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Human-jaguar conflicts and the relative importance of retaliatory killing and hunting for jaguar (*Panthera onca*) populations in Venezuela

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ABSTRACT

Retaliatory killing of large carnivores in response to their attacks on cattle is recognised as one of the most important factors causing worldwide declines of large carnivores. Conversely, hunting is believed to have been largely eliminated due to national and international protection measures. We studied the prevalence of human-jaguar conflict and the relative importance of retaliatory killing and hunting for jaguar populations in Venezuela by means of field interviews with hunters and ranchers. To predict the spatial distribution of retaliatory killing or hunting we fit a linear regression model. We registered 387 jaguar attacks on livestock and 22 attacks on humans. Subsistence/commercial hunting appeared the most common cause of human-caused jaguar mortality (52%) and retaliatory killing was less common (38%). Jaguars were also killed because of public fear, attacks on pets, by trophy hunters, and in car accidents. Public motivations to kill jaguars did not change through time, suggesting that the protection system introduced in 1996 has not been effective. Methods and tools used in retaliatory killing were different, more sophisticated, and probably more efficient than those used in hunting. However, products collected from harvested jaguars did not differ between motivation groups and included skins, canines, skulls, meat, fat, and cubs. Our model indicated that subsistence/commercial hunting is prevalent over most of the areas still inhabited by jaguars. On the contrary, retaliatory killing was mostly predicted for the areas where jaguars have already gone extinct, suggesting that it is an important driving factor of jaguar extirpations.

1. Introduction

Large carnivores often kill livestock and in some circumstances they can attack humans, both leading to human–carnivore conflict. These conflicts are widespread and are regarded as one of the main causes of the worldwide decline of large carnivore populations (Treves and Karanth, 2003; Ripple et al., 2014). The jaguar (*Panthera onca*) is the third largest felid species in the world, after lion (*Panthera leo*) and tiger (*Panthera tigris*). In contrast to its two larger cousins, jaguars attack humans very rarely, however their attacks on cattle are common and cause frequent retaliatory killing of jaguars (Hoogesteijn et al., 1993, 2011, 2014; Packer et al., 2005; Gurung et al., 2008; Neto et al., 2011).

Commercial and subsistence hunting may also contribute to the declines of large carnivores. From 1950 through the 1970s, in response to the fashion industry's demand for the skins of felids, intensive hunting for jaguars took place throughout all of South and Central America. This prolonged intensive hunting has been regarded as one of the main factors responsible for a 50% decline of jaguar range in the 20th century (Fitzgerald, 1989; Swank and Teer, 1989; Sanderson et al., 2002; Payán and Trujillo, 2006). International campaigns against hunting and the introduction of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 1975 resulted in the legal protection of jaguars in several countries, and it was believed that jaguar hunting was stopped or largely reduced

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(Nowell and Jackson, 1996; Cavalcanti et al., 2010; de Oliveira et al., 2012). However, some studies have indicated that jaguar hunting unrelated to livestock depredation still exists and may affect jaguar populations even inside protected areas (Carvalho and Pezzuti, 2010; Garcia-Alaniz et al., 2010; de Carvalho Jr and Gonçalves-Morato, 2013). Further research into the motivation, magnitude, and relative importance of various reasons for hunting jaguars is needed (Desbiez and de Paula, 2012).

Retaliatory killing aims to eliminate a predator of livestock, while hunting has a goal of obtaining various products or benefits from killing an animal. Hunting can be categorized as commercial, subsistence, or sport/trophy hunting but the first two categories possibly overlap widely and are difficult to separate (Redford and Robinson, 1991; Corlett, 2007; Sánchez-Mercado et al., 2016). It has been suggested that retaliatory killing may seriously affect populations of large carnivores (Hoogesteijn et al., 1993, 2002). Unregulated hunting may also have a negative effect on densities of many wildlife species in tropical ecosystems (Madhusudan and Karanth, 2002; Peres and Palacios, 2007) and may affect demography and population dynamics of large carnivores (Newby et al., 2013). However, it is not clear which of these two impacts is more detrimental to large carnivore populations. Based on our current knowledge it could be hypothesised that subsistence/commercial hunting for jaguars, if it still exists, should be rather restricted to large forested and low human populated areas, where legal control is more difficult. On the contrary, retaliatory killing should be limited to cattle breeding areas and there should be no or little spatial overlap between retaliatory killing and hunting. Techniques used in hunting and retaliatory killing, their efficiency and consequent impacts on jaguar populations are poorly studied. Swanepoel et al. (2015) have demonstrated that retaliatory killing of leopards in South Africa was characterized by a constantly higher kill rate and had more severe demographic consequences for leopard populations than recreational sport hunting. However, the impact of subsistence/commercial hunting can be different than sport hunting, because it can be more frequent and more widespread. The efficiency of hunting can also depend on techniques used by hunters. Some techniques, like the use of guns and dogs can have a very heavy impact on hunted animal populations and increased access to modern techniques by local people generally leads to increased hunting pressure on wildlife (Robinson and Redford, 1991; Koster, 2008).

In this paper we analysed a large set of data on human-jaguar conflicts and human caused mortality of jaguars, collected across Venezuela. First, we wanted to test if human-jaguar conflict was actually the main reason of jaguar killing, as was supposed by various studies. Further, we wanted to identify actual motivations of jaguar killing and estimate their relative importance and prevalence. We also aimed to compare methods and tools used in subsistence/commercial hunting and retaliatory killing to infer their potential efficiency and impact on jaguar populations. We fit a regression model to predict the spatial patterns in relative frequency of retaliatory killing and subsistence/commercial hunting using anthropic and environmental factors as predictive variables. Finally, we compared the spatial predictions of this model with the current range of the jaguar in Venezuela to infer the role of each of these impacts in jaguar extirpations.

2. Methods

2.1. Study area

Venezuela occupies an area of 916,445 km^2 and has a population of 28.9 million people (INE, 2011), most living in cities in the north. Approximately 725 thousand indigenous people live in Venezuela, however, only 270 thousand of them inhabit rural areas of the country, mostly in Amazonas, Bolivar, Zulia, and Delta Amacuro states (INE, 2011). Large-scale habitat transformations have occurred mainly north of the Orinoco River, while the south has retained more pristine habitats (Rodríguez, 2000; Huber and Oliveira-Miranda, 2010). According to data of the Venezuelan Ministry of Agriculture and Land there were about 12.7 million of cattle, 2.8 million of pigs, 1.1 million of goats, 0.6 million of sheep, 0.2 million of buffalos, and 0.2 million of horses registered in Venezuela in 2008 (MAT, 2010).

At an international scale, the jaguar is classified as 'Near Threatened' and in Venezuela as 'Vulnerable' (Caso et al., 2008; Jedrzejewski et al., 2015). Jaguars have been officially protected in Venezuela since 1996 (Venezuela, 1996a, 1996b), but habitat alterations, poaching and retaliatory killing due to conflicts with cattle breeding continue to affect the species (Hoogesteijn et al., 1993, 2002; Jędrzejewski et al., 2011; Jędrzejewski et al., 2017).

