods

Data for this study were derived from an ongoing jaguar distribution project undertaken by the Jaguar Conservation Fund (JCF), in which a systematic mapping of the species' occurrence in Brazil is in process. Although JCF's database includes jaguar occurrence in protected and non-protected areas, for this analysis we only considered state and federal reserves, as well as indigenous lands. This last category – areas traditionally occupied by Indians and used by them permanently - was included because they contribute significantly to habitat protection throughout Brazil (Rylands & Brandon 2005). To design the sampling method across the country we adopted the mapping system by the Brazilian Institute for Geography and Statistics (IBGE), in which Brazil is divided into 3,055 quadrants of approximately 50 x 50 km. Throughout Brazil, we compiled jaguar records from the existing scientific literature, JCF initiated surveys and other research, and interviews with locals. The current jaguar distribution analysis we created considers records from 1997 to the present. Quadrants with jaguar records were classified as "with jaguar presence." An entire protected area (PA) was classified as "with jaguar presence" if the PA had at least one jaguar record within its boundaries. PAs were also classified as "with jaguar presence" if jaguars had been registered in a quadrant adjacent to the PA. We will refer to these PAs with jaguar presence as Protected Jaguar Areas (PJAs). Data on protected areas came from the following sources: IBAMA (Brazilian government agency for the environment), MMA (ministry for the environment), FUNAI (Brazilian government agency for indigenous affairs).

To estimate the size of jaguar populations in PJAs, we used biome-specific jaguar density estimates based on camera-trapping data from the existing literature (Table 1), and multiplied density with PJA size. We only considered areas >100 km², as any fragments smaller than this threshold failed to support a pair of jaguars. (Table 1). We excluded APA (Areas of Environmental Protection) and RPPN (Private Reserves) from our analysis due to weak protection for the former and the lack of precise geo-referenced information for the latter. Several PJAs that are directly connected to each other are considered as a single area with a contiguous jaguar population.

Table 1. Jaguar density estimates for each Brazilian biome based on camera-trapping data.

Biome	Jaguar density (individuals/100km²)	Reference
Amazon	2.84	Silver *et al.* 2004
Cerrado	2.00	Silveira 2004
Caatinga	2.65	JCF, unpublished data
Atlantic Forest	2.22	Cullen *et al.* 2005
Pantanal	10.3	Soisalo & Cavalcanti 2006

In order to group protected jaguar populations into categories of viability, we performed a population viability analysis (PVA) using the computer program VORTEX 9.3 (Lacy *et al.* 2007). As demographic data for the species is incomplete, we used an existing Vortex model for the jaguar (Eizirik *et al.* 2002) and adjusted some of the demographic parameters based on empirical data from ongoing Jaguar Conservation Fund field studies of jaguar populations in four different Brazilian biomes (input parameters of the model can be requested from the lead author). We ran this model several times with varying initial population sizes and determined the time of population persistence with a 0.95 probability (TP95). With these values, we then performed a piecewise linear regression using the software package STATISTICA 7 (StatSoft, Inc. 2005) to determine minimum and maximum population size for the following viability categories: TP95 of up to 10 years (1), from 11 to 50 years (2), from 51 to 100 years (3), from 101 to 150 years (4), from 151 to 200 years (5) and longer than 200 years (6). We considered the last category as long-term viability. We then compared the mean PJA size and respective population size among biomes using a Kruskal-Wallis test for *k* independent samples, and the distribution of viability categories among biomes using a Chi² test, both implemented in the software package SPSS 13.0 for Windows (SPSS Inc., Chicago IL).

Results should be understood comparatively: In estimating size of jaguar populations in PAs using a single biome-specific density estimate, we do not consider the specific vegetation of each PA, nor differences in their level of protection. In addition, the idea of estimating minimum viable populations in general has received considerable critique (reviewed by Beissinger 2002), and it is recommended to interpret results comparatively. Specifically, our PVA model does not consider biome-specific differences in vital rates or external influencing factors due to a lack of quantitative information and the scope of this study. Also, the surroundings of any reserve play a major role for the performance of any protected population within a reserve (Woodroffe & Ginsberg 1998; Ranganathan et al. 2008). Nevertheless, we are confident that even within these limitations, this analysis gives an overview of how well the jaguar is protected within 50% of its global range.

Results

We counted 1,166 PAs in Brazil, the majority located in the Amazon (42%), followed by the Atlantic Forest (31%), Cerrado (21 %), Caatinga (5 %), and the Pantanal (1%). From this reserve network, we identified 298 PJAs (individual areas or blocks of adjacent areas) > 100 km². Combined, PJAs covered an area of 1,969,374 km², or about 25% of Brazil's land area.

Most PJAs are located in the Amazon (n = 167), corresponding to 42.9 % of the entire biome's area, followed by the Cerrado (n = 60, 5.6 %), Atlantic Forest (n = 49, 2 %), Caatinga (n = 16, 1.6 %), and Pantanal (n = 6, 2.7 %).

Mean PJA size varied among biomes ($H = 52.224$, $df = 4$, $p > 0.001$), ranging from 431 km² in the Atlantic Forest to 10,993 km² in the Amazon (Table 2). Mean population size also differed among biomes ($H = 64.942$, $df = 4$, $p < 0.001$), ranging from 10 individuals (SD = 12) in the Atlantic Forest to 311 (SD = 1137) in the Amazon (Table 2). We estimated that all Brazilian PJAs hold about 55,500 jaguars. Of those, 93.6 % occupy Amazonian PJAs, followed by 4.2 % in the Cerrado, and only 0.9 %, 0.8, and 0.6% Atlantic Forest, Pantanal and Caatinga, respectively (Table 2).

Based on our population model, a minimum population with TP95 of 200 years was 85 individuals. We calculated population size for the six viability categories as: 1 (TP95 up to 10 years) ≤ 18, 2 (TP95 up to 50 years) ≤ 41, 3 (TP95 up to 100 years) ≤ 59, 4 (TP95 up to 150 years) ≤ 73, 5 (TP95 up to 200 years) ≤ 85, and 6 (TP95 over 200 years) > 85.

Fifty-one percent of all estimated jaguar populations (n = 153) fall into viability category 1 (Table 3), accounting for about 2 % of all protected jaguars, while populations in viability category 6 (19 %, n = 56) account for 90% of protected jaguars Brazil-wide. The distribution of viability categories (Fig. 3) differs significantly between biomes ($Chi^2 = 55.693$, $df = 20$, $p < 0.001$). With 29% (n=48) of its populations falling into the highest viability category with a TP95 more than 200 years, the Amazon is the only biome that holds more long term viable populations (category 6) than expected. In contrast, the Atlantic Forest holds none, the highest category being 4 (TP95 up to 150 years; Table 3). Apart from the Amazon, all biomes have >50% of their protected jaguar populations in the lowest viability category.

Discussion

The jaguar can be found throughout most of Brazil, but our analyses show that its conservation status differs widely across the five Brazilian biomes. Our results corroborate that the Amazon is unique among Brazilian biomes with respect to jaguar conservation: It is the biome with the largest percentage and absolute area of PAs that hold jaguars, and, consequently, harbours the vast majority of the country's protected jaguar population. Mean population size of more than 300 individuals implies that a considerable proportion of all populations has a high probability of long-term survival. While the agricultural frontier is moving into the Amazon, bringing a predicted habitat loss of 50% over the next decades (Costa *et al.* 2005), the extensive system of large and often connected PAs in the Brazilian part of the Amazon plays a key role for long-term conservation of the jaguar Brazil-wide and range-wide.

Cited as another stronghold for the species (Sanderson *et al.* 2002), the Brazilian Pantanal shows a very small number of PJAs and protected jaguars (Table 2). However, due to its environmental characteristics – the seasonal flooding of most of its area – 87 % (MMA 2007[a]) is still covered by native vegetation. Extensive cattle ranching, the primary human activity in the Pantanal (Harris *et al.* 2005), and an extraordinarily abundant fauna (Swartz 2000)

Table 2. Statistics (number, size and estimated protected jaguar population (PJP)) of protected areas > 100km² with jaguars (Protected Jaguar Areas - PJA) in the five Brazilian biomes the species occurs in.

Biome	No. PJA	Mean size of PJA (SD) km²	Total area of PJAs km²	Mean PJP (SD)	Total protected jaguars
Amazon	167	10,993 (40,057)	1,816,302	311 (1,137)	51,920
Cerrado	60	1,936 (3,592)	116,156	39 (73)	2,332
Caatinga	16	734 (1,269)	11,749	20 (34)	327
Atlantic Forest	49	431 (530)	21,093	10 (12)	479
Pantanal	6	679 (971)	4,073	70 (100)	420
TOTAL Brazil	298	6,674 (30,391)	1,969,374	186 (862)	55,477

Table 3. Distribution of protected areas > 100km² with jaguars (Protected Jaguar Areas - PJAs) in the five Brazilian biomes the species occurs in, ranked in six viability categories (1 – 6), based on different time of population persistence wit 0.95 probability (TP95).

Biome	1 (TP95≤10 yrs)	2 (TP95≤50 yrs)	3 (TP95≤100 yrs)	4 (TP95≤150 yrs)	5 (TP95≤200 yrs)	6 (TP95>200 yrs)
Amazon	64	30	14	7	4	48
Cerrado	33	12	4	2	2	6
Caatinga	11	4	0	0	0	1
Atlantic Forest	42	6	0	1	0	0
Pantanal	3	1	0	0	1	1
TOTAL Brazil	153	54	18	10	7	56

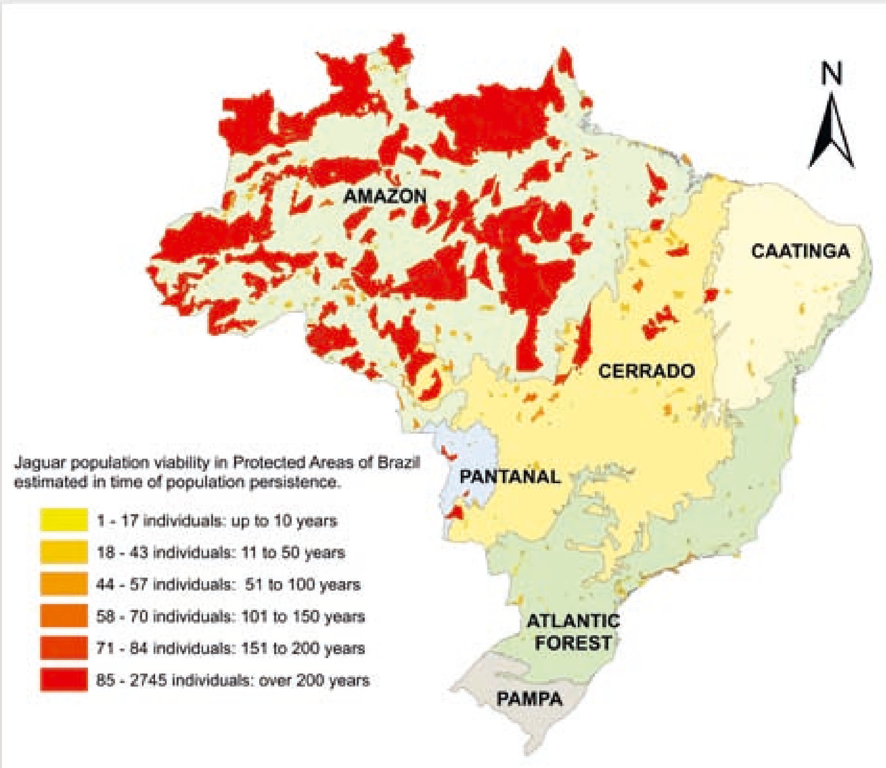

Fig. 3. Map of Brazil with protected areas and indigenous lands larger than 10,000 hectares where jaguar are known to be present (protected jaguar area - PJA); colors code for jaguar population viability derived from estimates of population size from a Population Viability Analysis. Connected PJAs were considered as a single area with a contiguous jaguar population.

support comparatively high jaguar densities (Soisalo & Cavalcanti 2006), even in non-protected areas. In addition, private reserves (RPPNs) probably play an important role for jaguar conservation in the Pantanal, as they are integrated into a landscape that still provides large tracts of native habitat and are generally well preserved. Also, the number of private reserves > 100 km² is higher than in other biomes, for example, in the state of Mato Grosso do Sul there are four (REPAMS 2008), while we are aware of only one in the entire Amazon biome. Therefore, our analysis underestimates the current contribution of the biome to the global jaguar population and range-wide jaguar conservation. Still, the unprotected jaguars of the Pantanal face serious threats. Conflict between cattle ranchers and jaguars is omnipresent, so hunting is a major problem (Crawshaw & Quigley 2002). Also, cattle ranching practices have become more intensive and as agriculture spreads into the floodplain loss of native habitat is increasingly becoming a problem (Harris *et al.* 2005). If this trend continues, the Pantanal may diminish as a refuge for jaguars.

Fig. 4. Fragmentation and isolation of native jaguar habitat by large-scale agricultural ventures in the Cerrado: One of the major threats to jaguar populations in Brazil's second largest biome. Photo by Jaguar Conservation Fund/Instituto Onça-Pintada.

The other three biomes are presented below in order of descending mean size of PJAs and current challenges to managers focused on the goal of maintaining jaguars over the long term. The Cerrado, Brazil's second largest biome, covers 22% of the country's land area. In contrast to the Amazon, however, this vast savannah-like region holds only 4 % of the country's protected jaguars. Populations also show a higher degree of fragmentation, with a mean population size of only 39 individuals. While natural vegetation still constitutes about 60 % to its area (MMA 2007[b]), the majority is under some degree of human influence and the biome is characterized by a fragmented landscape (Cavalcanti & Joly 2002; Fig. 4). A major threat to the species' persistence is the isolation of populations too small to be viable over the long term. Large-scale crop plantations most likely present barriers to jaguars so that the species depends on corridors of gallery forest (Fig. 5) for movement between suitable areas; however, hydroelectric dams disrupt these corridors (Silveira & Jácomo 2002). Much remains unknown about jaguars in the Cerrado (Silveira & Jácomo 2002), but information about the species' ability to use the fragmented landscape is crucial to understand its chances for long-term persistence, as protected areas alone cannot guarantee the jaguar's future.

