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Carcass utilization and bone modifications on guanaco killed by puma in northern Patagonia, Argentina

Cristian A. Kaufmann*, Daniel J. Rafuse, Mariela E. González, María C. Álvarez, Agustina Massigoge, Nahuel A. Scheifler, María A. Gutiérrez

INCUAPA-CONICET, Facultad de Ciencias Sociales, Universidad Nacional del Centro de la Provincia de Buenos Aires, Av. del Valle 5737, B7400JWI Olavarría, Buenos Aires, Argentina

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A B S T R A C T

Inspired by the early fieldwork of G. Haynes with large sized predators in wilderness areas, the following paper presents data on bone damage patterns in a sample of guanacos killed by one of the largest predators in South America, the puma (*Puma concolor*, Felidae, Carnivora). We describe the bone modification pattern on the carcasses, including skeletal part representation, bone fractures, and tooth marks. Also, tooth mark modifications on bones collected from a puma enclosure at a local zoo were analyzed. Our results indicate a light modification of guanaco carcass by puma; bone damages located mainly in the upper portions of rear and forelimbs, rib cage, and scapular and pelvic girdles; and the presence of a low percentage of fractured bones. Scores, pits, and punctures are the best represented tooth marks. On average, punctures are 3.5–5 mm in diameter, although larger tooth impressions are observed. The light consumption of guanaco by the puma would provide a potential source for scavenging by other carnivores and humans.

1. Introduction

The identification of bone modification patterns created by different carnivores has become one of the major research interests within actualistic taphonomy in the last three decades. The results of this line of investigation help to recognize the important role of carnivores in archaeological site formation, and to understand human–carnivore interactions through time. Carnivores accumulate, transport, and destroy bones in a patterned way that we need to identify in order to distinguish their action from human behaviors. Most scientific production concerning this subject deals with large African carnivorous mammals (e.g., Sutcliffe, 1970; Blumenschine, 1986; Brain, 1981; Haynes, 1983; Marean and Spencer, 1991; Domınguez-Rodrigo, 1999; de Ruiter and Berger, 2000; Selvaggio and Wilder, 2001; Domínguez-Rodrigo et al., 2010); although in recent years, the list of carnivores studied has greatly expanded, including carnivores of different taxonomic groups, sizes, and geographic regions (Andrés et al., 2012; e.g., Jackson and Jackson, 1999; Elkin and Mondini, 2001; Njau and Blumenschine, 2006; Montalvo et al., 2007; Pobiner et al., 2007; Delaney-Rivera et al., 2009; Yravedra et al., 2011; Westaway et al., 2011; Lloveras et al., 2012; Burke, 2013; Saladié et al., 2013; Rafuse et al., 2014; Sala et al., 2014; Cohen and Kibii, 2015; Young et al., 2015).

The research program conducted by Gary Haynes in North America over the last three decades investigates the bone modification patterns generated by different large carnivorous mammals, particularly wolves and bears (Haynes, 1980a, 1981, 1982, 1983; Sala et al., 2014). His broad vision of taphonomy has led him not only to discuss the role of carnivores in the formation of faunal assemblages and the equifinality between carnivore and human bone modifications (e.g., spiral fractures, tooth marks, etc.), but also to explore the potential information offered by carnivore damage for paleoecological inferences. The work of G. Haynes has been a major source of inspiration for the development of taphonomic research programs in the southern cone of South America (Mondini, 1995, 2003; