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NEW HISTORICAL RECORDS OF THE JAGUAR (*Panthera onca*) IN PATAGONIA

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Resumen: En este estudio se realizó una revisión exhaustiva de documentos históricos de la época de contacto con los europeos para evaluar la presencia histórica del jaguar (*Panthera onca*) en la Patagonia. Dado que no existen registros escritos con anterioridad a la llegada del hombre europeo, entonces se buscó evidencia suplementaria en restos fósiles, etnografía, topónimos y nombres indígenas para la especie. La evidencia disponible señala que la especie pudo haber alcanzado la región del Estrecho de Magallanes, Chile. Aunque la información es escasa para permitir un análisis del patrón de distribución pasado en Patagonia, a escala regional se identificaron tres áreas de ocupación: noroeste de Patagonia, sur continental de Chile, y áreas cercanas a puertos naturales de la costa Atlántica. El jaguar sobrevivió en el norte de la Patagonia Argentina y el Estrecho de Magallanes, Chile, hasta fines del siglo XIX, y se extirpó de la región centro-sur de Chile durante el siglo XVII. Se discuten brevemente los probables factores que contribuyeron a la declinación y extinción del jaguar en la Patagonia.

Palabras clave: Presencia histórica, *Panthera onca*, Patagonia.

Abstract: An exhaustive review of written historical documents from the time of European contact was completed in order to examine the historic presence of the jaguar (*Panthera onca*) in Patagonia. Since prior to the arrival of the Europeans there are no written records, therefore supplementary evidence has been sought in fossil remains, ethnography, toponyms and indigenous names for the species. There is evidence to suggest that the species may have occurred as far south as the Estrecho de Magallanes, Chile. Although the available evidence is scarce to enable an analysis of the former distribution pattern in Patagonia, at a regional scale three main areas of occupation can be identified: north-western Patagonia, southern continental Chile, and the vicinity of natural ports in the Atlantic coast. It is known that the jaguar survived in northern Argentine Patagonia and the Estrecho de Magallanes, Chile, until the late 19th century, and was extirpated in south-central Chile during the 17th century. Probable factors contributing to the decline and extinction of the jaguar in Patagonia are briefly discussed.

Key words: Historical occurrence, *Panthera onca*, Patagonia.

INTRODUCTION

The jaguar (*Panthera onca*) is the largest of the American cats, and morphologically it is similar to the leopard (Emmons, 1987). It occurs in a wide variety of habitats ranging from dense rainforest to shrub lands (Nowak, 1991), and is strongly associated with rivers, streams and dense marshes (Cabrera and Yeppes, 1960; Hoogesteijn and Mondolfi, 1992). This cat is an excellent swimmer and a good tree climber (Cabrera and Yepes, 1960). The jaguar is an opportunistic predator with a preferable crepuscular-nocturnal activity that takes advantage of a wide variety of prey, generally according to availability (Emmons, 1987).

Formerly, its range included the southern part of North America, all of Central America and South America as far as northern Patagonia (Redford and Eisenberg, 1992; Seymour, 1989). By the end of the 20th century, the jaguar's geographic distribution has been reduced significantly by hunting for the fur trade, persecution for livestock depredation and habitat loss (Seymour, 1989). In South America this species is considered extirpated over most of eastern Brazil, Uruguay and all but the northernmost portions of Argentina (Arra, 1974; Nowak, 1991; Perovic and Herrán, 1998).

The former southern extent of the jaguar in Argentina is uncertain. Carman (1984) suggested that the Rio Negro was the southern distributional edge as late as the 19th century. Other authors referred to its presence in Patagonia but have not provided the sources of information (Ambrosetti, 1894; Cabrera, 1934; Cabrera and Yepes, 1960; De Angelis, 1972; Lehmann Nitsche, 1907; Rusconi, 1967). According to Azara (1838), it was present in the Atlantic coastal areas around the 1800s. In Chile the jaguar is not currently mentioned as occurring in earlier times.

Efforts to examine the former presence of *P. onca* in Patagonia require an exhaustive analysis of its historical records of occurrences. Hence, the objective of this paper is to review all the written historical records available for this species in order to shed light on its former range, and to analyze the factors that might have caused its decline in this territory. Since prior to the arrival of the Europeans there are no written records, therefore other sources of information such as fossil remains, rock art, indigenous names for the jaguar, and toponyms have been used.