Although almost five times the size of the Pantanal, the Caatinga holds only about 300 protected jaguars due to the small fraction of protected area in this biome (1.6%, MMA 2007[c]). The semi-arid climate and poor soil limit large scale agriculture and cattle ranching, and about 60% of its area still maintains the native vegetation cover (MMA 2007[c]), however, these blocks are fragmented (Castelletti *et al.* 2004). The rural population is extremely poor and poaching is common (Leal *et al.* 2005), threatening the jaguar's prey base. The protected areas fail to protect the full range of the biome's biodiversity (revised by Leal *et al.* 2005) and, with predominantly low numbers, also do not protect long-term viable jaguar populations. Both degradation and lack of an efficient protected areas system, in combination with a lack of information about distribution, ecology and status of the jaguar in the Caatinga (Oliveira 2002) indicate an alarming conservation situation of the species in this biome.

The Atlantic Forest holds a number of PJAs comparable to the Cerrado (49 and 60, respectively), but 86% are in the lowest viability class. Only one PJA (Serra do Mar) provides some longer term perspective for jaguar conservation. Overall, the biome has suffered the highest incidence of habitat loss in Brazil, with 71 % of its area under anthropogenic use (MMA 2007[d]) and the remaining native vegetation is extremely fragmented (Gascon *et al.* 2000). In addition to the lack of sufficiently large protected areas, poaching of potential prey species (Cullen Jr. *et al.* 2000, Leite & Galvão 2002) and hunting of the jaguar due to livestock predation (Azevedo & Conforti 1999, as cited in Conforti & Azevedo 2003) have been reported even from within protected areas. Simulations indicate that it might be more important to primarily address these factors, rather than the lack of connectivity between populations (Cullen Jr. 2006). Overall, the jaguar's protection status in Brazil's most troubled biome is certainly the most critical throughout the country.

Conclusion

The problem of reserves being too small to protect viable populations of wide ranging carnivores is universal and has long been acknowledged (e.g. Schoenwald-Cox 1983, Ranganathan *et al.* 2008). We show that the same principle holds true for jaguars in most of Brazil: Only in the Brazilian Amazon does the existing protected areas system alone have the potential to conserve the species over the long term. Although on the national conservation agenda (Silva 2005), the creation of new protected areas oftentimes generates conflicts with local communities and is limited by competing human demands (Margules & Pressey 2000, West *et al.* 2006). This analysis points out the major differences in protection status of the jaguar throughout the five Brazilian biomes. From a management perspective, our data show that throughout most of the national territory, long-term jaguar conservation will depend on approaches integrating non-protected landscapes. Therefore, analyses of the specific ecological, cultural, socio-economical and environmental realities at the biome and regional level identifying specific threats and opportunities for jaguar conservation are necessary to develop an efficient conservation plan for the jaguar in Brazil.

Fig. 5. Corridors of riparian forest can provide habitat for jaguars and movement paths between suitable areas (Photo Jaguar Conservation Fund/Instituto Onça-Pintada).

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Humans and Jaguars in Five Brazilian Biomes: Same Country, Different Perceptions

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Human perceptions of and attitudes towards wildlife are important aspects of conservation as they indicate and reflect potential impacts on species populations. This study focused on identifying perceptions of the jaguar within local communities in five Brazilian biomes (Caatinga, Cerrado, Pantanal, Amazon and Atlantic Forest) using interviews for adolescents and adults, and thematic drawings for children. The majority of the public interviewed was in favor of jaguar conservation. In general, people presented positive perceptions and values of the jaguar, although there were differences between the biomes in perception of the species and values attributed toward it. Children's perceptions did not necessarily reflect that of the adults across the biomes. Results highlight the need for regionalized programs addressing the human aspect of jaguar conservation.

The relationship between humans and jaguars has several dimensions and has been documented in ancient and present times (Saunders 1998; Conforti & Azevedo 2003; Zimmermann *et al*. 2005; Palmeira & Barrela 2007). In general, it is acceptable to assume that many humans around the globe show admiration for large cats (Saunders 1998). They have been used as symbols since ancient cultures to today's modern society. In Pre-Columbian America, the jaguar was the most prominent symbol of power and strength (Benson 1998); today, its name stands for a luxury car brand. However, on a smaller scale, looking at communities that share space with them, perceptions change and are closely related to local culture and shaped by each area's religious history, ethical standards and conflicts with the species.

Brazil-wide demands for food production (crops and beef) combined with incentives for the expansion of agriculture and cattle ranching (Young 2005) have brought rapid conversion of jaguar habitat. At the same time, and based on the different local socio-economical circumstances, communities in each biome have developed distinct feelings towards native species like the jaguar, including fear, respect, and anger. These relations are commonly observed worldwide where humans live in close proximity to populations of wild animals (Manfredo & Dayer 2004).

Efforts to protect wildlife are often related to species that people admire for their beauty, power, charisma or exoticism (Sergio *et al*. 2006). On the other hand, aggressive responses, such as efforts to eliminate species or retaliation (Fig. 1), are usually directed towards those species that are perceived as competitors to human activities or risk to human life (Fanshave *et al*. 1997; Zimmerman *et al*. 2005). Considering that human perceptions and attitudes towards a species are determinant for its conservation (e.g. Marker *et al.* 2003; Lindsey *et al*. 2005), it is implicit that understanding these trends is key to guiding species conservation efforts.

In this study, we evaluated people's opinions about jaguars based on their perceptions and values attributed to the species across five biomes. We aimed to interpret perceptions while considering the distinct cultural aspects of the sampled communities. We also briefly discuss implications for jaguar conservation in the country's different biomes.

Material and Methods

Study area

We sampled one community site in each of five distinct regions of Brazil, located in different Brazilian biomes: Pantanal, Cerrado, Amazon, Caatinga, and Atlantic Forest. Although each area represents environmental, socio-economic and cultural characteristics typical for the biome, we do not consider that our data necessarily reflect the average perception of each biome as a whole. The study followed two major criteria for site selection: 1) that the area had confirmed past and present jaguar occurrence, and 2) that the traditions and socio-economics of the local community reflected the general customs expected for most of the biome. The site locations and human populations (IBGE 2007) for these regions is as follows:

- Cerrado (CER): Surrounding Emas National Park (ENP), central Brazil, municipality of Mineiros and Chapadão do Céu, State of Goiás; Alto Taquari, State of Mato Grosso; and Costa Rica, State of Mato Grosso do Sul (between 18º 00' S / 52º 54' W and 18º 62' S / 53º 20' W), with an area of 18,369 km^2 and a human population of 74,813 inhabitants;
- Caatinga (CAA): Ecological Corridor that includes the Serra da Capivara National Park and the Serra das Confusões National Park (between 9º 00' S / 42º 48' W and 9º 28' S / 43º 34' W); Municipality of São Raimundo Nonato, Coronel José Dias and Caracol, State of Piauí, with an area of 4,699 km^2 and a population of 45,551 inhabitants;
- Amazon (AMA): Surrounding Cantão State Park (CSP) (between 09º 08' S / 50º 00' W and 09º 50' S / 49º 50' W); Municipality of Caseara and Marianópolis, State of Tocantins; and Santana do Araguaia, state of Pará, with an area of 15,374 km^2 and a population of 58,193 inhabitants;
- Pantanal (PAN): Municipalities of Miranda, Aquidauana and Bodoquena, State of Mato Grosso do Sul (between 20º 14' S / 55º 47' W and 20º 30' S / 56º 43' W); with an area of 24,945 km^2 and a population of 77,053 inhabitants;
- Atlantic Forest (ATF): Atlantic Forest Corridor, including the surroundings of Intervales State Park, Alto Ribeira Touristic State Park, and Carlos Botel-

Fig. 1. For subsistence farmers, any livestock loss due to jaguar predation may represent large economical damage, therefore retaliation over cattle killers or even preventive killing of jaguars is common (Photo Jaguar Conservation Fund/Instituto Onça-Pintada).

ho State Park (between 24º 17' S / 48º 37' W and 24º 84' S / 49º 00' W), municipality of Apiaí, Iporanga, Guapiara, Ribeirão Grande, and São Miguel Arcanjo, State of São Paulo, with an area of 3,799 km^2 and a population of 87,434 inhabitants.

Interviews

We distributed interviews equally among the five study areas and sampled a public comprised of adolescents (15 and 19 years of age), adults (20 to 59 years) and elderly people (60 years or older). Interviewees were chosen randomly from the local population. We used a semi-structured questionnaire with open and closed questions and opted for individual interviews without the presence of a third person. The questionnaires were divided in two sections: 1) Profile of the interviewee; and 2) Perception of the jaguar and values attributed to it.

We chose a qualitative approach for analysis of the open questions as this is a pioneer study that demands familiarization with the language of the studied public and the types of answers given. To analyze open questions we established two variables (e.g. Rey 2002): 1) perceptions of the jaguar, and 2) values attributed to the jaguar.

For the variable "*perceptions of the jaguar,*" we analyzed answers to the questions "*Have you ever seen a jaguar*?" indicating the person's recognition of the species, followed by "*Where did you see a jaguar*?," in order to identify how the person could identify the species (e.g. from television, seeing them at a zoo, etc.). Lastly, we asked "*What do you think of the jaguar?*" Based on the responses obtained to this question, we established levels of how the jaguar is perceived: dangerous (causes threats to human life), beautiful, or both (beautiful and dangerous). We recognize that with this approach re-sampling or sampling in other areas can result in more or different response categories from the ones we obtained in this study, however, this line of analysis allows general identification of the image of the species in the different regions.

For the variable "*values attributed to the jaguar,*" we analyzed answers to the questions "*Do you think the jaguar should be eliminated from nature*?," followed by "*Why*?" Answers to the latter question indicated values that justify positions of favoring the species' elimination or favoring its protection. Results pointed to five classes of values attributed to the jaguar: (1) anthropocentric - those that show the necessity to conserve the jaguar so that future generations can enjoy its beauty, or condition its existence on the species not posing any risk to humans; (2) religious - those that consider the jaguar as sacred, a divine creature; (3) economical - those that condition the existence of the jaguar on the presence or absence of economical losses caused by it; (4) moral - those that condition the jaguar's existence on it being protected by law; and (5) ecological - those that acknowledge the jaguar's ecological importance, even if not explicitly stating its role in the food chain.

To be able to discuss results in a socio-cultural context, we also recorded length of residency in the particular region, literacy/education level, and knowledge of jaguar attacks in the region.

Drawings

Hand drawings were used to evaluate the perception of the jaguar by children between the ages of six and 15 years. For this exercise, children from public schools were first presented with pictures 24 x 30 cm in size of the typical vegetation of the biome they lived in. The children were then asked to draw three animals that, in their opinion, inhabit this environment. This exercise had the goal to evaluate the frequency at which the jaguar appeared among these three animals. Subsequently, we asked the children to draw a situation of them encountering a jaguar in the wild (Fig. 2). Lastly, each child was asked individually to tell a short story about their drawing, to complement analysis of the encounter described by them. Using both pieces of information, we interpreted encounter situations as: a) positive (where there is interaction but the jaguar does not represent any danger to humans); b) negative (jaguar attacking human, or human attacking jaguar); or c) neutral (where there is no interaction between the jaguar and the human).

Table 1. References of the jaguar stated by members of rural communities in five Brazilian biomes when asked "*What do you think of the jaguar?*" expressed in percent (n for each area ≈ 200).

Reference	Amazon	Cerrado	Caatinga	Atlantic Forest	Pantanal
Dangerous	21.0	15.4	28.5	37.8	15.0
Dangerous and beautiful	11.2	9.0	14.5	13.4	6.0
Beautiful	60.9	68.2	37.5	39.8	71
Nothing	1.5	1.0	6.0	4.0	3.5
Others	5.4	6.5	11	4.5	3.5
No answer	0.0	0.0	2.5	0.5	1.0

Table 2. Values attributed to the jaguar by members of rural communities in five Brazilian biomes, expressed in percent (n for each area ≈ 200).

Value	Amazon	Cerrado	Caatinga	Atlantic Forest	Pantanal
Anthropocentric	24.4	19.4	33.5	30.8	20.5
Ecological	20.5	22.4	6.0	15.4	38.5
Economic	24.9	6.0	3.0	6.0	5.5
Religious	29.8	44.8	45.5	30.3	34.5
Moral	0.0	3.5	2.5	5.5	0.0
Others	0.5	1.5	7.0	9.5	1.0
No answer	0.0	2.5	2.5	2.5	0.0

Statistics
To compare results within each biome we used a binomial test for questions answered with either "*Yes*" or "*No*," and for the first drawings where the jaguar appeared or not. We used a Chi-square test to analyze questions responded with several categories of answers, interaction categories in the second drawing, and to compare results between biomes. Analyzes were processed using the software SPSS 13.0 for Windows (SPSS Inc., Chicago IL).

Results
Profile of the interviewees
We conducted 1,007 interviews. Age of the majority of the interviewees (74%) ranged from 20 to 59 years. Most interviewees were born in the sampled region in the Pantanal (84%), Caatinga (92%), and Atlantic Forest (94%), while in the Cerrado and Amazon area, rates of interviewees born there were distinctly lower (26% and 17%, respectively). Fundamental education, comprised by the first eight years of school, was the most frequent level of education in all study areas (PAN = 54%; AMA = 44.4%; CER = 42.8%; ATF = 39.8; CAA = 38.5%). In the Caatinga and Amazon areas, we observed the highest rate of illiteracy (30.5% and 21%, respectively).