2.2. Data acquisition

Between 2009 and 2015, we conducted field interviews in rural localities across Venezuela to collect data on human-jaguar conflicts and human caused mortality of jaguars. We intended to cover the whole territory of the country, however, our possibilities of visiting the most distant areas, especially in the Amazonas state, were limited. We interviewed hunters (41%), ranchers (31%), and other local residents (28%) who were likely to have had direct contact with jaguars. Our interviews had qualitative and semi-structured character, with a set of standard guiding questions (Edwards and Holland, 2013). Through them, we attempted to document reliable records of jaguar attacks on humans and attacks on livestock as well as records of jaguar mortality, including all types of hunting, highway mortalities, and jaguars found dead due to natural causes. We also recorded any other reliable information concerning jaguar presence, including direct observations, prey remains, fresh tracks, etc. Exact location, date, and the detailed description of each reported case were noted. In the case of livestock depredation we noted the numbers and species of animals killed by jaguars. In the case of jaguar mortalities we asked about the motivations/reasons to kill them, techniques and tools used for hunting, and products obtained and utilized from the harvested animals. We did not ask purposely if the products were sold and about the amount of income obtained to avoid potential bias in answering other questions (Solomon et al., 2007). However, the interviewed persons often provided this information themselves (15% of cases when a jaguar was killed). All the interviewed persons were informed about the scientific and conservation goals of our survey. Interviews that we considered unreliable (inconsistencies between provided information, weakness of provided evidence on identification of carnivore species, e.g. only records of tracks or attacks on medium livestock only) or that were missing year or exact location were discarded. More details on the process of collecting and validating our interview data are provided in Jędrzejewski et al. (2017).

2.3. Data analysis

We categorized jaguar mortality in the two main groups: retaliatory killing and subsistence/commercial hunting. The term "subsistence/commercial hunting" here refers to hunts oriented to receive products or benefits from harvested animals and not related to cattle depredation. Distinguishing between subsistence and commercial hunting was impossible, because sale of products from the harvested animal was mostly opportunistic (Sánchez-Mercado et al., 2016). We distinguished also a category "others" that included other motives, less often mentioned in the interviews. This category included: sport hunting (i.e. for trophies), attacks on people, fear of jaguars, killing hunting and domestic dogs, killing jaguars during on-going deforestations. To determine if retaliatory killing and subsistence/commercial hunting differed in respect to their potential impact on jaguar populations we compared hunting techniques, tools used for hunting, and obtained products between these two harvest categories. To see if there were any temporal changes in prevalence, incidence or motivations of killing

Table 1
Human caused mortality of jaguars and motivations of hunters to kill a jaguar, expressed as percentages of all cases when it was possible to determine motivation to kill a jaguar or reason of its death. Two periods distinguished: 1940–2000 (no protection period) and 2001–2014 (full legal protection period). Differences between the two distinguished periods were tested with the two sample *t*-test between percentages ($^{**}p < 0.01$).

Years	Hunting for subsistence or for income			Total subsistence/ commercial hunting %	Sport hunting %	Livestock depredation %	Attacks on dogs %	Fear or attacks on people[a] %	Deforestation %	Killed by car on a road %	*N* records with determined motivation or reason of jaguar death	*N* records when motivation was not determined	*N* total
	Targeted hunting for jaguar %	Chance encounter during a hunt for other game species %	During a hunt, not specified better %										
1940–2000	3,2	20,4	27,1	50,7	1,8	40,3	2,3	4,5	0,0	**0,5**	221	11	232
2001–2014	7,3	8,3	36,9	52,5	0,3	37,2	1,3	3,0	1,7	**4,0****	301	6	307
All years	5,6	13,4	32,8	51,7	1,0	38,5	1,7	3,6	1,0	2,5	522	17	539

[a] Included 5 cases of retaliatory killing of jaguars because of attacks on humans and 14 cases of fear as motivation to kill a jaguar.

jaguars we compared data between two periods: 1940–2000 and 2001–2015. We selected this time division as it roughly corresponds to the end of the period of large scale habitat changes (i.e. deforestations, Pacheco et al., 2011), and to non-protection vs. protection periods (jaguar protection in Venezuela was introduced in 1996 and we assumed that it took four years to implement). We used a two sample *t*-test between percentages to test for differences between hunting motivations or time periods.

To evaluate the spatial pattern in the relative importance of retaliatory killing and subsistence/commercial hunting we fit a multiple regression model to our data. For this analysis, we limited mortality data to the period 2001–2015, because large scale deforestation conducted before 2001 (Pacheco et al., 2011) could have an impact on human-jaguar conflicts. To have a measure of the prevalence of retaliatory killing compared to hunting at any locality, we assigned 0 to the records of hunted jaguars and 1 to jaguars killed in retaliation. Then, we used the kriging function of ArcGis (ESRI Redlands CA, USA), to calculate an interpolated value for each point based on the value at that location and 5 other nearest neighbour points. Kriging is a geostatistical method that has been widely used to interpolate spatial data in animal distribution studies (e.g. Monestiez et al., 2006; Hengl et al., 2009; Nazeri et al., 2015). In this technique, the interpolated value depends upon the distance between data points and the values predicted by a semivariogram model reflecting general spatial autocorrelation of the data (Fortin et al., 2002). This way, for each data point we obtained a "retaliation/hunting" index that reflected the ratio of records of jaguars killed in retaliation to records of hunted jaguars. This index could have any value between zero and one, zero when all local points represented hunted jaguars; one when all local points represented jaguars killed in retaliation. We treated this index as a dependent variable and fitted a set of multiple regression models to it based on four candidate predictive variables that potentially could have an impact on human-jaguar conflicts (Supplementary materials, Table A1). These variables included: (1) forest cover as we assumed that in the forested areas hunting should be more common, (2) cattle density which should be correlated with retaliatory killing, (3) human population density that should be related with human-jaguar conflicts in general, (4) a code indicating if an area was legally protected (value 1) or not protected (value 0). We standardized all raster data to a 1 km × 1 km pixel size. We applied a log-transformation to human population density, which had considerable skew (Quinn and Keough, 2002). We selected the best model based on the Akaike Information Criterion (AIC, Akaike, 1973, Burnham and Anderson, 2002), and we considered only the models with all regression coefficients significantly different from zero. To check if the regression coefficients of the best models were robust, we used bootstrap resampling with 5000 replications and calculated bias values of the estimates. We tested standard regression assumptions of the best model by examining residual plots (plots of the standardized residuals as a function of standardized predicted values), histograms, and normal probability plots (Tabachnick and Fidell, 1983). We projected the best model across the whole of Venezuela and overlaid it with the current jaguar range in the country (Jędrzejewski et al., 2017). In addition to the regression analysis, we calculated spatial correlations between various categories of jaguar records (e.g. retaliatory killing, hunting, livestock depredation, etc.). For this, we divided the area of Venezuela into a grid of approximately 150 km by 150 km cells. For each cell we calculated the number of jaguar records of each category and divided it by the final cell size to obtain a standardized number of records. Then we computed Pearson correlation coefficients between the numbers of jaguar records of different types to check for spatial relationships. All spatial analysis was conducted using ArcGIS 10.1 (ESRI Redlands CA, USA). All of the statistical analyses were performed with SYSTAT 13.0 (Systat Software, Inc., San Jose, CA, USA) and SPSS ver. 20 (IBM SPSS Statistics).