METHODS

Study area

Patagonia is a territory of more than 1,000,000 km^2 located between latitude 36° S and 55º S. The topography of this territory is dominated in the west by the Andean Cordillera and in the east by dissected plateaus that give way to low, flat and undulating plains (Dimitri, 1972). The Andes play a crucial role in determining the climate of Patagonia since they impose a barrier to the moist westerly winds, producing a rain shadow effect to the east. A marked vegetation gradient parallels the climatic trend (Dimitri, 1972).

In the Andean and coastal cordilleras of Chile and in some extensions across the Andes into Argentina, high rainfall (800-4,000 mm/y) allows mixed temperate rain forests. Mixed deciduous woodland is found along the eastern flanks of the Andes where precipitation is lower (400-800 mm), and the xeric Patagonian steppe occurs on the eastern lower parts with less than 200 mm/yr. Towards the south cold areas and high rainfall (2,000-5,000 mm/y) support the Magellanic moorland extending along the south-western Chilean archipelago to 48ºS. The Andes contain over 20,000 km^2 of glaciers that are mostly concentrated south of 45°S (Masiokas *et al*., 2008). Mountain rivers have a pluvial regime, with two main discharge periods, one of them is due to heavy winter precipitation and the other to water melt from ice and snow on the Andes mountains. The rivers of the steppe are fed mainly by pluvial precipitation from the west

Historical records

Written historical records were obtained from different sources: *i*) contemporary published studies, and *ii*) journals of early explorers, expedition narratives, and chronicles of Jesuit clergymen. The year 1522 is used as a research baseline for the historical data. I have omitted early accounts whose faunal descriptions remain uncertain. The historical records collected on the jaguar were divided into two main categories: *i*) direct references; *ii*) indirect references. The latter are based upon second-hand information, and not on personal observation. In this case, only written documents of historic significance were considered. Direct references are provided by travellers and explorers. Their records include direct sightings of the species, and observation of tracks and preyed animals by the jaguar. Jaguar tracks have been included in this study because they present some differences from those of puma (*Puma concolor*-Hoogesteijn, 2001). However, since tracks of similar appearing species can be affected by many factors, and an accurate identification relies on the observer's expertise (De Angelo *et al*., 2010), this evidence has been considered valid only if accompanied by direct sightings. Additionally, records on preyed animals by the jaguar have been treated as circumstantial evidence.

Toponyms

Geographic and toponymic dictionaries have been used for the compilation of place-names (Coni, 1951; Erize, 1990; Latzina, 1891; Riso Patron, 1924; Zucarelli *et al*., 1999). I searched for toponyms formed with the words "jaguar", "tigre" and "nahuel" (= tiger, in Mapudungun language spoken in central Chile and west central Argentina by the Mapuche people). Except for settlements, human landmarks (such as schools, farms, etc.) have been excluded from the results. The method used was to compare the compiled toponyms with the historic records and the ethnographical evidence. Forty-three toponyms were analyzed in this review. Once the information was gathered, the