Perception of the jaguar
In all study areas, the majority of interviewees knew what a jaguar was. The Amazon study area showed the highest rate of interviewees that did not know (26.3%), followed by the Cerrado (15.9%), Caatinga (8.5%), Pantanal (7%) and Atlantic Forest (1%). In the Pantanal, 78% stated that they had seen a jaguar in its natural environment. For the other areas, this value ranged from 34.3% in the Cerrado, 18.5% in the Caatinga, and 17.4% in the Atlantic Forest to 0% in the Amazon. Television was the main source of information for recognizing jaguars in the Atlantic Forest (50.7%) and the Caatinga (54.5%), while in the Cerrado and Amazon sources of information varied, ranging from circus, zoos and photos to skins and skulls found in hands of locals.
Among the observed levels of perception (dangerous, beautiful, or the combination of both) "beautiful" was predominant for all biomes (Table 1). Answers were not distributed equally between levels, and deviation from uniform distribution was significant ($20.025 < Chi^2 < 161.783$, df = 2, $p < 0.001$). Perceptions also differed significantly between the five biomes ($Chi^2 = 74.767$, df = 8, $p < 0.001$). In the Pantanal, Cerrado and Amazon, perception of beauty were represented more than in the Atlantic Forest and the Caatinga, where perception of danger was found more often than in the other biomes (Table 1). Overall, the number of interviewees that had heard of an incidence of a jaguar attacking a human ranged from 29.5% in the Pantanal, followed by the Cerrado and Caatinga (27.4% and 27%, respectively), and considerably lower in the Atlantic Forest and Amazon (8% and 4.4%, respectively).

Table 3. Interpretation of drawings from school children (age 6 to 15 years) in five Brazilian biomes when asked to draw an imaginary encounter between themselves and a jaguar; interaction of both characters was classified as positive, negative, or neutral.

Biome	Neutral (%)	Positive (%)	Negative (%)
Cerrado (n=21)	52.4	0.0	47.6
Pantanal (n=9)	11.1	11.1	77.8
Caatinga (n=12)	0.0	41.7	58.3
Amazon (n=13)	7.7	38.5	53.8
Atlantic Forest (n=15)	13.3	40.0	46.7

Values attributed to the jaguar
Throughout all study areas, a significant majority (85.5%) believes that the jaguar should not be eliminated ($p<0.001$). The highest rate of answers in favor of elimination of the species were encountered in the Amazon area (33.2%), followed by the Atlantic Forest (15.9%) and the Caatinga (11.5%) and a considerably lower rate in the Pantanal and Cerrado sites (3.5% both). Within biomes, the five classes of values (anthropocentric, economic, ecological, religious, and moral) were not attributed equally to the jaguar ($53.220 < Chi^2 < 177.425$, df = 4, $p < 0.001$). The predominating value in the Amazon, Cerrado and Caatinga was religious (Table 2), anthropocentric in the Atlantic Forest, and ecological in the Pantanal. Frequency of the five values differed significantly among biomes ($Chi^2 = 165.784$, df = 16, $p < 0.001$).

Fig. 2. Child drawing an imaginary encounter situation between herself and a jaguar (Photo Jaguar Conservation Fund/Instituto Onça-Pintada).

Perception of the jaguar by children

A total of 75 drawings (35 girls and 40 boys; average of 15 per biome) from students ranging in age between six and 15 years old were collected and analyzed.

In the Amazon, the jaguar appeared spontaneously among the three species in 50% of the first drawings. All other biomes showed a lower number of first drawings with a jaguar (ATF=40%, PAN=22%, CAA=13%, CER =9%), in the Cerrado and Caatinga the difference was significant ($p<0.001$ and $p=0.007$, respectively).

Regarding the second drawings, positive interaction was highest in the Caatinga, at 41.7%. Rates in the other biomes ranged from 40% in the Atlantic Forest to 0% in the Cerrado (Table 3). The Pantanal presented the highest incidence of negative interaction, at 77.8%, while in all other biomes negative interaction was present in about 50% of the drawings (Table 3). Twenty percent of these negative interactions in the Cerrado and 40% in the Caatinga and Amazon, involved humans attacking a jaguar. This was not observed in the other two biomes. Neutral interaction was represented in 52.4% of the drawings in the Cerrado, more than in any other study area (Table 3). Frequencies of the three types of interaction differed significantly between biomes (Chi^2= 21.259, df=8; $p=0.006$). Drawings were generally coherent with the content of stories told.

Discussion

Considering that behavior is the result of interaction between perceptions, values and social rules integrated by an individual throughout his lifetime (Rodrigues *et al.* 1999), understanding people's perceptions can then be an essential tool to form favorable opinions about conservation of the jaguar. For example, in the Pantanal, extensive cattle ranching has been the major economic activity for over the past two centuries and consequently, the jaguar-rancher conflict has a long history. However, although jaguars are hunted in retaliation for cattle predation (Zimmermann *et al.* 2005), we observed in this study a clear desire to conserve the species, which is often highlighted as a regional flagship species. This is an important aspect for the species' conservation and demonstrates how perception can differ from observable actions (Bandura 1973).

The Caatinga and Atlantic Forest biomes presented strongest perception of the jaguar as dangerous (Figure 3). Generally, this perception occurs as a result of folklore and traditions (Wilson 2004, East and Hofer 1998) and a response to attacks on humans (Saberwal *et al.* 1994; Wilson 2004; Palmeira & Barrela 2007). In the Caatinga, 27% of the interviewees claimed to know of attacks by jaguars on humans. An interesting analogy to this perception can be observed in cave paintings of the region, dated back to at least 5000 b.c. (N. Guidon, personal communication), showing what seems to be a large cat attacking a human (Fig. 3). In the Atlantic Forest, although few interviewees (8%) claimed to know about jaguar attacks, fear of the jaguar was an important reference, a tendency also observed in the surrounding area of Iguaçu National Park (Conforti & Azevedo 2003).

Of all biomes, the Pantanal showed the highest percentage of ecological value attributed to the jaguar (Table 2). The long coexistence of cattle ranchers and jaguars in this biome could have lead to a better understanding of the species' ecological role. The second highest incidence of interviewees recognizing the ecological value of the jaguar was observed in the Cerrado, although the local population does not have a history of coexistence with the species, as large scale agricultural occupation of the landscape was initiated in the early seventies and accompanied by immigration into this region (Ribeiro *et al.* 2005). However, this could be explained by the sampled area being located in the surroundings of Emas National Park, a locally well known reserve that protects jaguars. The Park may have brought public awareness about biodiversity related issues. Also, this region is dominated by agricultural activities with virtually no jaguar-rancher conflict, favoring, in turn, tolerance of the species.

At the Amazon study site, located in the so-called arc of deforestation and characterized by a strong jaguar-livestock rancher conflict, the number of interviewees attributing an economical value to the jaguar was three to six times higher than in any other biome. Also, one third of the interviewed public thought that the jaguar should be eradicated. The progressive expansion of the agricultural frontier in this region has brought in immigrants from other parts of Brazil (Young 2005), which could be causing a lack of identification with the local wildlife. Independent to the value attributed, most interviewees throughout all biomes agreed that the jaguar should not be eliminated from nature.

The perceptions and values discussed here are also present in the children's minds, with the prominent attitude being fear. Fear of animals among children is common and diminishes or is replaced by other fears with increasing age (Ferrari 1986; Bleichmar 1991; Roazzi *et al.* 2001). The negative interaction characterizing the jaguar as a threat to human life is common in all biomes (Table 3), while the figure of the brave human (attacking the jaguar) occurred only in the Cerrado, Amazon and Caatinga.

Human-jaguar interactions presented in the second drawing did not necessarily reflect the predominating perception or value attributed to the jaguar by adults. For example, in the Atlantic Forest presented a high score of neutral interaction, although the reference of the jaguar as dangerous corresponded to 37.8% of the adults' answers. On the other hand, for the Amazon, the larger proportion of adults in favor of eliminating jaguars seemed to have influenced the children as they showed the highest incidence of drawings presenting a human attacking a jaguar.

Conserving a wide-ranging species with high conflict potential and a wide distribution like the jaguar has to incorporate the human dimension and recognize its uniqueness in different environmental, cultural and socio-economical settings. Several studies have proposed environmental education as a tool for mitigating conflicts between humans and wildlife (Conforti & Azevedo 2003; Zimmermann *et al.* 2005; Palmeira & Barrela 2007). While educational activities could strengthen positive tendencies observed in the Cerrado and Pantanal study areas, they can also lay the groundwork for understanding the ecological importance of the jaguar and demystify it where it is predominately seen as a threat to human lives, like in the Atlantic Forest and Caatinga. Considering that children have not yet completely internalized locally typical perceptions and values, environmental education should preferentially be directed towards this age class (Conforti & Azevedo 2003; present study). Their fear of the jaguar should be considered in such activities.

This study can be seen as a starting point to investigate how different local perceptions of the jaguar influence people's behavior and how this knowledge can complement political and ecological conservation efforts for the species in Brazil.

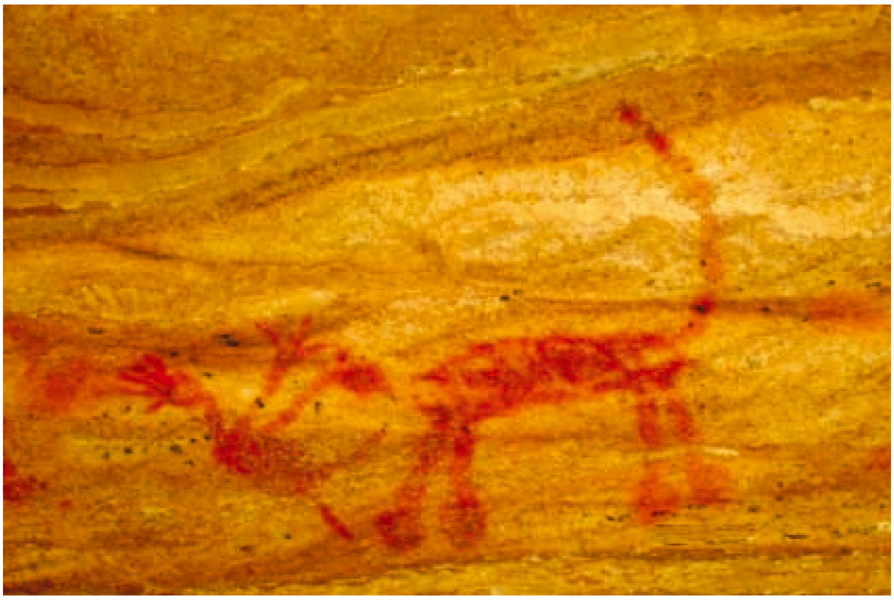

Fig. 3. Cave painting from the Serra da Capivara National Park, Caatinga of Northeastern Brazil representing a jaguar attacking a human, dated back to approximately 5000 BC (Photo Jaguar Conservation Fund/Instituto Onça-Pintada).

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Domestic Livestock Predation by Jaguars in Brazil

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Like other large predators, jaguars can prey on domestic livestock and are often killed in retaliation to this. The management of this conflict is not an easy task, as appropriate management measures depend on local landscape characteristics, herd husbandry practices, and the scale of the problem, as well as social situation and culture In Brazil, the conflict between jaguars and ranchers has a considerable impact on jaguar populations. A lack of governmental help does not alleviate the problem. Here, the applicability of techniques used worldwide to manage the conflict between large predators and humans to examine management options for the jaguar-rancher conflict across the country's different biomes is evaluated. Major conflict zones in Brazil are mapped. Property zoning is recommended for the Amazon and smaller properties in the Pantanal. For the Caatinga, Atlantic Forest and partially the Cerrado, smaller scale approaches like guard animals or electric fences are applicable. Major conflict zones are located in the northwest of Brazil. Apart from the technical challenge, there is, a political issue that must be tackled, namely, ascertaining who is responsible for developing and executing control measures for predator-human conflict in the country.

The exponential increase in human populations, combined with the world's demand for food, is creating ever-growing habitat conversion and fragmentation (Timan *et al.* 2001). Human population growth and expansion, and the resulting habitat loss, tend to increase the conflicts between people and wild animals, as the latter are forced to live closer to humans and their domestic livestock. Large carnivores, such as the jaguar, which require extensive areas and a stable natural prey base to live, are pushed into situations where they compete with humans for food and space. As a result, killing predators in reaction to or to prevent domestic livestock predation can have a considerable impact on carnivore populations. The jaguar is no exception to this trend: Though widely distributed, habitat conversion poses a major threat to the species (IUCN/SSC Cat Specialist Group, 1996). Known to prey on domestic livestock throughout its range (e.g. Rabinowitz 1986; Palmeira *et al.* 2008), hunting of jaguars in retaliation can seriously threaten local populations (IUCN/SSC Cat Specialist Group 1996; Fig. 1).

Although the above described predator-human conflict is increasing worldwide (see Treves & Karanth 2003), we still lack adequate solutions and management actions, the applicability of which is highly dependable on local factors. Actions can either prevent or increase tolerance for livestock predation and vary according to landscape characteristics, herd husbandry practices, and the scale of the problem (Conover 2002). Moreover, geographic accessibility to conflict sites, combined with operational costs, can determine the viability of any proposed method. Thus, the identification and implementation of proper management practices demands good knowledge of the conflict site and its specific ecological, social and cultural characteristics.

With this in mind, we have selected from the literature the most common solutions used around the globe to mitigate conflict between large carnivores and humans, and have assessed their applicability and potential efficiency, based on our own experiences, in the management of jaguar-rancher conflict across the different Brazilian biomes. To obtain a comprehensive picture of the problem in Brazil, we analyzed and mapped the potential jaguar-rancher conflict zones in the country.