3. Results

3.1. Jaguar-human conflicts

We interviewed 485 hunters, ranchers, and other local people across Venezuela and collected 923 jaguar records from the period 1940–2015. Among them there were 22 reliable reports of jaguar attacks on humans that included 4 cases when a person was killed. At least 7 of these attacks were provoked by hunters trying to kill a jaguar.

There were 387 records of jaguar attacks on livestock. Depredation cases included attacks on cattle (79% of depredation records), horses (12%), pigs (11%), donkeys (9%), mules (3%), sheep (4%), and goats (1%). In 37 cases also dogs (mostly hunting dogs) were killed.

3.2. Jaguar mortality

3.2.1. Reasons and motivations to kill jaguars

Our data included information on 381 live jaguars and 539 jaguars killed by humans. Among human killed jaguars, we could determine the cause of death or motivation of killing in 522 cases (Table 1). Subsistence/commercial hunting was the most frequent reason for human caused jaguar mortality (51.7%) and was followed by retaliation to livestock depredation (38.5%). However, this second group included also cases of preventive killing of jaguars (when jaguars were only detected inside a ranch, without killing livestock). Fear of jaguars, attacks on dogs (usually hunting dogs), sport hunting for trophies, and killing by loggers during on-going deforestations were declared as other reasons to kill jaguars. Thirteen jaguars (2.5%) were killed unintentionally in accidents with cars (Table 1).

In the group of jaguars killed in subsistence/commercial hunting, most were killed in a chance encounter during a hunt for other game

Table 2
Comparison of hunting methods used in three groups of jaguar hunting distinguished by declared motivations to kill a jaguar. Percentages of hunting methods used in each group of hunting were calculated based on number of hunts with determined methods. Differences between subsistence/commercial hunting and retaliatory killing were tested with the two sample *t*-test between percentages (***$p < 0.001$, *$p < 0.05$).

Hunting motive	Waiting hidden[a]				Active searching/chasing			Walk-and-seek-chance encounter		Trapping				Poisoning %	*N* records with determined methods	*N* records with undetermined methods	*N* total
	At the jaguar prey carcass %	At a live bait[b] %	On a trail %	Imitating jaguar roaring[c] %	Following tracks, near prey %	Using dogs %	Using horses and lasso %	On foot %	From a boat %	Cage trap %	Gun-trap %	Hole trap – excavated %	Cubs trapped[d] %				
Subsistence/commercial hunting	0,0	4,4	5,3	5,3	0,0	7,1	0,9	55,8	15,9	0,0	0,9	0,0	4,4	0,0	113	157	270
Retaliatory killing	28,7***	6,9	0,0*	3,0	5,0*	31,7***	2,0	4,0***	0,0***	12,9***	0,0	1,0	1,0	4,0*	101	100	201
Other (sport, fear, attacks on people, attacks on dogs, deforestation)	16,7	11,1	0,0	16,7	0,0	33,3	0,0	11,1	5,6	0,0	5,6	0,0	0,0	0,0	18	20	38
Total	13,8	6,0	2,6	5,2	2,2	19,8	1,3	29,7	8,2	5,6	0,9	0,4	2,6	1,7	232	277	509

[a] On the ground or in the tree.
[b] Mentioned: calves, cows, horses, pigs, goats, dogs.
[c] From the boat or from the tree, using an empty bucket or shells of tapara fruits.
[d] Cubs trapped in dens or after killing mother.

species or presumably in opportunistic hunts for any game species. However, in at least 29 cases jaguars were killed during an intentional hunt for this species (Table 1).

There was little statistical difference, concerning the reasons of jaguar killing between older (1940–2000) and recent (2001–2015) subsets of data. Only road mortality of jaguars statistically increased in recent years (Table 1).

3.2.2. Methods and tools used to hunt and kill jaguars

We obtained hunting method for 232 jaguar hunts (Table 2). The highest proportion of jaguars was killed in chance encounters while walking or moving by boat with a gun or (occasionally) spear and seeking other game animals (37.9% in total). Active searching and chasing with dogs was the second most common technique (19.8%). Waiting hidden, either near a carcass (remains of livestock killed by jaguar) or near a live bait (a calf, adult cow, pig, goat or dog), was another common method (19.8%). Fairly common was hunting by calling a jaguar with an imitation of roaring, performed by the hunter with the help of empty taparo fruit shells (*Crescentia cujete*) or with the hunter's head inside of a plastic bucket (5.2%). Metal cage traps, baited with pigs, goats, calves or dogs were also used. Other less common methods were gun traps installed at a prey carcass, putting poison at a carcass, chasing with horses and catching with lasso (Table 2), the latter recorded in open savannahs in Guárico and Apure states. Cubs were usually physically captured by hand after killing their mother or excavating them from a den.

For 307 records it was possible to determine the tools used in jaguar hunts (Table 3). Guns were used in 86.3% of hunts and dogs in 24.4% (Photo B1). A fairly common tool used mostly in Orinoco Delta by Warao indigenous people were spears (4.2%, Photo B2). Various types of traps were used, with cage traps baited with live animals being most common (13 cases, Photo B3). Poison was declared to be used in four cases. Some of the recorded hunts concerned killing a swimming jaguar from a boat. In those cases the hunters used other, simple tools like machetes, axes or paddles (Table 3).

Methods and tools used for retaliatory killing were statistically different from those used in subsistence/commercial hunting (Tables 2 and 3). In retaliatory killing, searching and chasing with dogs, waiting at prey carcass as well as using traps and poison was more common, while walking or boating and seeking or waiting on animal trails was more frequent in subsistence/commercial hunts. We recorded twelve cases of retaliatory killing when the ranchers hired and paid a specialised hunter, called in Venezuela a "tigrero" or "mata tigre" to kill a jaguar (these cases involved four different hunters). However, also among regular forest hunters we met four persons who specialised in killing jaguars for selling skins and other products.

3.2.3. Collecting products from hunted jaguars

For 195 cases we obtained information on the products collected from a jaguar and sold or utilized by hunters and their families (Table 4). These included skin, canines, skull, or claws (90.2%, Photos B4, B5), meat for own consumption or sale (17%), fat for medicines or (occasionally) for magic purposes (10.3%, Photo B6), jaguar cubs to be sold as pets (6.3%, Photo B7). Only one person admitted that the jaguar carcass was discarded and no products were collected. Interestingly, there were no statistical differences between different motivation groups in respect to products collected (Table 4).

3.2.4. Spatial distribution of human-jaguar conflict and jaguar hunting

The distribution of records of jaguars killed in retaliation was moderately correlated with the distribution of depredation records ($r = 0.46$), both occurring mostly in the northern, and especially in the north-western part of Venezuela (Fig. 1). Records of jaguars hunted in subsistence/commercial hunts were distributed more evenly across the country (Fig. 1). The distribution of hunted jaguars was highly correlated ($r = 0.78$) with the distribution of life jaguar records not

Table 3
Comparison of tools used in three groups of jaguar hunting distinguished by declared motivations to kill a jaguar. Differences between subsistence/commercial hunting and retaliatory killing were tested with the two sample *t*-test between percentages (***$p < 0.001$, *$p < 0.05$).

Hunting motive	Guns %	Dogs %	Spear %	Lasso %	Traps[a] %	Poison %	Other %	*N* total hunts with determined tools	*N* hunts with undetermined tools	*N* total hunts recorded
Subsistence/commercial hunting	88,0	**17,7**	**5,7**	0,6	**0,6**	**0,0**	**7,0**	158	112	270
Retaliatory killing	84,0	**30,4***	**0,8***	1,6	**11,2*****	**3,2***	**0,8***	125	76	201
Other (sport, fear, attacks on people, attacks on dogs, deforestation)	83,3	37,5	12,5	0,0	4,2	0,0	4,2	24	14	38
Total	86,3	24,4	4,2	1,0	5,2	1,3	4,2	307	202	509

[a] 13 cage traps, 2 gun traps, 1 excavated hole trap.

related to cattle depredation (observations, tracks, etc.). Retaliatory killing and hunting co-occurred in the northern part of the country, although at the a national scale the spatial correlation between them was only 0.30 (Fig. 1).

The best model explaining spatial variation in the retaliation/hunting index included all four candidate predictive variables (Table 5). This model predicted high values of this index, i.e. the prevalence of retaliatory killing, at high cattle and human population densities and low forest cover (Table 6). On the contrary, low values of the retaliation/hunting index, thus prevalence of subsistence/commercial hunting, were predicted at high forest cover and low human and cattle densities. Legal protection of an area had a negative effect on the predicted values of the index, meaning that inside the protected areas hunting was more likely to occur than retaliatory killing (Table 6). Spatial prediction of this model (Fig. 2) showed that subsistence/commercial hunting was prevailing in most of the current jaguar range (85% of its area), while retaliatory killing was dominant on a fairly small fraction of jaguar range (2%). Conditions promoting prevalence of retaliatory killing were found in Venezuela mostly outside current jaguar range, on areas where jaguars had already been extirpated. Our model predicted that both retaliatory killing and hunting co-occurred in equal proportions on 13% of current jaguar range and on extensive areas outside of this range (Fig. 2).

4. Discussion

4.1. Motivations and reasons of jaguar hunting

Contrary to assumptions by several authors that jaguar hunting has been largely stopped (e.g. Cavalcanti et al., 2010; de Oliveira et al., 2012), our results suggest that hunting for subsistence or for commercial purposes is still the most common motivation for human caused jaguar mortality in Venezuela. Although other studies have indicated that jaguar hunting may still occur (e.g. Zeller, 2007; de Carvalho Jr and Gonçalves-Morato, 2013) the incidence, prevalence, and widespread nature of this were unexpected. Despite legal protection of jaguars, hunting is widespread, it occurs everywhere where jaguars still exist, and is not limited to large forest tracts. Jaguars were hunted mostly during regular hunts for other game species and in the majority of cases with the same methods as other game species.

There have been very few studies examining human motivations to kill jaguars. Moreno et al. (2015) demonstrated, that in Panama, retaliatory killing was responsible for 98% of human caused mortalities and only 2% of jaguars were killed for other reasons, like fear or commercial hunting. In our study, retaliatory killing was the second most important reason of jaguar deaths. Marchini and MacDonald (2012) pointed to fear as an important motivation to kill jaguars in Brazil. It is possible there is some variation between countries and localities depending on local traditions, beliefs, and differences in law enforcement. In Venezuela, fear of jaguars was a less important factor. Interestingly, sport hunting for trophies, which is often mentioned in the jaguar literature (e.g. Zeller, 2007) was of marginal importance in Venezuela. Other motivations, like killing dogs (mostly hunting dogs) by jaguars and killing jaguars by loggers during on-going deforestation were less often encountered in our interviews. Road mortality of jaguars seems to be a growing problem and obviously it has increased during the last fifteen years. Jaguars killed on roads have been reported also in other countries (e.g. Srbek-Araujo et al., 2015). Motivations to kill jaguars are probably partially overlapping. Regardless of which motivation was declared, the frequency of collecting various products, especially pelts and canines, was very similar. This likely indicates, that a prevailing market for jaguar pelts and canines provides additional stimulus to ranchers to kill jaguars that attack cattle.

4.2. Human-jaguar conflict

Lions, tigers, and leopards often attack both livestock and humans and this behaviour creates a strong human–carnivore conflict resulting in fear and frequent retaliatory killing of these felids (Packer et al., 2005; Johnson et al., 2006; Inskip and Zimmermann, 2009; Athreya et al., 2011). In contrast, our and other studies show that jaguar attacks on humans are very rare and mostly provoked by humans (Neto et al., 2011; Hoogesteijn et al., 2011, 2014; Iserson and Francis, 2015). Thus, there is an important difference between human's attitude to jaguars and to other large felids. Our data indicate that jaguars are primarily perceived as game species, which can be hunted for various benefits, and are additionally killed to protect livestock from depredation. This distinction may have implications for jaguar conservation strategies.

Table 4
Comparison of products collected from harvested jaguars between the three classes related to hunting motivations. Two sample *t*-test between percentages was calculated to check statistical significance of differences between motivation groups. No statistical differences were detected.

Hunting motive	Skin, fangs, skull, claws %	Meat %	Fat %	Cubs %	Carcass discarded %	*N* hunts with determined carcass use	*N* hunts with undetermined carcass use	*N* total
Subsistence/commercial hunting	88,4	15,6	12,2	8,8	0,0	147	123	270
Retaliatory killing	93,2	22,0	3,4	1,7	1,7	59	142	201
Other (sport, fear, attacks on people, attacks on dogs, deforestation)	94,4	11,1	16,7	0,0	0,0	18	20	38
Total	90,2	17,0	10,3	6,3	0,4	224	285	509