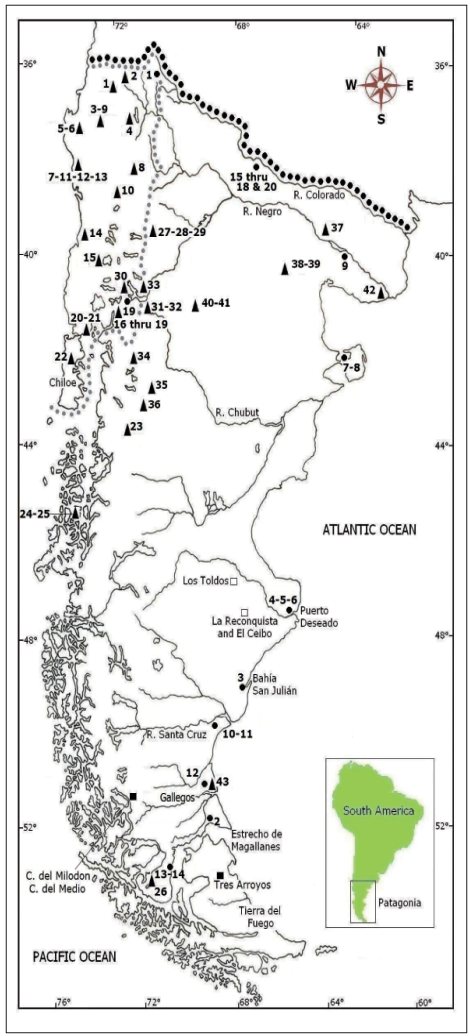

Figure 1. Map of Patagonia. Black dotted line = northern limit of the study area; gray dotted line = approximate distribution of 16th century indigenous populations of north-western Patagonia mentioned in the text; filled dots = historical records; filled triangles = toponyms; open squares = rock art sites; filled squares = archaeological sites. See Tables 1 and 2 for identification of numbers. Note that some place names are superposed.

place names were separated into two groups: a) Chile and Andean region of Argentina, b) extra-Andean Argentine Patagonia. This classification is based on the landscape characteristics of the territory in terms of forest cover, permanent water and prey availability.

Ethnography and fossil remains

To address the gap in the historical evidence on the jaguar, I resorted to the ethnographic information and fossil evidence. The most useful documents for the ethnographic data are the chronicles of the Spanish conquest and colonization. Evidence from iconography has been also included in this study. However, it is worth noting that rock paintings may not represent the fauna of the area as hunter-gatherers may have depicted animals they encountered during long distance travels. Consequently, these data have been taken with care. This study includes the paleontological information on *P. onca* although this species has left very little evidence in the fossil record.

RESULTS

Historical records

A total of 20 historical records were found for Patagonia for the period 1558 through 1897. Table 1 shows a chronological listing of the records collected in this study. In some cases, if relevant, the original text is quoted. The last jaguar sightings in northern Argentine Patagonia were at the end of the 19th century, and in southern Chile the species was probably still present in the 1850s. Written records place the jaguar in ten areas of occupation, eight in Argentina (natural ports in the Atlantic coast and northern Argentine Patagonia), and two in Chile (south-central Regions and the Estrecho de Magallanes). In the Argentine steppe the historic records are mainly associated to five of the eight main rivers in Argentine Patagonia: Colorado, Negro, Deseado, Santa Cruz, and Gallegos. Direct sightings resulted in eight of the ten localities, and in six of the total collected records, pumas and jaguars have been differentiated from each other. Occurrence records varied among geographical areas, time periods and human presence. Sighting observations of jaguar in the extra-Andean Patagonia coincide with voyages of discovery and exploration and the British hydrographic missions to survey the southern coasts of South America. In the case of northwestern Patagonia, the written records of 17th century strongly correlate to the Spanish-Creole colonization.

There are three records of special interest for southern Patagonia in late 19th century for they refer specifically to the "jaguar". The first account is John Mac Douall's (Table 1, ref. 12), who acted as auxiliary accountant during the voyage of the "Beagle" in 1826 and 1827 under the command of Cap. Pringle Stokes. Mac Douall observed a jaguar in Cabo Buen Tiempo (51º 56'S, 98º 06' W), Santa Cruz, Argentina, the same locality where Cap. Stokes named a peaked hill "Monte Tigre" (51º 33' S, 69º 08'W-Fitz-Roy, 1839). The

second account applies to William Mogg (Table 1, ref. 13), who formed part of the crew of the "Beagle" commanded by Cap. Robert Fitz Roy. Mogg reported on the occurrence of the jaguar in the eastern shores of the Estrecho de Magallanes in his diary written in 1828. Victor de Rochas made a similar testimony when he undertook a voyage to the Magellanic channels in 1856-59 as surgeon of the French Navy. His description of the jaguar and the puma has been quoted in Table 1, ref. 14.

It is unusual to find the jaguar described in the early accounts as abundant, plentiful or very numerous. Jaguars were apparently plentiful in the vicinity of Lago Nahuel Huapi, Argentina (O'Connor, 1884) until the end of the 19th century, and in the region at about the same latitude but in Chilean territory (Bibar, 1966). On the contrary, occurrence records in the extra-Andean Patagonia were sparse and haphazard.