Material and Methods

Identification and management of jaguar-rancher conflict

Management alternatives for predator and depredation control tested to date vary widely and can be very species-specific. Therefore, the first step in determining the most appropriate method to be used is to identify the predator responsible for the depredation. In the case of the jaguar, signs at a kill site could be confused with those left by a puma (*Puma concolor*) or by a large domestic dog. Thus, first, we compiled from our own experiences and the scientific literature the characteristics and evidence typically found at a jaguar kill site. We then assessed management measures for the predator-human conflict used worldwide from the literature. Each of the measures was evaluated in terms of the operational, financial, political and socio-economic aspects and then overall rated as "recommended" or not. For this exercise, we took into account the conflict scenario expected for each Brazilian biome, given average property size, vegetation cover, predominant landscape features and local culture regarding the jaguar.

Jaguar-rancher conflict control measures can be classified according to three different approaches and scales, and we characterized each of the evaluated measures according to scale they address:

Problem animal - This approach concentrates on the individualization of the problem. Although any jaguar coexisting with cattle may eventually and occasionally prey on cattle, some individuals show a tendency to prey more consistently, inflicting greater financial losses to the ranchers. Generally, they are young animals in search of a territory, females with cubs, or old or injured individuals that have become unable to hunt wild prey (Rabinowitz 1986; Pitman *et al*. 2002). Management efforts should thus be specifically directed towards the problem animal rather than towards the entire carnivore population, which can coexist peacefully with domestic cattle.

Domestic herd - This approach adopts a “passive” point of view, focusing on herd management within the area of conflict. It is the traditional approach used by humans since ancient times (Linnell *et al*. 1996), utilizing, for example, night enclosures for livestock. The identification of the conflict at the herd level may also reveal problems associated with inadequate husbandry practices, avoiding the need to invest in alternative actions against depredating carnivores. For example, the absence of basic care (e.g. vaccination programs) makes domestic animals more vulnerable to predation (Pitman *et al*. 2002).

Landscape - This approach occurs at the environment level. The amount of wildlife damage depends in part on the landscape and land-use patterns in the broad area encompassed by the conflict site (Conover, 2001). The habitat and its degradation by human activities should also be considered; for example, the natural vegetation around and within pastures. Due to the cover they provide, areas close to forests and springs are more likely to be visited by predators (Pitman *et al*. 2002). Michalski *et al.* (2006), working in the Alta Floresta region (Northern Brazil), concluded that landscape variables such as distance to the nearest riparian corridor, proportion of forest area around farm headquarters, and the interaction between the distance to the corridor and the distance to the town are important predictors of the occurrence of predation events.

Fig. 1. Jaguar cubs killed in the Pantanal by ranchers in retaliation to cattle predation (Photo Jaguar Conservation Fund/Instituto Onça-Pintada).

Results

Characterizations of a jaguar kill

Jaguars prey on a wide variety of wild animals, and may take domestic livestock as well, including pigs, horses and especially cattle. However, it is important to consider that they can also act as scavengers, feeding occasionally on carcasses (JCF, unpubl. data). Determining which type of predator is responsible for a kill can be difficult, although size can be an indicator. Prey smaller than 250 kg can be taken by any of the sympatric predators (e.g., jaguars, pumas, domestic dogs), while kills greater than 250 kg can be definitively attributed to jaguars, since above this biomass the jaguar is virtually the only predator capable of preying on such large animals.

Kill – When analyzing a jaguar kill, some details should be taken into account: a) jaguars generally leave teeth marks in heavy dense bones such as the femur, the cranial base region or in the upper/lower part of the neck, causing fractures and ruptures of the vertebrae; b) many large prey are killed by jaguars breaking the neck, and it is

Distribution of potential jaguar conflict

In order to estimate and map the major expected jaguar conflict zones in Brazil, we overlaid the current jaguar distribution (see Tôrres *et al*, this volume) with cattle abundance (heads of cattle per municipality) in the country (IBGE 2005). The zones were outlined as blocks of continuous jaguar presence and high cattle density, where conflicts are most likely to be present across the landscape.

Table 1. Methods used worldwide to control and/or prevent livestock predation by carnivores, characterization as to what scale of the conflict they address, and an assessment of their applicability for controlling/preventing jaguar livestock predation in the different Brazilian biomes. Methods considered as “Recommended” were marked with an “X” and those recommended depending on the property characteristics were marked with a “P” (partially).

Method	Scale	Amazon	Atlantic Forest	Caatinga	Cerrado	Pantanal
Killing of problem animal	Problem animal	X			P	X
Guard animals	Herd	X	X	X		
Visual barrier	Problem animal	X		X		
Electric fence	Herd	X	X	X		
Protection collar	Herd					
Financial compensation	Problem animal / herd	X	X	X	X	X
Visual/audial stressors	Herd					
Propane explosives	Herd					
Herd management	Herd	P	X	X	P	P
Electronic guard	Herd					
Removal of problem animal	Problem animal	X	X	X		
Non-lethal shots	Problem animal					
Zoning of property	Landscape	X	X	X	X	X

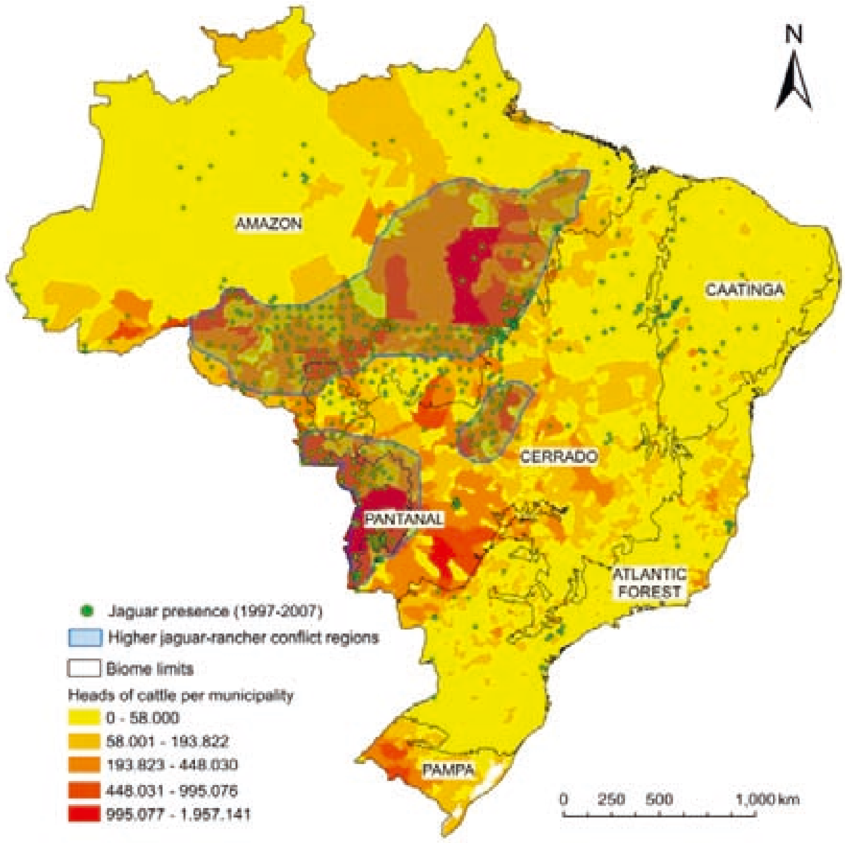

Fig. 3. Expected jaguar-rancher conflict zones in Brazil determined by current jaguar distribution overlapped with cattle abundance per municipality.

common to see the head of the animal turned backwards; c) unlike pumas, it is uncommon for jaguars to bite the throat to kill the prey by suffocation; d) in general, jaguars start to eat at the foreside of the prey, and later the ribs and medial portion of the carcass; their preferred parts are the throat, the lower part of the neck, the hump and the chest, leaving the forelimbs untouched; small animals, such as calves, are generally entirely consumed; e) generally, jaguars do not cover the carcass with leaves and dirt as does the puma, but instead can drag it for distances as far as 1.5 km and hide it in vegetative cover (Pitman *et al*. 2002).

***Kill site* -** When looking at a fresh kill scene it is important to check for fresh tracks. Compared to pumas and dogs, jaguar tracks are more rounded, their width is greater than their length and the toes are more rounded (for details see Miller and Jug 2001).

It is important to combine both evidence (the kill) and scenario (the environment) and analyze if there is enough evidence to determine the predator. For instance, any of the sympatric predators can visit and eat parts of an existing kill and therefore confound the evidences. Only a careful analysis of all factors can yield an accurate identification of the predator.

Conflict control measures

We compiled 13 methods used to prevent, mitigate and/or eliminate large carnivore conflict (Table 1, for a description of the methods see Appendix I; a list of references used for this compilation can be obtain from the lead author upon request). Of those, 5 address conflict at the level of the problem animal, 8 address herd management, and 1 acts at a landscape scale. One method is applied at more than one level: financial compensation for livestock losses to predation can be seen as a kind of insurance, working at the herd level, while this measure can also be used to create tolerance for a problem animal where removal or elimination is not recommended. Among the five biomes, the Amazon was eligible for 8 of the management measures, followed by the Caatinga (7), Atlantic Forest (6), Cerrado, and Pantanal (4, both). Land use patterns may vary significantly within a biome. Therefore, when analyzing the applicability of the methods, we attributed the term "partially" to those methods that we considered could only be implemented in restricted situations or regions of the biome.

Distribution of potential jaguar conflict

Combining herd size for each of the 2,193 municipalities in Brazil with current jaguar distribution (Tôrres *et. al.* this volume), we identified three expected conflict zones in the country, all located in the northwestern portion of the country (Fig. 2).

Discussion

Amazon Rainforest

In the Amazon Rainforest, jaguar-livestock conflict is concentrated in the region known as the arc of deforestation (Fig. 2). This region is characterized by properties where a considerable portion of the natural forest has been converted into non-native pastures, leading to a convergence of jaguar habitat and cattle ranching. For this biome, we suggest the use of property zoning, that is, establishing delimited zones for cattle graze, safeguard and drinking points away from bush areas, reducing the chances of encounters with jaguars. Financial compensation for livestock losses caused by jaguars may also be considered; however, as this measure is not readily applicable at a large scale, mainly due to financial restrictions, it should be an alternative only for key areas where the loss of a single jaguar has considerable impact on its local population. The killing of a problem jaguar is only recommended when all other methods have failed, and only after a careful and thorough analysis of the situation.

Atlantic Forest

The agricultural structure of this biome is characterized by properties whose land ownership and/or occupation are long established, going back to colonial times. Cattle predation by jaguars is restricted to areas that still retain remnants of original forest: these are the southeast portion of the Coastal Atlantic Forest in the São Paulo and Paraná States and the portion of the Mesophile Atlantic Forest in the São Paulo, Mato Grosso and Paraná States. For this biome, the introduction of guard animals may be tested to prevent jaguar attacks, as this method has been shown to work well with pumas (Rogério Cunha, personal communication). Electric fences are also recommended for small properties with intensive livestock management. Financial compensation for livestock losses is recommended at a local scale, accompanied by social-educational programs on how to prevent conflicts. Considering that properties in this biome are usually small, zoning is recommended as a viable alternative. The removal or translocation of a problem jaguar should be considered only in the most extreme cases, as jaguars are particularly threatened in this biome.

Caatinga

In comparison to the other Brazilian biomes, the Caatinga is the most adverse region for cattle ranching. Properties sizes are, on average, smaller and would favor localized management methods. Its harsh climatic conditions and dense semi-arid vegetation hinder extensive cattle enterprises. However, ranchers in this region usually raise cattle on a subsistence scale and are too poor to invest additional money in jaguar avoidance methods. Poverty among the Caatinga ranchers is already responsible for poor husbandry practices of their small herds of dairy cattle and goats. Although small properties and small herd size allow for the use of more localized management options, most of them would be too expensive for the rancher to implement without an outside sponsor. We recommend electric fences and visual barriers as potential methods to be tested, because they can be effectively applied to small to medium scale properties. Considering the critical status of the Caatinga jaguar (Sollmann *et al*., this volume), we do not recommend killing of problems animals as a management alternative.

Cerrado

In the Cerrado, conflict is mainly concentrated in an area near the Amazon border. Herd management and property zoning are recommended for smaller properties (up to 200 hectares). In this case, we consider that methods such as guard animals, electronic guards (automatic devices that emit a series of audio/visual stressors) and electric fences should be tested. A compensation program might be considered in joint collaboration between governmental and non-governmental organizations. However, this alternative should be prioritized around key jaguar populations. For example, in Emas National Park, State of Goiás, where no more than 30 jaguars are though to live, we should not risk to lose a single individual due to jaguar-rancher conflict. Methods such as visual/auditive stressors or propane explosions should be tested in a long-term experiment in order to verify responses from problem-jaguars.