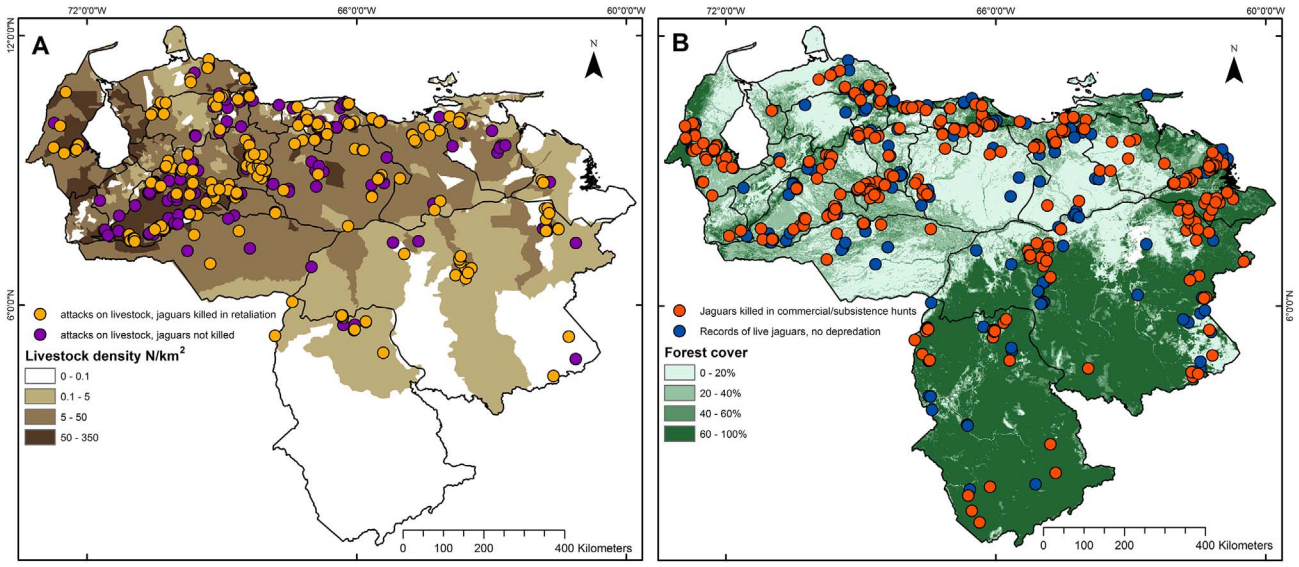

Fig. 1. Spatial distribution of records of retaliatory killing and subsistence/commercial hunting of jaguars, and records of live jaguars in Venezuela. A. Distribution of records of livestock depredation by jaguars, with a division to jaguars killed in retaliation and not killed, and spatial variation in cattle density. B. jaguar records not related to livestock depredation, with the division to jaguars killed in subsistence/commercial hunting and records of live jaguars, and forest cover.

Table 5
Model selection results for models predicting values of the retaliation/hunting index.

Model No	Variables	AIC	dAIC	wAIC
1	Canopy, human density, cattle density, area protection	− 6.45	0,00	0,79
2	Canopy, human density, area protection	− 3.37	3,08	0,17
3	Human density, cattle density, area protection	− 0.53	5,92	0,04
4	Canopy, human density	4,75	11,20	0,00
5	Human density, area protection	5,69	12,14	0,00
6	Human density	19,88	26,33	0,00
7	Canopy	22,69	29,14	0,00

Table 6
Parameters of the best model predicting values of the retaliation/hunting index (i.e. the prevalence of retaliatory killing compared to hunting) over the territory of Venezuela. $R^2 = 0.20$, Standard Error = 0.24, $p = 0.0000$, $N = 273$.

Effect	Coefficient	Standard Error	Std. coefficient	*t*	*p*-Value
Constant	0.43435	0,05	0,00	9,50	0,0000
Canopy	− 0.00216	0,00	− 0.17	− 2.81	0,0053
Log (human density)	0.04005	0,01	0,19	3,15	0,0018
Cattle density	0.00129	0,00	0,14	2,24	0,0257
Area protection	− 0.10324	0,03	− 0.18	− 3.21	0,0015

4.3. Differences in hunting methods and their potential efficacy in killing jaguars

Methods and tools used in retaliatory killing were statistically different than those used in subsistence/commercial hunting. In retaliatory killing people use more sophisticated and specialised methods, like following them with dogs, waiting at prey carcass, using traps and poison. The use of dogs may substantially increase hunting efficiency (Robinson and Redford, 1991; Koster, 2008). Other techniques used in retaliatory killing can be also highly efficient. A common practice of hiring specialised hunters to kill jaguars in retaliation may additionally increase efficiency. Our data confirm the findings of Swanepoel et al. (2015) that retaliatory killing can be more effective than other types of hunting and possibly leads to higher kill rate and heavier impact on carnivore populations. Fairly common in Venezuela is jaguar killing by attracting jaguars with imitation of roaring. A similar method was reported from Mexico (Garcia-Alaniz et al., 2010), Belize (Rabinowitz, 2000), and Bolivia (Hoogesteijn and Mondolfi, 1992). The use of this method as well as hunting with spear confirms that jaguar hunting is deeply rooted in Venezuelan society.

4.4. Products used from killed jaguars

Independent of the reasons and motivations to kill a jaguar, almost all interviewed hunters collected skins and canines, and often also skulls, claws, meat, and fat. Frequently, they sold the products obtained from jaguars. Thus, it is very difficult to distinguish between commercial and subsistence hunting and even retaliatory killing has several similarities to hunting in respect to the products utilized from killed jaguars.

Unexpectedly consumption of jaguar meat was common in our study and has possibly been underestimated. Consumption of jaguar meat and use of jaguar fat for medicines and magic purposes is probably common all over jaguar range and have been noted also in other studies (Balaguera-Reina and Gonzalez-Maya, 2008; Garcia-Alaniz et al., 2010; González-Maya et al., 2010; Srbek-Araujo, 2015).

4.5. Spatial patterns and importance of hunting and retaliatory killing for jaguar populations

Various human impacts, and especially deforestation, hunting, and retaliatory killing have been proposed as the main factors responsible for jaguar declines (e.g. Nowell and Jackson, 1996; Zeller, 2007). Which of them exerts the strongest effect on jaguar populations is not clear. Our study shows that hunting is in general more frequent and more widespread than retaliatory killing. However, subsistence/commercial hunting is prevailing over vast areas still inhabited by continuous jaguar populations, thus it may not lead to fast jaguar extirpations. Hunting in large forested areas of Venezuela may not be very intense. Our data show that it is mostly opportunistic as in most cases jaguars are not main target. Moreover, subsistence/commercial hunting prevails in sparsely populated areas, mostly inhabited by indigenous people. Results of our interviews indicate that the majority of indigenous people, especially in southern Venezuela, hunt jaguars only occasionally, when they feel threatened by the proximity of a jaguar or when jaguars kill their dogs. Non-indigenous hunters kill

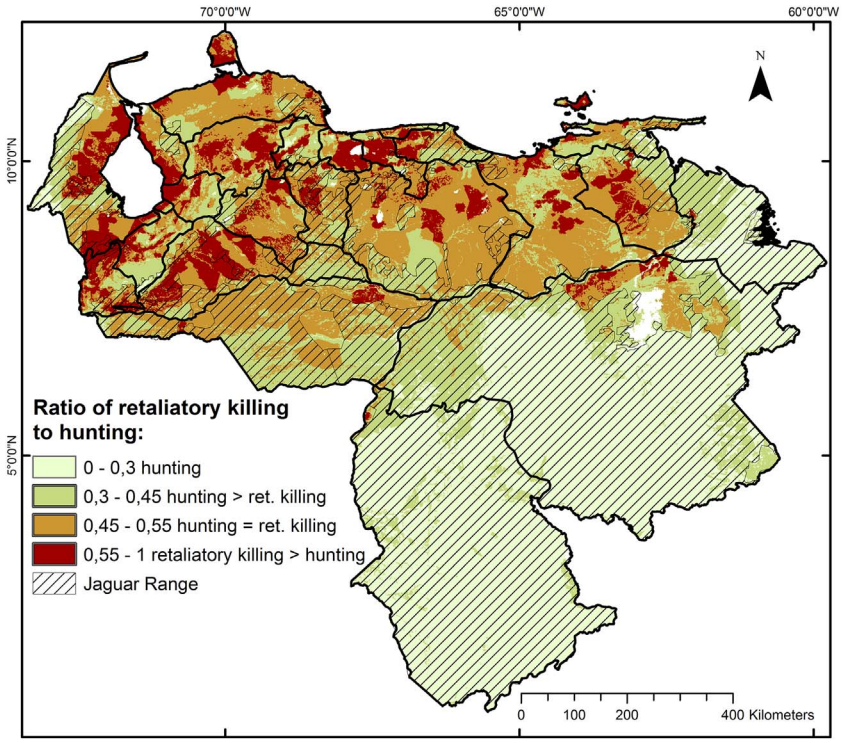

Fig. 2. Spatial distribution of values of the retaliation/hunting index (i.e. the prevalence of retaliatory killing compared to hunting) predicted by the best regression model, compared with the current jaguar range in Venezuela (after Jędrzejewski et al. 2017).

jaguars at any chance, but impact of such hunting is possibly related to density of hunters, which in turn should be related to human population density. Thus, in the forested areas with sparse human populations opportunistic hunting seems to have limited impact on jaguar populations.

On contrary, retaliatory killing, although not as widespread as hunting, seems to be highly detrimental for jaguar populations. It involves more sophisticated and more efficient hunting methods than the opportunistic subsistence/commercial hunting. Moreover, the comparison of our model predictions with current jaguar range suggests that retaliatory killing is likely one of the drivers of jaguar extirpations, because it is predicted to occur mostly outside of the current jaguar range, i.e. in the areas where jaguars have already been extirpated. Moreover, cattle depredation by jaguars and resulting retaliatory killing of jaguars are often related with the process of deforestations (de Oliveira et al., 2012; Carvalho et al., 2015). Deforested areas are quickly converted to pastures with high cattle density which entice jaguars to come out of the remaining forests, kill cattle and be killed in retaliation. Jędrzejewski et al. (2017) has demonstrated that jaguar populations have been reduced in Venezuela mostly during the last 75 years and that probability of jaguar occurrence is low in the areas with high human impacts and low forest cover. Thus, the appearing mechanism leading to jaguar extirpations involves deforestations, cattle breeding, and retaliatory killing. Additionally, jaguars disappear faster when retaliatory killing overlaps with hunting performed by numerous hunters in more populated regions. Results of our modelling strongly support this interpretation. First, importance of retaliatory killing is increasing with growing livestock and human population densities, and with declining forest cover. Second, overlapping of retaliatory killing and hunting is also predicted mostly for the areas where jaguars have gone extinct in recent decades.

Our results demonstrate the importance of protected areas for jaguar conservation. Inside the protected areas retaliatory killing is obviously limited. Although protection do not stop hunters to enter and hunt inside, the legal protection of an area prevent it from cattle breeding and from deforestations which appears most important for jaguar persistence.

4.6. Implications for conservation

Our data show that the relative importance of hunting and retaliatory killing has not changed in time, suggesting that both impacts have remained at the same level and that the introduction of legal protection of jaguars in 1996 (Venezuela, 1996a, 1996b) has not been effective. Solutions are not simple and rather they should not include increasing persecution of hunters. Hunting is deeply rooted in rural communities and widely accepted as an important activity. The recent political and economic crisis in Venezuela makes the situation even more difficult, as for many people wild meat is an important source of animal protein. Development of ecological education seems to be the most appropriate and most promising way of limiting jaguar hunting. Retaliatory killing is equally difficult to control. In the future, a system of environmental services payment combined with eco-tourism, education and propagation of anti-predation strategies in cattle management could be a possible solution for Venezuela and elsewhere (Hoogesteijn et al., 2005; Hoogesteijn and Hoogesteijn, 2008, 2014; Quigley et al., 2015). Nevertheless, this and other studies (e.g. Jędrzejewski et al., 2011; Jędrzejewski et al., 2017) indicate that controlling deforestation and creating more protected areas would be the most important protection measures that could slow down the process of jaguar population declines.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.03.025.

References

Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N., Caski, F. (Eds.), Proceedings of the Second International Symposium on Information Theory. Akademiai Kiado, Budapest, pp. 267–281.

Athreya, V., Odden, M., Linnell, J.D., Karanth, K.U., 2011. Translocation as a tool for mitigating conflict with leopards in human-dominated landscapes of India. Conserv. Biol. 25, 133–141.

Balaguera-Reina, S., Gonzalez-Maya, J.F., 2008. Occasional jaguar hunting for subsistence in Colombian Chocó. In: Cat News 48. pp. 5.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Springer-Verlag, New York, pp. 327.

de Carvalho Jr, E.A.R., Gonçalves-Morato, R., 2013. Factors affecting big cat hunting in Brazilian protected areas. In: Tropical Conservation Science 6. pp. 303–310.

Carvalho, E.A., Pezzuti, J.C., 2010. Hunting of jaguars and pumas in the Tapajós–Arapiuns Extractive Reserve, Brazilian Amazonia. Oryx 44, 610–612.

Carvalho Jr., E.A., Zarco-González, M.M., Monroy-Vilchis, O., Morato, R.G., 2015. Modeling the risk of livestock depredation by jaguar along the Transamazon highway, Brazil. Basic Appl. Ecol. 16, 413–419.

Caso, A., López-González, C., Payán, E., Eizirik, E., de Oliveira, T., Leite-Pitman, R., Kelly, M., Valderrama, C., 2008. Panthera onca. In: The IUCN Red List of Threatened Species 2008http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T15953A5327466.en. (e.T15953A5327466).

Cavalcanti, S., Marchini, S., Zimmermann, A., Gese, E., Macdonald, D., 2010. Jaguars, livestock, and people in Brazil: realities and perceptions behind the conflict. In: Macdonald, D.W., Loveridge, A.J. (Eds.), Biology and Conservation of Wild Felids Oxford University Press, pp. 383–402.

Corlett, R.T., 2007. The impact of hunting on the mammalian fauna of tropical Asian forests. Biotropica 39, 292–303.