Toponyms

Thirty-nine place names containing the word "nahuel" and four named for "tigre" exist or have existed in Patagonia (Table 2). Toponyms embodying the word "jaguar" were not found. At regional scale, the abundance of landmarks of Mapuche origin could be related to the symbolic importance of the jaguar to the natives that continued to provide sources for place names long after its extinction. Place name density could be an indicator of the historical abundance of the species. The bulk of toponyms found in northwestern Patagonia may indicate that this region represented preferred ecological conditions for jaguars. By contrast, the extra-Andean Patagonia was mostly a vacant region defined by its low human population and its scarcity in toponyms. This could be explained by the assumption that the species was already scarce at the arrival of the early settlers. Another interpretation could be that the jaguar may have been scattered thinly across this region.

Ethnography

Evidence is scarce to infer the role played by the jaguar in the lives and thinking of the Patagonian natives. In south-central Chile and adjacent areas of Argentina, several ethnic groups derived from the Mapuche culture (see Figure 1) and exploited the jaguar for meat, shelter and clothing (Bibar, 1966; Obregón Iturra, 1991; Rosales, 1877). Furthermore, the hides had a commercial value among the Puelches who traded them in Chillán, Bio-Bio Region, in return for agricultural, textile and manufactured articles provided by the Mapuches (Núñez de Pineda Bascuñán, 1984). At the continent's southernmost tip, the terrestrial hunters of the Estrecho de Magallanes, Chile, also hunted the jaguar but relied primarily on guanaco (*Lama guanicoe*), puma and the South American ostrich (Rochas, 1861; Tavener, 1955).

In early chronicles jaguar symbols are mentioned. For example, Mapuches and Huilliches placed two poles crested with tigers or other animals' figures against the

Table 1. Chronological listing of historic records of *Panthera onca* in Patagonia. Reference numbers match those in Figure 1. Text transcriptions appear between quotation marks.

#	Locality	Source	Date	Evidence	Bibliographical reference
1	Andean flanks and valleys (40° S) , Chile	G. de Bibar	1558	"Hay muchos guanacos y leones y tigresy zorros y venados pequeños y unos gatos monteses y aves de muchas maneras".	Bibar 1966
2	R. de la Posesión, Chile	P. Sarmiento de Gamboa	1580	The footmarks of tigers and lions were seen.	Sarmiento de Gamboa (1950)
3	Pto San Julián, Argentina	J. Narborough	1670	"Près le port Saint-Julien on aperçut des animaux semblables au tigres, soit des jaguars, soit des couguars [puma]..."	Malte-Brun (1817)
4	Pto Deseado, Argentina	J. Byron	1764	Tracks of a large tiger were found.	Hawkesworth (1774-85)
5	Pto Deseado, Argentina	J. Byron	1764	Guanacos depredated by tigers were found.	Hawkesworth (1774-85)
6	Pto Deseado, Argentina	J. Byron	1764	"The men who first came up to the well found there a large tyger lying upon the ground".	Hawkesworth (1774-85)

Table 1. Continue...

#	Locality	Source	Date	Evidence	Bibliographical reference
7	Golfo San Jose, Argentina	J. de la Piedra	1779	They found "... escrementos de guanacos, carneros de la tierra, tigres y gamos..."	Piedra (n/d)
8	Golfo San Jose, Argentina	J. de la Piedra	1779	Tiger tracks were found.	Piedra (n/d)
9	R. Negro, Argentina	J. I. Perez	1780	A killed tiger was found.	Carman (1984)
10	R. Santa Cruz (Arg.)	A. Cabrera and J. Yepes	1780	"... existen documentos fehacientes que en 1780 aún había tigres en el alto río Santa Cruz, en Patagonia, …"	Cabrera and Yepes (1960)
11	R. Santa Cruz, Argentina	R. Lehman Nitsche	1782	While Viedma was traveling with the Indians inland to the Andes, they mentioned the existence of tigers (nahuel) and pumas (pagni) in the area.	Lehmann Nitsche (1907)
12	R. Gallegos, Argentina	J. Mac Douall	1826	"The guaguar, or South American tiger, was seen prowling and skulking among the rocks near the	Mac Douall (2009)

Table 1. Continue...