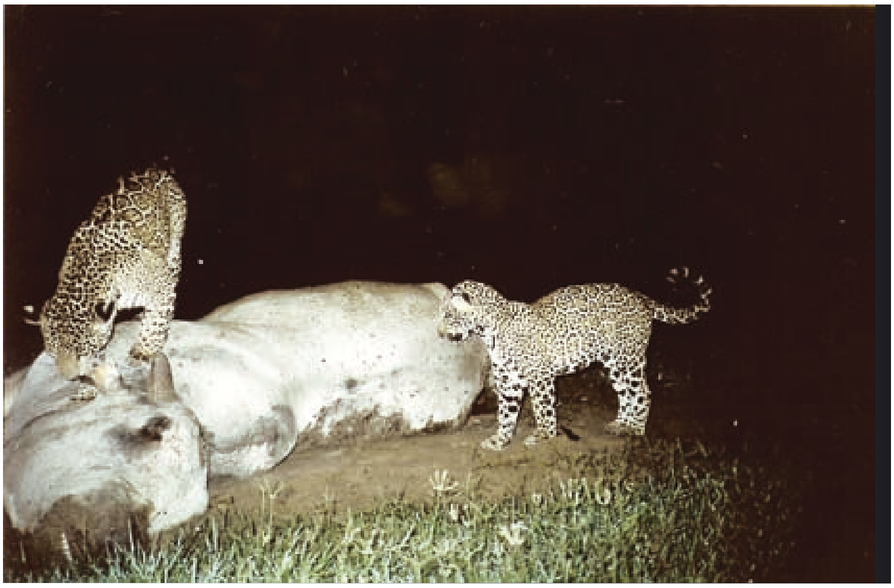

Fig. 5. Jaguar cubs feeding on a bull killed by their mother on a Pantanal ranch (Photo by Jaguar Conservation Fund/Instituto Onça-Pintada).

Pantanal

The Pantanal constitutes the third major jaguar-rancher conflict zone in Brazil. The biome is a seasonal flood plain with vast areas of natural pastures that offer good conditions for grazing. About 95% of the Pantanal is privately owned, of which some 80% is used for extensive cattle ranching. To increase cattle density on their lands, ranchers have been converting natural grasslands into exotic pastures since the early seventies. This long rancher presence has enabled jaguars to live close to cattle and incorporate them in their diet since the early stages of their lives (Fig. 3). Ranches in the Pantanal are usually large, where some may reach several hundred thousand hectares. We therefore consider herd management as alternative only for properties up to 1.000 hectares. As the Pantanal is very heterogeneous in terms of vegetation cover and habitat distribution, property zoning may not be applicable to all regions. Financial compensation programs should be applied in key areas. The killing of problem jaguars should be considered only where high abundance of the cat is proven. Sport hunting as a management tool could be tested in this biome. However, the killing of problem animals is recommended only in extreme cases and should never be considered as the first option.

The jaguar-rancher conflict dilemma in Brazil: who is responsible for what?

Usually governmental institutions around the world base their actions regarding predator-human conflict on three distinct strategies that can be summarized as: 1) eliminating the predator (Treves & Naughton-Treves 1999, Treves & Karanth 2003); 2) regulated harvest (Harbo & Dean 1983, Okarna 1993, Landa *et al*. 1999, Angst 2001, Treves & Karanth 2003) and; 3) preservation, through full legal protection (Karanth *et al*. 1999, Rangarajan 2001), sometimes along with compensation programs (Montag 2003, Naughton-Treves *et* al. 2003, Treves & Karanth 2003). However, when searching for

Brazil's official experience and statistics (state and federal) on managing the jaguar-rancher conflict there is virtually nothing available in the scientific literature or governmental database.

In Brazil, hunting has been regulated since 1967, when the first Fauna Law was created (Law 5197-67-03/01/1967). In this law, the Brazilian State declares itself as proprietary of all the wildlife species, forbidding hunting in all circumstances, except for scientific purposes. A later complement of this law (Law 9605-1998) states that the "destruction" of wild animals is permitted when considered as "pests" to agriculture and public health. On the other hand, permits to eliminate such pests can only be given by a not specified (?) "competent authority."

The Brazilian Constitution of 1988 says that the State and the people should preserve and defend the environment, but that the State should be responsible for preserving and restoring essential ecological processes, thus providing ecological management of species (Art. 225). The Federal Government is responsible for the establishment of general directions (Art. 24) and states and municipalities have powers to legislate over specific issues, including hunting, fishing, and nature conservation (Art. 23 & 24). Later, the Law for *Environmental Crimes* (Law 9605-1998) complemented the one from 1967, extending to prison the punishment to those that hunt endangered species such as the jaguar. Therefore, based on the current Brazilian legislation, the aspect of management of a predator such as the jaguar still relies, in practice, on the goodwill of the government to implement the law for pest control and determine who has the responsibility to execute it.

The existing techniques to eliminate, reduce or compensate losses from jaguars still seem unsustainable in a large country with such heterogeneous landscapes as Brazil, where land use and management practices vary among the five distinct biomes. There is no formal and official authorization or government statistics of predator management in the country. It still stands as if this problem did not exist nor needed any special attention. Therefore, jaguar management in Brazil seems to be more of a political than a technical challenge.

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Supporting Online Material SOM

www.catsglorg/catnews/03_specialissue/jaugar_barzil/content_jaguar_barzil.htm

Appendix I: Description of conflict control measures

Jaguar Conservtaion Genetics

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Information on genetic aspects of jaguar populations is still scarce. Initial studies have surveyed genetic diversity parameters and assessed the geographic differentiation among individuals on a continental or sub-continental scale, but so far little has been accomplished with respect to investigating regional or local jaguar populations. Moreover, different studies have employed different sets of molecular markers, posing potential problems for the future development of comparative analyses across study sites and ecosystems. Here we review the current status of jaguar genetic studies, present a new set of microsatellite markers that may be useful for jaguar population genetic studies, and survey the molecular diversity of two adjacent wild jaguar populations, sampled in the Brazilian Pantanal region. Our results suggest that this set of markers is highly efficient for jaguar genetic studies, and that moderate to high levels of variability are present in wild jaguar populations, at least in the surveyed areas of the Pantanal. This contribution may be useful as a review of jaguar genetics, as well as a baseline empirical work that might support future in-depth investigations of these and other free-ranging populations of this felid.

The use of molecular tools to investigate genetic, ecological and behavioral aspects of wildlife populations has gained immense popularity in recent years, allowing unprecedented probing into multiple components of organismal biology which were previously inaccessible. In addition to its scientific relevance, knowledge of such aspects is often a critical component for the design of adequate conservation strategies on behalf of species and ecosystems. Genetic data are required to understand long-term demographic history and dynamics, and to characterize social structure and patterns of dispersal and territoriality. They are also useful for assessing evolutionary potential and inferring census and effective population sizes, which are important components of Population Viability Analyses. The field of Conservation Genetics encompasses a diverse array of methodological approaches involving the use of genetic information to tackle these and other issues of conservation concern.

Jaguars (Fig. 1) are an elusive species whose population biology has been historically difficult to study, and only recently has been the focus of in-depth investigation made possible by technological and analytical innovations. If ecological investigations of jaguars are now the focus of multiple studies at various field sites, genetic analyses of this species are still in their infancy, having been severely limited by the practical difficulty in sampling biological materials representative of natural populations. A range-wide assessment of genetic diversity and evolutionary history has been performed, and studies addressing regional or local-level issues are starting to become feasible, as improved methods for biological sampling become incorporated in this scientific discipline. Here we (i) review the history of jaguar conservation genetics and the current state of the field, (ii) discuss the advantages and prospects of developing a set of molecular markers that can become standardized for jaguar population genetics, and (iii) present novel preliminary data describing the levels of microsatellite diversity in a natural jaguar population, that of the southern Brazilian Pantanal.

Although the jaguar had been included in previous genetic studies addressing phylogenetic questions with the use of molecular markers (e.g. Johnson & O'Brien 1997), its intraspecific levels of diversity had not been investigated until 2001. In that year, a study employing mitochondrial DNA (mtDNA) sequences encompassing a segment of the control region (CR) and 29 nuclear microsatellite loci addressed the genetic diversity and demographic history of jaguars, based on 44 individuals sampled from Mexico to southern Brazil (Eizirik *et al*. 2001). That study revealed that this species exhibits a shallow mtDNA structure, compared to other felids, with low differentiation among geographic regions. The shallow structure, with low inter-regional differentiation, was inferred to have been caused by a rather recent population expansion, *ca.* 300,000 years ago, followed by a history of demographic connectivity over a continental scale. No support was observed for the classically recognized jaguar subspecies, a finding that had also been reported on the basis of morphological data (Larson 1997). The major pattern that emerged from that data set was a phylogeographic partition between the northern and southern portions of the range, likely a function of reduced historical gene flow across the Amazon River. The levels of diversity detected in the hypervariable microsatellite loci were quite high and also indicative of large scale gene flow across the range of the species.

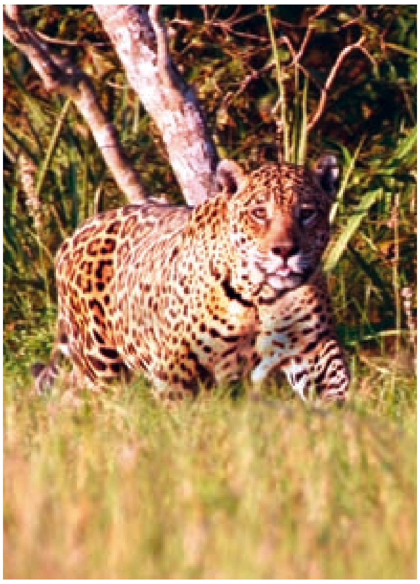

Fig. 1. Female wild jaguar in its natural habitat in the Pantanal (Photo L. Leuzinger).

No major partitions were detected with those markers, but four moderately differentiated regional groups could be discerned. The partition likely induced by the Amazon River could still be detected, but its intensity was lower than that observed with the female-transmitted mtDNA marker, suggesting that male-mediated gene flow across the river could play a role in the historical geographic homogenization in this species. This hypothesis has so far not been thoroughly tested (but see Ruiz-Garcia *et al.* 2006), and requires more detailed sampling of local populations, particularly throughout the Amazon region. Likewise, the precise magnitude of genetic differentiation among any regional populations could not be fully tested in that study, due to the sparse sampling available for each locale, and the range-wide scope of the analyses.

Subsequent to that study, to our knowledge only three scientific papers have addressed genetic aspects of jaguar populations (Moreno *et al*. 2006, Ruiz-Garcia *et al*. 2006, Soares *et al.* 2006). All three studies have employed microsatellite loci as molecular markers, allowing an assessment of the performance of these hypervariable nuclear segments to investigate this species. These loci are currently the markers of choice for population level studies of most wildlife species, as their high mutation rates and Mendelian inheritance allow the detailed probing into demographic, behavioral and ecological questions. We will briefly review the scope and findings of these three papers, and focus on the comparison of the microsatellite loci employed, aiming to evaluate the current status of marker standardization among studies.

Moreno *et al*. (2006) analyzed 39 jaguar individuals sampled in Brazilian zoos, using four microsatellite loci, three of which had been used by Eizirik *et al*. (2001). These three loci presented high levels of allelic diversity in this captive population (no analysis of natural populations was included), with 9-12 alleles identified in each of them. Ruiz-Garcia *et al*. (2006) addressed the population genetics of Colombian jaguars, including a total of 62 individuals from that country and 22 additional samples. Twelve microsatellite loci were employed, four of which had been previously used by Eizirik *et al*. (2001), and three overlapping with those of Moreno *et al*. (2006) (one of which did not overlap with Eizirik *et al*. [2001]). They also found high levels of diversity and some evidence of genetic continuity (*i.e.* no differentiation) between areas located to the north and to the south of the Amazon River. This finding might disagree with the initial inference by Eizirik *et al.* (2001), but the sampling schemes and geographic scopes were different between the two studies, and so were most of the molecular markers employed. Further analyses with designed sampling and standardized markers are still required to test this hypothesis. Finally, Soares *et al*. (2006) employed seven microsatellite loci (all of which had previously been used by Eizirik *et al.* [2001]) to perform a paternity analysis in a jaguar population in the Brazilian Cerrado biome. Only four individuals were analyzed, and three of them were related to each other, so little inference can be made on the levels of genetic diversity in that population using these data.

An overall conclusion of this brief assessment is that still very few studies have been performed on jaguar genetics, highlighting the need for further work on this topic. Moreover, many of the employed markers were not shared among studies, precluding direct comparisons of the levels of genetic diversity identified in different areas. It would be thus important to develop a set of markers that is standardized for jaguar genetics, presenting high amplification success and allelic diversity in this species, and allowing for cross-study comparisons of variability measures. Although such rough comparisons of diversity could be made across studies as long as the loci were the same, a more refined goal would be to have data sets that could be integrated in meta-analyses.

One challenge to such integration is the lack of reproducibility of the precise allele sizes across different laboratories and genotyping devices, especially in the case of dinucleotide microsatellite markers (whose repeat unit is 2 nucleotides long). This type of locus is more difficult to score reliably, and more prone to inter-lab variation in allele assignment (E.E., personal observation). However, they are very abundant in the genome, and more frequently identified in screens for variable markers than other types of repeats. Most of the microsatellite markers originally described for the domestic cat (*Felis catus*) were dinucleotides (*e.g.* Menotti-Raymond *et al.* 1999), and this set of loci served as the basis for most population genetic studies performed with wild felids so far. As a consequence, most loci applied in the studies reviewed above were dinucleotide repeats: 27 out of 29 loci in Eizirik *et al*. (2001), four out of four loci in Moreno *et al*. (2006), 11 out of 12 loci in Ruiz-Garcia *et al*. (2006), and six out of seven loci in Soares *et al*. (2006). In spite of the variability reported for these markers in these studies, it may be better to base a standardized microsatellite set for jaguars on other types of loci, such as tetranucleotides (composed of 4-bp repeat units), whose allele scoring is more reliable and reproducible. Given that several trinucleotide and tetranucleotide loci have been reported for the domestic cat (*e.g.* Menotti-Raymond *et al*. 1999, 2005), we aimed to assess their performance in jaguars, and to test whether they may serve as a basis for a standardized panel of population-level markers for this species.