Desbiez, A.L.J., de Paula, R.C., 2012. Species conservation planning: the jaguar national action plan for Brazil. In: Cat News 7. pp. 4–7.

Edwards, R., Holland, J., 2013. What Is Qualitative Interviewing? University of Edinburgh. Bloomsbury Publishing, London, pp. 124.

Fitzgerald, S., 1989. International Wildlife Trade: Whose Business Is It? World Wildlife Fund, Washington, DC, USA, pp. 459.

Fortin, M.J., Dale, M.R., Ver Hoef, J.M., 2002. Spatial analysis in ecology. In: El-Shaarawi, A.H., Piegorsch, W.W. (Eds.), Encyclopedia of Environmetrics. John Wiley & Sons, Ltd., Chichester, pp. 2051–2058.

Garcia-Alaniz, N., Naranjo, E.J., Mallory, F.F., 2010. Human-felid interactions in Three Mestizo communities of the Selva Lacandona, Chiapas, Mexico: benefits, conflicts and traditional uses of species. Hum. Ecol. 38, 451–457.

González-Maya, J.F., Charry, D.Z., Arévalo, Á.H., Cepeda, A.A., Reina, S.B., Uribe, C.C., Angel, C., 2010. Traditional uses of wild felids in the Caribbean region of Colombia: new threats for conservation? Lat. Am. J. Conserv. 1, 64–69.

Gurung, B., Smith, J.L.D., McDougal, C., Karki, J.B., Barlow, A., 2008. Factors associated with human-killing tigers in Chitwan National Park, Nepal. Biol. Conserv. 141, 3069–3078.

Hengl, T., Sierdsema, H., Radović, A., Dilo, A., 2009. Spatial prediction of species' distributions from occurrence-only records: combining point pattern analysis, ENFA and regression-kriging. Ecol. Model. 220, 3499–3511. http://dx.doi.org/10.1016/j.ecolmodel.2009.06.038.

Hoogesteijn, R., Hoogesteijn, A., 2008. Conflicts between cattle ranching and large predators in Venezuela: could use of water buffalo facilitate felid conservation? Oryx 42, 132–138.

Hoogesteijn, R., Hoogesteijn, A., 2014. Anti-predation strategies for cattle ranches in Latin America: a guide. In: Panthera Eckograf Soluções Impressas Ltda., Campo Grande, MS, Brazil, 978-85-912016-2-4, pp. 64.

Hoogesteijn, R., Mondolfi, E., 1992. El jaguar: Tigre americano. Armitano, Caracas, Venezuela, pp. 182.

Hoogesteijn, R., Hoogesteijn, A., Mondolfi, E., 1993. Jaguar predation and conservation: cattle mortality caused by felines on three ranches in the Venezuelan Llanos. In: Symposium of the Zoological Society of London 65. pp. 391–407.

Hoogesteijn, R., Boede, E.O., Mondolfi, E., 2002. Observaciones de la depredación de bovinos por jaguares en Venezuela y los programas gubernamentales de control. In: Medellín, R.A. (Ed.), El jaguar en el nuevo milenio. Fondo de cultura económica FCE-Universidad nacional autónoma de México. UNAM-Wildlife Conservation Society, pp. 183–197.

Hoogesteijn, R., Hoogesteijn, A., González-Fernandes, A., 2005. Ganadería y ecoturismo, dos actividades productivas, compatibles y sustentables en hatos de sabana inundable. In: Romero, R., Salomón, J., de Venanzi, J. (Eds.), XX Cursillo sobre bovinos de carne. Universidad Central de Venezuela. Facultad de Ciencias Veterinarias, Maracay, Venezuela, pp. 23–77.

Hoogesteijn, R., Tortato, F.R., Hoogesteijn, A., Payan, E., Marchini, S., 2011. Interacciones humanos/jaguares. Son realmente peligrosos los jaguares para los seres humanos? In: Simposio: Coexistencia entre grandes carnívoros y el ser humano en América: Estado actual y soluciones prácticas 15. Mesoamericana, pp. 343.

Hoogesteijn, R., Hoogesteijn, A., Tortato, F.R., 2014. Peligrosidad del jaguar para los humanos, realidad o exageración? In: Simposio Internacional: Conservación de felinos en las Américas, pp. 8–9 (23 al 26 de Mayo del 2014, Sarapiquí, Costa Rica, Panthera Costa Rica).

Huber, O., Oliveira-Miranda, M.A., 2010. Ambientes terrestres de Venezuela. In: Rodríguez, J.P., Rojas-Suárez, F., Giraldo Hernández, D. (Eds.), Libro Rojo de los Ecosistemas Terrestres de Venezuela. Provita, Shell Venezuela, Lenovo (Venezuela), pp. 29–92.

INE, 2011. XIV Censo Nacional de Población y Vivienda. In: Redatam, S.P. (Ed.), Instituto Nacional de Estadística (INE), . Venezuela. http://www.ine.gov.ve/CENSO2011.

Inskip, C., Zimmermann, A., 2009. Human-felid conflict: a review of patterns and priorities worldwide. Oryx 43, 18–34.

Iserson, K.V., Francis, A.M., 2015. Jaguar attack on a child: case report and literature review. Western Journal of Emergency Medicine 16, 303.

Jędrzejewski, W., Abarca, M., Viloria, Á., Cerda, H., Lew, D., Takiff, H., Abadía, É., Velozo, P., Schmidt, K., 2011. Jaguar conservation in Venezuela against the backdrop of current knowledge on its biology and evolution. Interciencia 36, 954–966.

Jedrzejewski, W., Abarca-Medina, M.R., Boede, E.O., Hoogesteijn, R., Isasi-Catalá, E., Carreño, R., Viloria, A.L., Cerda, H., Lew, D., González-Fernández, A.J., Perera, L., y Puerto Carrillo, M.F., 2015. Jaguar, *Panthera onca*. In: Rodríguez, J.P., García-Rawlins, A., y Rojas-Suárez, F. (Eds.), Libro Rojo de la Fauna Venezolana, Cuarta edición. Provita y Fundación Empresas Polar, Caracas, Venezuela. (Downloaded from: animalesamenazados.provita.org.ve/content/jaguar-0).

Jędrzejewski, W., Boede, E.O., Abarca, M., Sánchez-Mercado, A., Ferrer-Paris, J.R., Lampo, M., Velasquez, G., Carreño, R., Viloria, A.L., Hoogesteijn, R., Robinson, H.S., Stachowicz, I., Cerda, H., Weisz, MdM, Barros, T.R., Rivas, G.A., Borges, G., Molinari, J., Lew, D., Takiff, H., Schmidt, K., 2017. Predicting carnivore distribution and extirpation rate based on human impacts and productivity factors; assessment of the state of jaguar (*Panthera onca*) in Venezuela. Biol. Conserv. 206, 132–142. http://dx.doi.org/10.1016/j.biocon.2016.09.027.