#	Locality	Source	Date	Evidence	Bibliographical reference
				beach, but on our approach it quickly made off…"	
13	Estrecho de Magallanes, Chile	W. Mogg	1827	The terrestrial hunters of the eastern shore of the Estrechode Magallanes "give chase to the first object they see,whether fox, guanaco, jaguar,ostrich or skunk". He further writes that "the skins are generally of the guanaco, skunk,fox, and sometimes of the jaguar,the latter being not so frequently caught".	Tavener (1955)
14	Estrecho de Magallanes, Chile	V. de Rochas	1856-59	"Le jaguar, si dangereux qui'il soit, est bien loin d'atteindre jamais aux proportions du vrai tigre d'Asie; sa taille est celle de la panthère; il est grisâtre, a tâches fauves bordées de noir. Le couguar [puma] est	Rochas (1863)

Table 1. Continue...

#	Locality	Source	Date	Evidence	Bibliographical reference
				beaucoup plus petit que le lion, san crinière, roux, avec des taches de même couleur plus foncée. Généralement long d'un mètre et haut de cinquante centimètres; il n'est nullement dangereux pour l'homme".	
15	R. Colorado, Argentina	E. Zeballos	1879	They saw a jaguar hunting an ostrich in the area comprised between rivers Colorado, Negro and Neuquén.	Zeballos (1994)
16	R. Colorado, Argentina	A. Doering	1879	Plenty of jaguar tracks were found near the rivers' banks.	Doering (1881)
17	R. Colorado, Argentina	A. Espinosa	1879	"Cazaron un tigre y se vio la rastrillada de otros seis. Se vio un león".	Espinosa (1939)
18	R. Colorado, Argentina	A. Espinosa	1879	A dead tiger was found.	Espinosa (1939)

Table 1. Continue...

#	Locality	Source	Date	Evidence	Bibliographical reference
19	L. Nahuel Huapi, Argentina	E. O'Connor	1883	"Abundan el guanaco, cisnal, ciervos, el puma o león de América, el gato montés y el tigre americano".	O'Connor (1884)
20	R. Colorado, Argentina	R. Lehman-Nitsche	1897	A tiger was killed.	Lehman-Nitsche (1907)

Table 2. Distribution of place names in Patagonia embodying the words "nahuel" and "tigre" applied to *Panthera onca*.

#	Toponym	Lat.	Long.	Type of feature
		CHILE AND ANDEAN REGION OF ARGENTINA		
		CHILE		
Biobio				
1	Nahuelcura	36° 59’	72° 37’	Adm. division
2	Nahueltoro	36° 29’	71° 46’	Population
3	Nahuelcura	37° 10’	72° 43’	Stream
4	Rucanahuel	37° 32’	71° 30’	Stream
5	Nahuelbuta	37° 47’	73° 02’	Hill
6	Nahuel	37° 18’	73° 22’	Stream
7	Nahuelbuta	38° 40’	73° 10’	Mountain range
8	Cordón Nahuel	38° 13’	71° 35’	Mountains
Araucania				
9	Nahueltripay	37° 44’	72° 42’	Stream
10	Nahuelcura	38° 55’	72° 00’	Stream
11	Nahuelco	38° 03’	73° 10’	Stream
12	Nahuelbuta	38° 01’	73° 15’	Stream
13	Nahualhuapi	38° 52’	73° 18’	Island
Los Ríos				
14	Nahuelhuenu	39° 41’	73° 13’	Stream
Los Lagos				
15	Nahuel	40° 11’	72° 22’	Island
16	Ñahuelhuapi	41° 25’	72° 22’	Locality
17	Nahuelhuapi	41° 23’	72° 20’	Boulder
18	Nahuelhuapi	41° 23’	72° 20’	Hot spring
19	Nahuel Huapi	41° 41’	72° 36’	Inlet
20	Nahuelhuapi	41° 50’	73° 29’	Point
21	Nahuelco	41° 53’	73° 10’	Point
22	Punahuel	42° 24’	73° 03’	Population
23	El Tigre	43° 43’	72° 01’	River

Table 2. Continue...