Materials and Methods

Assessment of tetranucleotide microsatellite loci for jaguar population genetics

We tested 20 trinucleotide/tetranucleotide microsatellite loci developed for the domestic cat (Menotti-Raymond *et al.* 1999, 2005). Two of them (FCA441, FCA453) had been previously used by Eizirik *et al*. (2001), and another (FCA391) was employed by Ruiz-Garcia *et al.* (2006). Five loci (FCA749, FCA751, FCA748, FCA732 e FCA559) did not present efficient amplification in jaguars in pilot runs, and were excluded from further testing. Another locus (FCA424) was monomorphic (*i.e.* bearing no variation) in the pilot sample, and locus FCA738 presented only two alleles; both of them were also excluded from further analyses. We thus focused on a panel of 13 loci (FCA742, FCA741, FCA740, FCA723, FCA453, FCA441, FCA391, F146, F124, F98, F85, F53 and F42) that presented good results for jaguars sampled across their range (not shown), and initiated an assessment of their performance in population-level studies. We are currently employing these markers in jaguar population genetic studies focusing on multiple sites located in the Brazilian Atlantic Forest, Pantanal and Amazon biomes. We describe below preliminary results from a screen for genetic variation in these markers in the southern Pantanal, based on samples collected at two nearby locations.

Genetic diversity of natural jaguar populations: the Brazilian Pantanal

Blood samples from 23 wild-caught jaguar individuals were obtained in two nearby areas within a seasonally flooded habitat in the southern region of Pantanal, Mato Grosso do Sul state, Brazil. The field sites were the Caiman Ecological Refuge (19.80° S / 56.27° W; n = 12) and San Francisco ranch (20.08º S / 56,60º W; n = 11) where field projects addressing jaguar ecology and conservation are currently being carried out.

Blood samples were preserved with EDTA and in some cases with a salt saturated solution (100mM Tris, 100mM EDTA, 2% SDS), and stored at 4°C or –20°C for most of the time prior to DNA extraction. Total DNA was extracted from blood samples following a standard phenol-chloroform protocol (Sambrook *et al*. 1989), and its quality and yield were assessed by analysis on an agarose gel. DNA extracts were amplified by PCR for the 13 microsatellite loci listed above. Every forward primer was 5'-tailed with an M13 sequence (Boutin-Ganache *et al*. 2001), and used in combination with an M13 primer that had the same sequence but was dye-labeled on its 5' end. PCR reactions were carried out for each locus separately, and products from 1 to 3 loci were diluted and pooled together based on yield, size range and fluorescent dye. Microsatellite genotyping was performed using a MegaBACE 1000 automated sequencer and the ET-ROX 550 size standard (GE Healthcare), and then analyzed utilizing the accompanying software Genetic Profiler 2.2.

We calculated the number of alleles, polymorphic information content (*PIC*), observed (H_O) and expected (H_E) heterozygosity for each locus, and tested for any evidence of departures from expectations of Hardy-Weinberg Equilibrium (HWE) and linkage equilibrium using CERVUS 2.0 (Marshall *et al*. 1998) and ARLEQUIN 3.1 (Excoffier *et al*. 2006). To quantify the power of individual identification with the set microsatellite markers applied here, we estimated the probability of identity (P_{ID}) index, *i.e.* the probability of any two individuals in the population randomly sharing identical genotypes for all the analyzed loci (Paetkau *et al*. 1998).

Results and Discussion

Of 13 primer pairs used, ten presented allele intervals compatible with a tetranucleotide repeat (FCA741, FCA740, FCA723, FCA453, FCA441, FCA391, F124, F85, F53, F42), two were trinucleotide repeats (F146 and F98) and one was a dinucleotide repeat (FCA742). One additional tetranucleotide locus (FCA741) was found to be monomorphic in this jaguar sample and was removed from the study.

All loci were in linkage equilibrium in both sampling locales after Bonferroni adjustments (Rice 1989 [α = 0.05]). Deviations from HWE expectations were tested for each of the two locations separately, and then combined. One locus (FCA441) was found to be out of HWE in the Caiman ranch population and another one (FCA742) in the San Francisco ranch population. In both cases, the deviation from HWE was no longer significant after application of the sequential Bonferroni correction. When both populations were combined in a joint analysis, a third locus (FCA740) appeared to depart from HWE expectations, but again the statistical significance of this result was lost after applying the sequential Bonferroni correction. These results indicate that the deviations observed prior to the correction may not bear any biological relevance, and for the present time we can infer that these markers meet HWE expectations for these populations.

The overall analysis of the 12 selected loci, employing the total sample of 23 individuals captured in both locales, revealed moderate to high levels of genetic diversity, with an average expected heterozygosity (H_e) of 0.7171, mean number of alleles per locus of 5.83, and mean Polymorphic Information Content (PIC) of 0.6592 (Table 1). Both populations exhibited considerable diversity (Table 2), a finding which will be refined with additional sampling in the

Table 1. Measures of diversity at 12 microsatellite loci characterized in this study for *Panthera onca* in the southern region of the Pantanal biome, Brazil.

Locus	*N*	No. of alleles	Allele size range	Ho[1]	He[2]	PIC[3]
FCA742	19	11	142-178	0.947	0.876	0.838
FCA740	23	5	300-316	0.652	0.739	0.681
FCA723	23	6	200-244	0.783	0.653	0.580
FCA453	22	6	192-216	0.818	0.715	0.656
FCA441	22	4	165-177	0.500	0.589	0.520
FCA391	23	6	215-243	0.870	0.776	0.727
F146	23	3	173-182	0.304	0.382	0.318
F124	23	7	203-231	0.870	0.769	0.715
F98	23	3	189-195	0.565	0.641	0.552
F85	22	7	139-183	0.773	0.834	0.790
F53	21	5	164-196	0.762	0.803	0.748
F42	22	7	251-275	0.864	0.830	0.785

[1]Observed heterozygosity; [2]Expected heterozygosity;
[3]Mean polymorphic information content.

Table 2. Measures of diversity at 12 microsatellite loci in two local populations of *Panthera onca* from the Brazilian Pantanal.

Population	*n*	Average expected heterozygosity	Average No. of alleles per locus	PIC*	No. of private alleles
Caiman E. R	12	0.6962	5.33	0.6226	17
San Francisco ranch	11	0.7088	4.42	0.6248	6

* Mean polymorphic information content

future. Since this is the first assessment of jaguar genetic diversity performed for local wild populations, and most of our molecular markers are different from those employed previously, the observed levels of variability cannot yet be directly compared to other studies. However, this scenario should change in the near future as other populations are currently being analyzed with these same markers. Given that jaguars are believed to be more abundant in the southern Pantanal region than in many other parts of their distribution, these preliminary data from this biome may serve as a baseline which may be helpful when assessing current levels of diversity in small, fragmented jaguar populations.

The estimated probability of identity (P_{ID}) using these markers in the joint Pantanal sample was 2×10^{-13}, indicating that it is extremely unlikely that any two individuals may bear the same composite genotypes at these loci (*i.e.* this estimate would imply that one would need to sample > 1 trillion jaguars to find two individuals with identical composite genotypes). This is very important in the context of allowing the individual identification of jaguars using molecular markers, such as in the case of non-invasive samples (e.g. scats, hairs) and forensic specimens, which are of direct interest to studies addressing ecological, behavioral and conservation-related issues (*e.g.* density estimates, kinship and social structure, patterns of dispersal and population connectivity). Given the power observed in this panel of 12 microsatellites, it is likely that a subset of these markers will still have very high precision in the discrimination of jaguar individuals in any local population, allowing the investigation of ecological and behavioral questions using non-invasive sampling (which often requires that one selects a smaller number of loci to minimize error rates and to facilitate thorough genotype checking via redundancy). We conclude that this set of markers holds good promise for building a standardized panel for jaguar population genetic studies, either by itself or in combination with some loci selected from previous studies.

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Diseases and Their Role for Jaguar Conservation

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Recent declines in free-ranging wildlife populations have highlighted the potentially devastating effect of infectious disease. Diseases are an increasing threat to wild felids due to habitat restriction and encroachment from domestic animals. Domestic animals can directly or indirectly enter in contact with natural felid populations, potentially disseminating pathogens and altering disease patterns. Although wildlife populations can have the ability to cope with perturbations such as diseases, the relative increase in mortality and morbidity in dwindling populations and the introduction of new pathogens can exert important effects on demography, creating great concern for any endangered species. However, the potential role of diseases in wild carnivore populations is still poorly understood, and this is especially true for the jaguar *Panthera onca*.

Although habitat fragmentation and hunting are considered the main threats to wildlife, diseases are an increasing concern for many of the most endangered carnivores (Laurenson *et al.* 2005). Diseases have always been present in wild felid populations, but can be devastating when occurring in populations that are already small or in decline, or suffering from malnutrition, stress or inbreeding (Murray *et al.* 1999). Emergence of more pathogenic strains, co-infections with other pathogens (Munson *et al.* 2007) and alterations in host-pathogen relationships can occur at any time. These can be responsible for epizooties, which may occur suddenly and with potentially disastrous consequences for endangered populations (Scott 1988; Cleaveland *et al*. 2006). In addition, environmental and demographic pattern alterations can cause the emergence and reemergence of infectious diseases and increase the occurrence of degenerative, neoplasic and genetic diseases (Daszak *et al.* 2000).

The transmission of infectious diseases between domestic and free-ranging carnivores is becoming increasingly common (Murray 1999). Jaguars and domestic animals occupying the same or adjacent environments can share much of the same pathogens. The most important factor probably is the contact between domestic and wild carnivore populations at the interface of their ranges (Bengis *et al.* 2002; Fig. 1), favoring the dissemination of infectious agents (Murray *et al*. 1999; Cleaveland *et al*. 2000; Daszak *et al*. 2000). Livestock predation represents an additional route of transmission of pathogens. Considering generalist infectious pathogens, domestic animals elevate the number of susceptible hosts, thus potentially elevating local prevalence of infectious diseases.

Wild animals dying of disease are rarely found; this is especially true for large carnivores like jaguars, which occur at low densities and have secretive behavior patterns (Murray *et al*. 1999). Thus, it is not just difficult to find appropriate biological material for epidemiological studies but also to justify to the authorities the importance of these studies or intervention in distressed wildlife populations (Artois 2001). One of the major tasks for effective disease monitoring programs for wild animals is the detection of early stages of new or reemerging diseases, essential for making correct decisions, avoiding serious losses of wildlife and minimizing economic and zoonotic impacts in livestock and humans (Morner *et al*. 2002; Dobson & Foufopoulos 2001; Bengis *et al*. 2002).

This paper presents a brief review concerning infectious and non infectious diseases reported in jaguars as available in current literature and focuses on the importance of addressing disease issues in jaguar conservation projects.

Infectious diseases

It is consensual that all members of the family Felidae are thought to be susceptible to the same pathogens (Fowler

Fig. 1. Interaction between jaguar and cattle, occupying the same environment in the Brazilian Pantanal (Photo Jaguar Conservation Fund/Instituto Onça-Pintada).

Fig. 2. Fracture of the upper left canine tooth of an adult female jaguar presenting exposure of necrotic pulp (Photo Jaguar Conservation Fund/Instituto Onça-Pintada).

1986). However, ecological and physiological patterns vary among wild felids and may be responsible for different patterns observed in the evolution of infectious diseases in felid species. In this paper we provide information collected from indexed databases regarding pathogens to which the jaguar has been reported exposed or infected both in captivity and in the wild. We have not attempted to present all pathogens to which jaguars might be susceptible, as it would be an impossible task due to spill-over from other species and the constant potential of change and emergence of pathogens. Similarly, we have not attempted to rank the presented pathogens as posing high or low risk of impact on host dynamics, neither to population nor individual levels, as profoundly significant differences exist among studies.

The selected diseases presented here should be interpreted with caution, as most studies consisted of case reports or serological surveys: Serological surveys for antibody detection are indicative of previous exposure to a particular disease agent or class of agents that share similar antigenic properties, but seldom yield information on time of exposure, morbidity or mortality. Molecular detection and culture methods allow for identification of infectious agents actually present in the animal. In both cases, correlation between the agents detected and development of disease depends on additional information, such as clinical examinations, necropsies, and histopathologic evaluations.

Among microparasites (viruses, bacteria, protozoa and fungi), the viruses have drawn considerable attention. Fifteen years ago, the Canine distemper virus (CDV), a common pathogenic virus of canids, was proven to be fatal to felids: it killed 30% of free-ranging lions in the Serengeti (Roelke-Parker et al. 1996) and caused epizooties in captive felids in the Panthera genus in North America, including a jaguar (Appel et al. 1994). In Brazil, first evidence of CDV exposure in free-ranging jaguars was recently reported by Nava (2007) in the Atlantic Forest, possibly associated with the presence of domestic dogs.

The most common viruses that affect the domestic cat have been reported in jaguars. The Feline leukemia virus (FeLV), mostly fatal in domestic cats, does not appear to be endemic in captive or free ranging wild populations (Kennedy-Stoskopf 2003), except for the European wild cat (Daniels *et al.* 1999, Fromont *et al*. 2000). In Brazil, captive jaguars have been shown exposed to the FeLV (Schmitt et al. 2003). Antibodies to Feline immunodeficiency virus (FIV) or closely related lentiviruses have been found in most felid species, including captive (Barr 1989) and free-ranging jaguars (Murray et al. 1999). The FIV is a lentivirus of domestic cats that causes immunodeficiencies and neurological signals (Worley 2001) but seropositive wild felids do not show overt clinical signs (Kennedy-Stoskopf 2003). In Brazil, evidence of FIV infection was detected in jaguars (Leal & Ravazzollo 1998). Another important virus, the Feline coronavirus (FCoV), responsible for the feline infectious peritonitis (FIP), a fatal immune mediated systemic disease that occurs worldwide (Simmons et al. 2005), has been reported in captive jaguars in Brazil, similarly to all other neotropic felid species in captivity and in a free-ranging ocelot in Brazil (Schmitt et al. 2003; Filoni et al. 2006). Most FCoV infected felids do not develop FIP, and may remain sources of infection. Some felid species, like the cheetah, have been shown more susceptible to fatal systemic disease (Evermann et al. 1988). To date, free-ranging (Fiorello 2006) and captive jaguars (Cubas 1996) have been found seropositive to Feline parvoviruses (FPV) as well. The FPV infection in felids may range from asymptomatic to varying degrees of unspecific clinical signs, gastroenteritis and a decrease in blood cells that can be lethal (Barker & Parrish 2001). Evidence of exposure to Feline herpesvirus (FHV 1) has been found in captive Brazilian jaguars (Batista et al. 2005).