Johnson, A., Vongkhamheng, C., Hedemark, M., Saithongdam, T., 2006. Effects of human–carnivore conflict on tiger (*Panthera tigris*) and prey populations in Lao PDR. Anim. Conserv. 9, 421–430.

Koster, J., 2008. The impact of hunting with dogs on wildlife harvests in the Bosawas Reserve, Nicaragua. Environ. Conserv. 35, 211–220. http://dx.doi.org/10.1017/S0376892908005055.

Madhusudan, M.D., Karanth, K.U., 2002. Local hunting and the conservation of large mammals in India. AMBIO J. Hum. Environ. 31, 49–54.

Marchini, S., Macdonald, D.W., 2012. Predicting ranchers' intention to kill jaguars: case studies in Amazonia and Pantanal. Biol. Conserv. 147, 213–221.

MAT, 2010. VII Censo Agrícola Nacional, 2008. Ministerio del Poder Popular de Agricultura y Tierras, República Bolivariana de Venezuela. http://censo.mat.gob.ve.

Monestiez, P., Dubroca, L., Bonnin, E., Durbec, J.P., Guinet, C., 2006. Geostatistical modelling of spatial distribution of *Balaenoptera physalus* in the northwestern Mediterranean Sea from sparse count data and heterogeneous observation efforts. Ecol. Model. 193, 615–628.

Moreno, R., Meyer, N., Olmos, M., Hoogesteijn, R., Hoogesteijn, A.L., 2015. Causes of jaguar killing in Panama – a long term survey using interviews. In: Cat News 62. pp. 40–42.

Nazeri, M., Madani, N., Kumar, L., Mahiny, A.S., Kiabi, B.H., 2015. A geo-statistical approach to model Asiatic cheetah, onager, gazelle and wild sheep shared niche and distribution in Turan biosphere reserve-Iran. Eco. Inform. 29, 25–32.

Neto, M.F.C., Neto, D.G., Haddad, V., 2011. Attacks by jaguars (*Panthera onca*) on humans in Central Brazil: report of three cases, with observation of a death. Wilderness Environ. Med. 22, 130–135.

Newby, J.R., Mills, L.S., Ruth, T.K., Pletscher, D.H., Mitchell, M.S., Quigley, H.B., Murphy, K.M., DeSimone, R., 2013. Human-caused mortality influences spatial population dynamics: pumas in landscapes with varying mortality risks. Biol. Conserv. 159, 230–239.

Nowell, K., Jackson, P., 1996. Status Survey and Conservation Action Plan Wild Cats. 421 IUCN/SSC Cat Specialist Group.

de Oliveira, T.G., Ramalho, E.E., de Paula, R.C., 2012. Red list assessment of the jaguar in Brazilian Amazonia. In: Cat News 7. pp. 8–13.

Pacheco, C., Aguado, Suárez I., Mollicone, D., 2011. Dinámica de la deforestación en Venezuela: análisis de los cambios a partir de mapas históricos. Interciencia 36, 578–586.

Packer, C., Ikanda, D., Kissui, B., Kushnir, H., 2005. Conservation biology: lion attacks on humans in Tanzania. Nature 436, 927–928.

Payán, E., Trujillo, L.A., 2006. The tigrilladas in Colombia. Cat News 44, 25–28.

Peres, C.A., Palacios, E., 2007. Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. Biotropica 39, 304–315. http://dx.doi.org/10.1111/j.1744-7429.2007.00272.x.

Quigley, H., Hoogesteijn, R., Hoogesteijn, A., Foster, R., Payan, E., Corrales, D., Salom-

Perez, R., Urbina, Y., 2015. Observations and preliminary testing of jaguar depredation reduction techniques in and between core jaguar populations. Parks 21, 63–72.
Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Presspp. 527.
Rabinowitz, A., 2000. Jaguar. One Man's Struggle to Establish the World's First Jaguar Preserve. Island Press, Washington, D.C. USA, pp. 378.
Redford, K.H., Robinson, J.G., 1991. Subsistence and commercial uses of wildlife in Latin America. In: Robinson, J.G., Redford, K.H. (Eds.), Neotropical Wildlife Use and Conservation. The University of Chicago Press, Chicago, pp. 6–23.
Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 1241484.
Robinson, J.G., Redford, K.H., 1991. Neotropical Wildlife Use and Conservation. University of Chicago Presspp. 520.
Rodríguez, J.P., 2000. Impact of the Venezuelan economic crisis on wild populations of animals and plants. Biol. Conserv. 96, 151–159.
Sánchez-Mercado, A., Asmüssen, M., Rodríguez-Clark, K.M., Rodríguez, J.P., Jędrzejewski, W., 2016. Using spatial patterns in illegal wildlife uses to reveal connections between subsistence hunting and trade. Conserv. Biol. 30, 1222–1232. http://dx.doi.org/10.1111/cobi.12744.
Sanderson, E.W., Redford, K.H., Chetkiewicz, C.L.B., Medellin, R.A., Rabinowitz, A.R., Robinson, J.G., Taber, A.B., 2002. Planning to save a species: the jaguar as a model. Conserv. Biol. 16, 58–72.
Solomon, J., Jacobson, S.K., Wald, K.D., Gavin, M., 2007. Estimating illegal resource use at a Ugandan park with the randomized response technique. Hum. Dimens. Wildl. 12, 75–88.
Srbek-Araujo, A.C., 2015. Opportunistic Consumption of Meat of Jaguar (Mammalia: Carnivora) in the Brazilian Amazon: A Case Report in the State of Pará. (Natureza on line) 13. pp. 50–52.
Srbek-Araujo, A.C., Mendes, S.L., Chiarello, A.G., 2015. Jaguar (*Panthera onca* Linnaeus, 1758) roadkill in Brazilian Atlantic Forest and implications for species conservation. Braz. J. Biol. 75, 581–586.
Swanepoel, L.H., Somers, M.J., Dalerum, F., 2015. Functional responses of retaliatory killing versus recreational sport hunting of leopards in South Africa. PLoS One 10, e0125539.
Swank, W.G., Teer, J.G., 1989. Status of the jaguar 1987. Oryx 23, 14–21.
Tabachnick, B.G., Fidell, L.S., 1983. Using Multivariate Statistics. Harper Collins College Publisherspp. 963.
Treves, A., Karanth, K.U., 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. Conserv. Biol. 17, 1491–1499.
Venezuela, 1996a. Presidencia de la Republica. Decreto No. 1485 del 11/09/96: Animales vedados para la caza. Gaceta Oficial No. 36.059. (7 Oct. 1996). (Caracas, Venezuela).
Venezuela, 1996b. Presidencia de la Republica. Decreto No. 1486 del 11/09/1996: Especies en peligro de extinción. Gaceta Oficial No. 36.062. (10 Oct. 1996). (Caracas, Venezuela).
Zeller, K., 2007. Jaguars in the New Millennium Data Set Update: The State of the Jaguar in 2006. Wildlife Conservation Society, New York, pp. 77.