#	Toponym	Lat.	Long.	Type of feature
Aysen				
24	Rainahuel	45° 40’	73° 51’	Island
25	Reinahuel	45° 40’	73° 52’	Bay
Magallanes				
26	Nahuel	53° 29’	73° 06’	Island
		ARGENTINA		
Neuquén				
27	Nahuel Mapi	39° 58’	70° 95’	Stream
28	Nahuel Mapi	39° 29’	71° 03’	Mountain
29	Nahuel Mapi	39° 35’	71° 15’	Mountain range
30	Nahuel Puñón	40° 55’	71° 50’	Lagoon
Neuquén-Río Negro				
31	Nahuel Huapi	40° 58’	71° 30’	Lake
Río Negro				
32	P. Nahuel Huapi	41° 09’	71° 09’	Plain
33	Nahuel Puñonco	40° 41’	71° 14’	River
Chubut				
34	Tigre	42° 27’	71° 45’	River
35	Nahuel Pan	42° 98’	71° 35’	Mountain
36	Nahuel Pan	43° 11’	71° 46’	Populated place
		PATAGONIAN STEPPE		
Río Negro				
37	Bajo de la Tigra	39° 26’	65° 16’	Depression

Table 2. Continue...

#	Toponym	Lat.	Long.	Type of feature
38	Nahuel Niyeu	40° 23’	66° 11’	Stream
39	Nahuel Niyeu	40° 30’	66° 33’	Populated place
40	Nahuel Niyeu	41° 18’	69° 40’	Gorge
41	Nahuel Niyeu	41° 18’	69° 35’	Populated place
42	Isla del Tigre	40° 75’	63° 11’	Island
Santa Cruz				
43	Tigre	51° 20’	69° 03’	Mountain

facade of the house, which symbolized the noble lineage of the family (Bibar, 1966; Mariño de Lovera, 1865). Likewise, the jaguar was a symbol of strength and power in warfare among the Mapuches whose defensive weapons included armors, shields and helmets surmounted by a crest made from tiger skin, or other animals selected for their character (Bibar, 1966). The importance of this feline is also illustrated in the large corpus of popular tales narrated by the Mapuche (Hernández, 2002).

The jaguar has been given several names in the native languages spoken in continental Patagonia which are: Mapudungun or Mapuche, Gününa küne, and Tehuelche (see, e.g., Coña, 1984; De La Grasserie, 1902; Lehmann Nitsche, 1914; Lenz, 1895-97; Molina, 1967; Outes, 1928). However, there is no evidence of presence or absence of a term referring to the jaguar in the Kawésqar or Alakaluf language spoken on Isla Wellington and in the Alakaluf of the Estrecho de Magallanes (P. Viegas Barros, pers. comm.).

Representations of felines are known from the Santa Cruz province, Argentina, where the most ancient rock art has been documented. Rock-art in this area focuses on animal expression being the most common figure the guanaco, the South American ostrich, and the feline less usual. Cat-like creatures believed to be jaguars come from two sites located in the central high plateaus of this province (Figure 1). At the first site, named El Ceibo Cave 6B, there is a feline image of 1,5 m long painted in red with the coat spots in black. Cardich (1979) inferred that the figure belonged to *P. o. mesembrina*, extinct some 10,000 years ago. He also indicated that an incomplete figure in red with black spots in a small cave of Los Toldos referred to the jaguar.

At the second site, named La Reconquista Cave 6, four feline figures are represented among guanacos and hand paintings. When Jean-Marie

Franchomme studied different aspects of rock art in rock shelters and caves of Santa Cruz, he attributed one of these images to the jaguar (extinct or recent) (Arrigoni, 1996; Franchomme, 1992). He based his assumption on the general spotting distribution, the open circles with a black central dot, the short black lines over the dorsal area, and the black tip tail (Ramírez Rozzi, 2002). The feline representations (of an extinct or actual cat) do not necessarily mean that the animal existed in the area. Similarly, absence of representations is not evidence of absence of the species.

Fossil remains

Fossil remains of *P. onca* have been reported in the middle Pleistocene of North America (Seymour, 1993). A comparative evaluation of museum specimens from throughout their range revealed that from the late Pleistocene jaguars decreased in size by 15%, based on cranial and dental measurements, or 25%, based on postcranial measurements (Seymour, 1993). The gradual size change involved the shortening of the limb bones, leaving the living species relatively larger headed and shorter limbed. Fossil jaguars in North America tend to be larger than most living specimens although there is some overlap with the largest race from southern Brazil (Seymour, 2003).