Among zoonotic bacteria, *Leptospira* sp, *Brucella* sp and *Bartonella hense-*

lae were already reported affecting jaguars. The *Leptospira* sp, responsible for causing a mild to severe disease, does not appear to be a major problem for felid species. Captive (Côrrea 2000, Guerra Neto *et al*. 2004) and free-ranging jaguars (Furtado *et al*. 2007; Nava 2008) in Brazil have been reported seropositive to *Leptospira* sp. Nava (2008) reported seropositive free-ranging jaguars for *Brucella* sp, an important zoonosis affecting livestock. Brazilian free-ranging felids may be a reservoir for *Bartonella henselae* (Filoni *et al.* 2006), which causes cat scratch disease in humans. Captive jaguars have been shown antibody positive to *B. henselae* (Yamamoto *et al.* 1998), and recently, Guimarães *et al.* (2008) detected this bacteria in a captive jaguar in Brazil. Captive jaguars have also been shown seropositive to the anthrax bacterium, *Bacillus antracis* (Abdulla *et al.* 1982).

Evidence of infection with the fungus *Pythium insidiosum* has been reported for jaguars (Camus *et al.* 2004).

Considering protozoa, captive (Silva *et al.* 2001) and free-ranging jaguars (Furtado *et al*. 2007) were reported as seropositive to *Toxoplasma gondii* in Brazil, but clinical signs have not been found. Felids are the only definitive host for Toxoplasmosis (Frenkel *et al*. 1970), but little is known about the role of wild felids in the natural epidemiology of *T. gondii* infection and its role as cause of mortality in wild felines.

Although macroparasites of free-ranging jaguars have not been extensively studied, a wide variety of endoparasites have been reported (Patton *et al*. 1986) and the nematode *Dirofilaria immitis*, the heart worm, has been observed in free-ranging jaguars (Otto 1974). Few records are available about ectoparasites of free-ranging jaguars (Durden *et al*. 2006; Sinkoc *et al* 1998; Labruna *et al*. 2005) although they can be possible vectors for other microparasites.

Non-infectious diseases

Data about non-infectious diseases in jaguars are even scarcer than for infectious diseases. In Brazil, even captive populations of jaguars are poorly clinically assessed and consistent programs designed to evaluate their health are lacking. A retrospective study about the morbidity and mortality of captive jaguars has been conducted in North America, and detected dental, gastrointestinal, integumentary and musculoskeletal diseases as being the most common causes of morbidity (Hope & Deem 2006). Likewise, a high incidence of neoplasia was detected in captive jaguars, possibly associated with longevity and husbandry in the captivity (Paul *et al*. 2002; Castro *et al*. 2003; Ramos-Vara *et al*. 2000). Degenerative spinal disorders (Kolmstetter *et al.* 2000) and impairment of hearing (Ulehlova *et al*. 1984) have been described in captive jaguars too. For free-ranging jaguars, incidence of dental fractures, especially in the canines, was observed in the Brazilian Pantanal (Jaguar Conservation Fund - JCF unpublished data; Fig. 2), Amazon and Atlantic Forest biomes (Rossi Jr. 2007). Considering that free-ranging jaguars frequently kill by biting through the skull between the ears (Schaller & Vasconcelos 1978), the oral evaluation is an important part of their physical examination.

Fig. 3. Blood collection from the femoral vein of a jaguar (Photo Jaguar Conservation Fund/Instituto Onça-Pintada).

Perspectives

The scarcity of indexed information on occurrence of infectious and non infectious diseases in jaguars supports the thesis that investigation of health aspects should be a relevant part of any project directed towards conservation of this endangered species. Available data on the subject is fragmentary, largely consists of case reports and cross-sectional serological surveys, and relied on small samples (Fig. 3). In addition, comparison of results from the existing surveys is difficult as different lab methods have been used and the selection of pathogens was opportunistic, arbitrary or directed by availability of funding and diagnostic tests. Unfortunately, more comprehensive studies and long term studies addressing the occurrence and effects of diseases are still lacking for wild jaguars.

While we consider that all survey designs are important, only detailed long term studies can provide a suitable understanding of the role of diseases in jaguar populations. The best approach would be interdisciplinary, interconnecting population studies with studies on pathogenesis of diseases and identification and characterization of pathogens. To achieve this, systematic data gathering on biological and clinical aspects in different geographical locations and designed for a growing number of pathogens, close monitoring of disease outbreaks and appropriate utilization of diagnostic methods are required. Studies on infectious diseases in free-ranging jaguars should be extended to prey species, livestock, and domestic carnivores. Captive jaguars should also be

Fig. 4. Testing biochemical properties of a captured jaguar's urine in the Pantanal of Mato Grosso do Sul (Photo Jaguar Conservation Fund/Instituto Onça-Pintada).

considered in studies aiming to understand the role of diseases for the species as they represent a valuable potential genetic reservoir for future restocking into nature.

Thus, we consider that not only adequate personnel and laboratorial support should be available to serve this demand, but also that constant funding resources are necessary. Fortunately, cooperation between universities and non governmental institutions has been a fruitful trend in Brazil. A central storage facility for biological material already exists for wild felids in Brazil represented by the National Center for Research and Conservation of Wild Predators (Centro Nacional para Pesquisa e Conservação de Predadores Naturais - CENAP), supported by the government. Non-governmental organizations are unifying their efforts towards conservation of jaguars through partnerships with diagnostic laboratories from universities. The Association Mata Ciliar was one of the institutions that started the systematic work with captive neotropical felids including jaguars, and continues to do so. The role of disease in wild jaguar populations in an ecological context is currently being addressed in various jaguar conservation projects in Brazil. To date, the Jaguar Conservation Fund (JCF) has an ongoing project assessing the health status of free-ranging jaguar populations in three Brazilian biomes: Cerrado, Pantanal and Amazon, through capturing, collecting biological samples (Figs 4 and 5) and radio-collaring jaguars. Samples from cattle and domestic dogs from the same areas are being collected to contrast the results from jaguar samples (Furtado *et al*. 2007). In addition, the JCF is developing a study with jaguar skulls to understand if and how oral injuries compromise the species' predatory behavior. In Southeastern Brazil, the Ecological Research Institute - IPÊ develops an epidemiological project in the Atlantic Forest where jaguars, their prey, and domestic animals are being sampled to study the occurrence of infectious diseases and epidemiological consequences of forest fragmentation (Nava 2008). The Instituto Pró-Carnívoros is initiating a project in the Pantanal to investigate the occurrence of selected infectious agents in free-ranging jaguars.

Conclusion

Although little information is currently available about the impact of diseases on jaguar population, it is broadly accepted that surveillances and monitoring programs are required for an adequate understanding of disease dynamics in wild jaguar. Only such monitoring will provide timely identification of increases in pathogens effects and allow for actions and further analyses to resolve possible outbreaks. Diseases should always be considered as an important factor in conservation biology.

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Fig. 5. Taking a blood sample from a jaguar during capture within a JCF project investigating epidemiology and possible disease transmission between jaguars and domestic livestock (Photo Jaguar Conservation Fund/Instituto Onça-Pintada).

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Studying Jaguars in the Wild: Past Experiences and Future Perspectives

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Jaguars have been studied in the wild since the late 1970's. However, compared with other large cat species, jaguars are still one of the least known. We describe capture methodologies and study methods used in jaguar research, their application, advantages and disadvantages. Over the years, capture methodologies have improved, primarily in relation to safety measures. Telemetry studies are shifting from VHF to GPS systems with the capacity to collect more information on the species. Among non-invasive methodologies, camera trapping is used to study jaguar density and feces collected with the help of detector dogs can provide information on diet, genetics, health and hormonal status. With improving methodologies and more published information about their applicability, studying jaguars in the wild will hopefully become less challenging.

The first scientific-based information on jaguars in the wild came mainly from anecdotal accounts of hunters in the mid-1970's (Guggisberg 1975; Almeida 1976). Soon after, a research project in the Pantanal investigated jaguar predation on capybaras by examining kills (Schaller & Vasconcelos 1977), followed by radio-telemetry investigations of jaguar movement patterns (Schaller & Crawshaw 1980). Since then, different methodologies have been tested for studying the species in the wild. Still, considering its large distribution, and in comparison to other large cats, little information is available on the jaguar. One of the evident explanations for this lack of knowledge is the difficulty associated with studying the species in its natural environment, considering its generally low population density and cryptic habits. Here, we summarize the methodologies in current use and discuss the future trend for jaguar studies in the wild. The authors cumulatively have experience with all methods described here.

Capturing Jaguars

There are three different techniques to capture jaguars in the wild: trained hounds, snares and live traps with bait. While all three methods are associated with some risk, they have different degrees of success, depending on the study area, field effort, climate, and experience of the capture team.

Capturing with trained hounds

Capturing jaguars with trained hounds is currently the most frequently used capture method. It involves releasing between four and 25 trained hounds on fresh jaguar spoor. The hounds follow the jaguar scent, chase the jaguar and force it to either tree or stop on the ground (Rabinowitz 1986; Schaller & Crawshaw 1980; Crawshaw & Quigley 1991; Silveira 2004; Soisalo & Cavalcanti 2006; McBride Jr. & McBride 2007; Azevedo & Murray 2007). Tree climbing when being followed by hounds was observed by the Jaguar Conservation Fund (JCF) in 74.4% of 43 jaguars captured in the Pantanal, Cerrado and Amazon. A short or long-range dart projector is used to dart the animal, preferably at the proximal region of the rear limb. After the jaguar has been darted, the dogs are leashed to reduce stress to the jaguar and allow it to descend from the tree before sedation takes effect. In JCF studies, 18.75% of jaguars that climbed a tree upon being chased by hounds descended from it after being darted. If the jaguar moves off, the hounds are released to lead researchers to the immobilized cat. If the jaguar stays in the tree after being darted, a capture net is set up to avoid traumatic falls and a "bed" of leaves is made below the net to prevent the animal from hitting the ground. However, if the jaguar becomes immobilized in the tree, a team member should be prepared to climb the tree, tie a rope to the animal's chest and lower it to the ground (Fig. 1). This procedure was necessary in 10% of the cases a jaguar was treed in JCF studies.

The use of hounds assures some selectivity in the capture, as the dogs are trained to track only animals previously identified by their tracks. This assures the researchers that jaguars and not pumas (*Puma concolor*) and adults, not cubs, are tracked. It is also an efficient method. Of the 43 successful captures undertaken by the authors, on average the target animal was immobilized after only one hour of tracking, and at a mean distance of 1.8 km from the hounds' release site. However, hounds used to capture jaguars should be experienced, obedient and well trained to chase only the target species. Although efficient, the method does offer some risks to all parties involved. For instance, the falling of an anesthetized jaguar from a tree can result in traumatic injuries of the animal. To avoid this some authors recommend not to dart a jaguar more than 5 meters up in a tree (Deem & Karesh 2005), but the risk of falling even from low or moderate heights still involves

Fig. 1. During captures with hounds, jaguars may become sedated up in the tree they seek refuge in. In these cases it is necessary to lower the animal down with a rope (Photo Jaguar Conservation Fund/Instituto Onça-Pintada).

the possibility of injury or death (McCown 1990; JCF unpublished data). While a capture net placed directly underneath the animal greatly reduces the risk of injuries, people setting the net have to get dangerously close to the jaguar. Also, setting the net may take from 10 to 15 minutes, enough time for the jaguar to jump to another branch or tree. Finally, it is important to consider that hunting of jaguars is prohibited in most of the jaguars' range countries and the contracting of hunters and hounds violates legal and ethical principles. For trained hounds and handlers to be a capturing option, the researcher should either hire experienced staff with hounds from existing scientific research or from countries where hunting is permitted.

Snaring jaguar

Leg-hold snares modified for research have been used to catch various large cats (Logan *et al.* 1999; Goodrich *et al.* 2001; McCarthy *et al.* 2005) A leg-hold snare consists of a ¼ inch thick stainless steel cable forming a loop that will close around the animal's foot when it steps on the trigger. The snare cable is attached to an anchor cable through a swivel that allows the captured animal to rotate freely – this swivel is critical to prevent injury. The snare loop has a one-way lock that prevents the loop from loosening. To avoid injuries, a slide stop has been added to the cable to prevent the loop from closing too tightly and cutting off circulation in the foot. The stop can be adjusted for the target species, allowing smaller non-target species to easily escape. A bungee cord and metal coil spring inserted in parallel in the cable work very well as shock absorbers. Snares can be set along trails, drainages, places where cat spoor are frequently found, or around kills and carcasses which function as bait. The success of the snares can be enhanced with a "caller," an MP3 player, with amplifier and speaker, that is programmed to continuously play recordings that may attract the cats and is hidden between two snares. Setting places should be carefully selected to avoid potential dangers for the trapped animal and the researches later trying to release it (e.g. sharp rocks, steep terrain, flash floods, sites too exposed to the sun, etc; Logan *et al.* 1999; Logan & Sweanor 2001). With snares and callers combined, the WWF AREAS-Amazonia study of jaguars in the Peruvian Amazon caught 17 jaguars in the Amazon of southeastern Peru (Fig. 2). No serious injuries or deaths caused by the snares were observed, only swollen paws and minor cuts. There are several methods that help avoid capturing non-target species. A branch can be placed above the snare to deflect ungulates. The trigger can be supported by either a firm sponge or three short pieces of metal strips from a measuring tape to insure that lighter mammals or birds cannot set it off. Still, snares should not be set at places frequently used by non-target species. One of the most important ways to avoid injuries is to check the traps at an appropriate frequency. Checking snares more than once per day and/or constant monitoring with some kind of device like VHF collars/radio transmitters (Logan, pers comm., Nolan 1984; Halstead 1995) is highly recommended. A further recommendation is to close traps when climate conditions are adverse and might cause hypothermia or overheating to the trapped animal (Powell & Proulx 2005). While there will always be a potential for injury or even death, with proper use, snares have generally proven to be an efficient method to capture large cats.

Live Traps

Cage traps baited with live animals (e.g., domestic pig or sheep) can be placed along natural trails, transect or roads (Rabinowitz 1986; Morato *et al.* 2002; Azevedo & Murray 2007). The trap may or may not allow the animal to have access to the bait. Jaguar trap dimension should be of approximate 0.90m x 0.90m x 2.0m with a strong enough welded wire mesh able to constrain the animal inside until the animal is anesthetized. Traps must be checked at least once per day to guarantee the captured animals' well-being. Also, the bait requires that food and water be regularly replaced. Traps must be set in the shade to avoid exposition of the bait or trapped animal to the sun.

Captured jaguars inside cages can be very aggressive and inflict serious injury to themselves by biting and hitting the cage (Fig. 3). The most common injury is teeth breakage (Rabinowitz 1987). To avoid this risk, traps should not be made with grating, should not allow the animal to get caught in any parts or dispose loose hard pieces that can be bitten or chewed by the cat. If left in the cage to recover after anesthesia, the animal can be aggressive and cause harm to itself, and there should be caution during release as the cat can turn back to a unprotected person instead of fleeing from the scene (Deem & Karesh 2005). Alternatively, the animal can be placed in a quiet, padded and protected area to recover and leave the site. Risks are involved with both recovery situation as even outside of the trap the jaguar can injure itself by falling, banging itself or drowning in a water puddle while not fully recovered. It is important to remember that with this methodology it can take a longer trapping effort to achieve a capture. The method also involves the risks of capturing non-target species. Another limitation to the use of this method is the expense: steel trap costs, along with transportation and operational costs of feeding the live bait and checking the trap, can become very high.

Fig. 2. Jaguar trapped on a snare by its front paw in the Peruvian Amazon (Photo S. Carillo-Percastegui).

GPS (Tracktag) versus VHF telemetry for tracking jaguars

While radiotelemetry is in general an excellent technique for determining jaguar home range size (Fig. 4), habitat use, movement patterns, and other spatial attributes (see Schaller & Crawshaw 1980; Rabinowitz & Nottingham 1986; Crawshaw 1995), its effectiveness in dense habitat such as the Amazon forest may be limited. The dense canopy of tropical forests reduces the range of radio signals to a few kilometers at best and ground accessibility is usually limited. The only viable large scale monitoring alternative is the use of small fixed-winged aircraft. This approach is limited to diurnal monitoring and tends to be very expensive. Additional problems associated with radiotelemetry are triangulation errors caused by low accuracy of the reading, bouncing signals or moving animals, as well as a bias of collected data towards more accessible areas. There is also a trade-off between the number of locations that can be collected for each individual and the number of individuals that can be monitored. Therefore, GPS collars have become popular for studying large cats (Anderson & Lindzey 2003; Hemson *et al.* 2005, McCarthy *et al.* 2005) and have been employed successfully in jaguar studies in the Atlantic Forest (Cullen *et al.* 2005; Cullen 2006), Pantanal (Soisalo & Cavalcanti 2006) and the Paraguayan Chaco (McBride & McBride 2007).

In late 2007, the World Wildlife Fund - US fitted four jaguars in the Amazon of southeastern Peru, with a new type of GPS system called TrackTag (NAVSYS Limited, West Lothian, UK). The TrackTag is an archival GPS unit with a capacity to store up to 30,000 locations in its on-board memory, adapted to fit on a VHF radio-collar. The tag has very low power requirements and its own light-weight energy source. Currently the tag must be retrieved and connected to a computer for data downloading and processing. However, the unit is currently being redesigned to include remote downloading capacity. Like other GPS collars, the unit can be set to collect locations at determined time intervals and can also be equipped with a timed drop-off mechanism. To date, the authors have recovered and processed five collars. Those collars recorded between 662 and 4,250 locations during 3.8 to 7 months that they collected data. This is between 10 to 100 times more data than would typically be collected from a VHF-based study. Cullen (2006) reported five to 15 times more data collected with regular GPS than with VHF collars, depending on density of forest cover.

Although the initial costs of the GPS collars were ten times the cost of a typical VHF collar, the quantity and quality of data collected far outweighs the added cost of purchase as they are more precise and unbiased by time of day or ease of access. While VHF collars are still useful for some studies where infrequent locations are needed, such as monitoring problem cats or reintroduced or translocated individuals, most

Fig. 3. Jaguar captured in Emas National Park, central Brazil with a cage trap baited with a live pig. Note that the cage is not properly designed. The jaguar should not have access to the cage bars as they may allow the animal to bite and injure itself. A metal mesh over the bars is recommended to prevent injuries (Photo Jaguar Conservation Fund/Instituto Onça-Pintada).

studies interested in collecting detailed data on the ecology of jaguars should probably consider using GPS collars. For relatively open areas a large number of different models are currently available; from simple store-on-board units, to units that automatically transmit data through a satellite or cell phone connection. For densely forested areas the TrackTags are a viable GPS option, and new more sensitive designs are currently being tested.

Camera traps for estimating jaguar density

Camera trapping to estimate large felid density was initially developed for tigers (Karanth 1995, Karanth & Nichols 1998), but was soon adopted for jaguar studies (Wallace *et al*. 2003), and has since been implemented throughout the species' range (Maffei *et al*. 2004; Silveira 2004, Silver *et al*. 2004, Cullen *et al*. 2005, Soisalo & Cavalcanti 2006, Salom-Perez *et al*. 2007). Camera trapping takes advantage of the unique spot (or stripe) pattern on each cat that permits individual identification of registered animals (Fig. 4). The information on photographic captures and recaptures of the different individuals can be analyzed with capture-recapture models to estimate abundance, which can be translated into a density estimate, dividing abundance by the sampled area. The study design has to consider two model assumptions: 1) All animals within the sampled area have a capture probability larger than 0, thus, cameras must be placed so that there are no internal gaps that could contain an individual's entire home range; and 2) The population under study is closed, i.e. during sampling, no losses or recruitments occur, so a maximum sampling period of two to three months is recommended (Silver 2004). When calculating the sampled area, a buffer around the outer camera trap polygon has to be considered, as portions of the home ranges of registered animals will be located outside of this polygon (Karanth & Nichols 1998). Estimates of buffer width can be obtained in various ways, and as density estimates are sensitive to buffer width, this is subject of ongoing discussion (e.g. Soisalo & Cavalcanti 2006).

Jaguars occur at low densities and consequently, large areas (several hundred km²) have to be sampled with a large number of camera traps (from 25 upwards) to guarantee sufficient data, both in number of individuals captured and in number of recaptures (Karanth & Nichols 2002), making these studies quite expensive (Maffei *et al*. 2004, Soisalo & Cavalcanti 2006) and work intensive. In tropical, open-habitat study areas, camera traps with passive heat-in-motion sensors are likely to be triggered frequently by direct sunlight or even daytime heat. Depending on the model, camera traps can produce more than 50% of pictures of hot air. This increases material costs and creates the need to check cameras more frequently to avoid sampling gaps. Due to financial and logistic constraints, under these conditions researchers may have to confine sampling to night time hours.

Even when functioning properly, only a small fraction of pictures will be of the target species, between 5% and 25% depending on study area, with success rates of two to four jaguar registers per 100 trap nights. To optimize success, traps need to be set at locations with a high probability of jaguar movement, such as roads or trails (Silver *et al*. 2004). This can conflict with the need to cover the entire sampled area without internal gaps, in which case additional trails may have to be opened. Depending on their accessibility, these trails increase time spent checking traps disproportionately. While Silver *et al*. (2004) found manmade trails to work well, the Jaguar Consrevation Fund observed low to no jaguar camera trapping success on such trails (JCF, unpublished data). Salom-Perez *et al*. (2007) suggested that differences in use of manmade trails existed between the sexes due to females being more timid. Several studies report a sex ratio of detected animals skewed towards males (Wallace *et al*. 2003; Silver *et al*. 2004; Salom-Perez *et al*. 2007), owing to the females' smaller home ranges and less movement, rather than an actual skewed sex ratio in the population.

Still, the advantages outweigh the drawbacks: Camera traps are non-invasive, can sample large areas continuously, and collect enough data for a reasonable density estimate within two to three months. Some of the drawbacks mentioned can be compensated, at least partially, with site specific sampling designs and choice of the right equipment. In terms of data analysis, capture-recapture models provide a sound statistical basis for density estimation, and data can also be used to investigate jaguar activity pattern and spatial distribution. Recently developed spatially explicit capture-recapture models that estimate density directly without the need to determine the size of the sampled area

(Borchers & Efford 2008) hold the potential for more flexible sampling designs and more accurate density estimates. Furthermore, with constant advances in the field of digital photography, a robust, battery-economic digital camera trap should not be too far away.

Using Scat Detector Dogs to Study and Monitor Jaguars

The use of scat-detection dogs is increasingly recognized as a valuable wildlife assessment and monitoring tool (Long *et al*. 2007a). Chosen for their drive for play-reward with a tennis ball, these dogs enable researchers to seek out scat samples of rare and otherwise difficult-to-study species (Fig. 5). The dogs are able to cover large areas, are non-biased in their sampling of gender, and have demonstrated accuracy in their ability to hone in on their targets while ignoring non-target species (Smith *et al*. 2003). In comparison with camera traps and hair snag survey methods, detection dogs have demonstrated superior effectiveness at locating species presence as well as number of individuals (Wasser *et al*. 2004; Harrison 2006; Long *et al*. 2007b). Scat samples can be used to understand wildlife movement, for diet and disease studies, as well as for DNA and hormone analyses (Wasser *et al*. 2004).

Scat detector dogs offer a valuable tool for non-invasive study of jaguar. In a study by at Emas National Park (ENP) and surroundings in central Brazil (Vynne *et al.* 2007), scat dog teams were employed over 12 months between 2004 and 2008 for a five species survey including jaguars. Of all putative jaguar samples (n=49), 80% were found off of roads or major trails, and thus would not have been encountered by human search teams alone. We found evidence of jaguar using open, grassland-dominant habitats bordering the agricultural matrix where jaguar had not previously been recorded.

While scat dogs may be the most effective survey method available for detecting presence of elusive species, the required field time is extensive as compared to other methods (Harrison 2006). This is likely to be even more exaggerated for the very wide-ranging jaguars. In the ENP study, we spent approximately 22 hours in the field for every putative jaguar scat encountered.

Fig. 4. Male radio-collared jaguar passing a camera trap station in Emas National Park, central Brazil (Photo Jaguar Conservation Fund/Instituto Onça-Pintada).

When jaguars are targeted as the focal species or sampling is restricted to known jaguar niche habitat, detection rates are expected to climb. For example, 90% (n=44 of 49) of the samples were found within the jaguar niche, realized by Silveira (2004) during a radio-collaring study. If we consider only survey days spent in the defined niche, we had an 88% probability of detecting a jaguar on a given field day. Studies in Cantão State Park (Amazon-Cerrado ecotone) and on a private reserve in the Pantanal, where jaguar densities are much higher and where dogs were trained only on jaguar and puma resulted in a much lower search time of about 1.3 hrs per putative large cat scat (Almeida *et al*. 2008).

Well-trained scat dog teams have a demonstrated high accuracy of honing in on target species from 93% to 100% (Smith *et al*. 2003; Vynne, unpublished data; Wasser *et al*., unpublished data). However, inexperienced handlers may inadvertently train dogs onto non-target species by misidentifying scat samples in the field and/or rewarding errantly interpreted dog search behavior. In our study, two experienced dog-handler teams had an 81% accuracy rate of collection for jaguar and puma scats, while a new handler-dog team collected 50% as non-target species. This can introduce significant costs in laboratory analyses or bias in cases where genetic confirmation is not being done prior to analysis. Thus, only experienced dog teams should be considered for use on a study (Long *et al*. 2007).

Another consideration of the method should be the objectives for the study. As jaguars cover extensive areas and have low defecation rates, we cannot expect to get detailed movement information. When physiological, genetic, presence/absence, disease and parasite, or diet information is warranted, however, scat samples will provide the most effective means of gathering this health panel of information. However, for some laboratory analyses, samples have to be reasonably fresh. In general, study design is crucial for effective sampling and professional outfits can provide advice for effective study design.

Conclusion

The choice of any methodology for studying jaguars depends on the purpose of the study, site location and the research team's experience and available resources. While jaguar capture is still the most reliable methodology for biological sample collection and necessary for telemetry studies, due to the risks involved in these procedures researchers tend to substitute them for non-invasive methodologies. Information of species-specific capture accidents and fatalities need to be published so that future captures do not repeat past mistakes. Camera traps and especially GPS col-

Fig. 5. Author Carly Vynne with scat detector dog surveying for jaguar scats in the surroundings of Emas National Park, central Brazil (Photo M. Baker).

lars are still relatively young technologies that continue to be improved and adapted to particular field situations, as demonstrated by the TrackTag collars used in the Amazon. Likewise, training of detector dogs is becoming more sophisticated allowing even identification of individuals from scats (Kerley & Salkina 2007). Until the last decade, the jaguar was the second least studied large cat in the world. With improving technology and analytical methods, the upwards trend in jaguar research stands a good chance to continue.

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