In South America the paleontological record has become the subject of debate about whether *P. onca* remains are present since the Late Pleistocene (Seymour, 1989; Arroyo-Cabrales, 2002), or since the lower to middle Pleistocene (Berman, 1994). The first jaguar remains were recovered from the Cueva del Milodon located in the Ultima Esperanza inlet of Chile, XII Region. A feline larger than the existing jaguar was represented by mandibular bones and a metapodial. The remains have been described by Roth (1899, 1904) and received different names until Cabrera (1934) assigned them to an extinct subspecies, *P. o. mesembrina*. Further excavations in the southernmost part of Patagonia led to the recovery of remains of this species at Cueva del Medio and Tres Arroyos (Latorre, 1998; Massone, 2002; Nami, 1985-86; Nami and Menégaz, 1991). At Tres Arroyos (53° 23°S; 68° 47°W), on the island of Tierra del Fuego, remains of *P. o. mesembrina* showed that the species had been present at this site at 11,085 ± 70 BP (Massone, 2002; Steele and Politis, 2009). The archaeological site of Cueva del Medio is located at roughly 250 km from Monte Tigre in Argentina where a jaguar was sighted in 1826 (Table 1, ref. 12). Interestingly, the most southern fossil jaguar remains in South America and the most northern ones in North America have been uncovered at sites located at roughly the same distance from the equator.

DISCUSSION

Written historical records have been widely used to depict the former distribution of mammals (Aubry *et al.*, 2007; Bowles, 1971; Timm *et al*., 1997; Tyler and Anderson, 1990).

To supplement this type of data some authors have resorted to the archaeological and ethnographical evidence, and toponyms (Aybes and Yalden, 1995; Bernard and Parker, 2006; Blench, 2000; Cox *et al*., 2002; Rostlund, 1960). However, early records are influenced by a number of constraints (Boshoff and Kerley, 2010). Here, the principal limitations in using historical accounts relate to the paucity of records prior to the 18th century, the lack of systematic observations and an unequal spatial coverage.

Another limitation has been the absence of geographical explorations of the extensive hinterlands. The first contacts occurred on the coast and it was many years later that the travellers and explorers moved inland along the river basins. The knowledge of the interior Patagonia was only further augmented after 1870. By that time, the jaguar was likely near extinction. Furthermore, sight records are likely to be influenced by particular characteristics of the species. Jaguars were rarely encountered by humans in the past and this is still true today. Possible factors responsible for the scarcity of sightings could be: *i*) the secretive and elusive nature of the species, *ii*) the inaccessibility of much of its preferred habitat, and *iii*) the predominantly nocturnal habits in feeding and movement. In addition to the above factors, it must be considered that the early explorers did not normally travel at night and kept to flat open areas. It seems that the chance of observing a jaguar in Patagonia in historical times was closely related to the length of time spent by the travelers in one spot, the spatial coverage, and the contact with the natives.

Written accounts show different levels of accuracy in the identification of species and locations of sightings. Despite the tendency of early observers to confuse similar-appearing species (Boshoff and Kerley, 2010), a large and charismatic feline like the jaguar should have been easily recognized if the observer had the chance to encounter it. The jaguar shows significant differences in terms of body size when compared with the other two spotted cats of Patagonia: *Oncifelis guigna* and *Oncifelis geoffroyi*. The body size of the jaguar varies geographically between 56-105 kg for adult males and 41-77 kg for adult females (Hoogesteijn *et al*., 1993). *O. guigna* weights around 2.2 kg, it stands approximately 220 mm at the shoulders and has an overall body length of between 500 and 680 mm (Greer, 1965). Body mass of the O. *geoffroyi* has been set to 4.26 ± 1.03 kg (Lucherini *et al*., 2006) and head and body length is 450-700 mm (Nowak, 1991). Whereas *O. guigna* is found in south-central Chile and adjacent Argentina in the Andean area, *O. geoffroyi* occurs throughout Argentina. Consequently, only the latter species could have been found in extra-Andean Patagonia.

It is certain that the jaguar is poorly represented in the written historical record, and the ethnographic and archaeological evidence for a territory of more than 1,000,000 km^2. The available evidence is too scarce to enable an analysis of its former distribution pattern in Patagonia. However, at a regional scale

three areas of occupation can be identified. First, the Andean region between latitudes 38ºS and 42ºS must have represented a preferred habitat for the species in terms of forest cover, permanent water and prey availability. Second, although the historical records for southern continental Chile are not geographically precise, on the basis of the ecological requirements of the species and the landscape characteristics, it is plausible to think that the natives have mainly hunted the jaguar in the forest and ecotone. Field studies in Venezuela and Brazil showed that the ecotones of vegetation types are also productive edges for the jaguar (Cullen, 2006; Scognamillo *et al*., 2003). Last, in the Patagonian steppe the jaguar occurrence is associated to the main rivers. Thus, the jaguar might have persisted in the vicinity of the major watercourses within the recent past. The opposite is true for the puma, a species more adapted to arid conditions, still occurring throughout much of its historical range.

It is unclear whether the historical observations of jaguar represent the end of a long-term process of decline, or whether the species became more vulnerable after the arrival of the Europeans. In the latter case there are plausible scenarios for the species' decline. In south-central Chile the last reference of the jaguar dates back to around 1674. This region was densely populated due to the favourable climatic conditions, and the natives mainly settled around the main river basins and lakes borders (Bengoa, 2003). With the arrival of the Spaniards in 1542, any land started to experience an environment disturbance through the introduction of livestock and exotic plants, and the mistreatment of natural resources (Torrejon and Cisternas, 2003). The last records of jaguar coincide with this period of land alteration through human activities. Conversely, vast tracts of the extra-Andean Patagonia have been unoccupied or very sparsely occupied, and the natural landscape remained pristine until the arrival of the pioneer settlers after the General Roca's campaign that rid Patagonia of the Indians in 1879 (Rey Balmaceda, 1976). The xeric conditions of this ecoregion must have played an important role in restricting the jaguar to the proximity of permanent water. Then, the settlement pattern of humans near courses and bodies of water most probably had a devastating impact on the jaguar populations. At a broader temporal and geographical scale, the range of this cat has contracted most rapidly in regions of drier habitat such as the Argentine Monte and Pampas, the arid grasslands of Mexico, and the southwestern United States (Caso *et al*., 2008).

Nevertheless, the most interesting point is not the jaguar's extinction in the Patagonian steppe but its appearance in this territory intersected by a small number of main rivers, and dominated by shrub-grassland vegetation. Seymour (1989) stated that jaguar prefer a warm, tropical climate, associated with water, and are infrequent in arid areas. As expected for an opportunistic stack-and-ambush hunter that relies upon surprise, areas with good cover are essential to approach its prey (Grant *et al*., 2005). The Patagonian

steppe is a complex landscape mainly characterized by plateaus or mesetas. This rugged terrain might have provided cover for hunting, and it is possible (and perhaps highly probable) that river valleys functioned as travel corridors. In addition, access to water most likely provided predictable locations for encountering prey. The apparent absence of significant jaguar populations in the arid and more open southwestern United States led Rabinowitz (1999) to believe that this region has never been more than marginal habitat at the extreme northern limit of its range. Similarly, the Patagonian steppe may have also played a marginal role in the southernmost extent of the jaguar in terms of lack of water and cover, and/or any other limiting factor.

To sum up, this study shows that it is highly probable that the jaguar's former distribution in Patagonia stretched as far south as the Estrecho de Magallanes, Chile. The explicit references to the jaguar for southern Patagonia reinforce the historic records for the rest of the extra-Andean region. The poor representation of the jaguar in the written historical records might be explained as a result of the progressive decrease of the species over time, its secretive and elusive behavior, or a low number of observers present in a huge territory. The sighting localities are mainly associated to the forest habitats in the wet landscapes and the main watercourses in the steppe. It is known that the species survived in northern Argentine Patagonia and the Estrecho de Magallanes region until the late 19th century, and was extirpated in south-central Chile during the 17th century. Its disappearance in the latter region seems to be related to the impact on the ecological balance of the region and the intensification of human settlement. In contrast, the arid characteristics of eastern Patagonia could have forced the animals to inhabit reduced habitats where the species became more vulnerable to hunting pressure. However, under wetter conditions the species might have been widely distributed in the past. The low abundance of the jaguar in this territory in historical times may have been the result of a decline in the species population, or the limited evidence available. The written records are scarce and difficult to verify. However, this information is valuable for delineating the historic range and habitat use by jaguars in Patagonia. In order to gain greater insight into the species, the evidence provided by faunal remains and ethnography (rock art and engravings) will be fundamental.

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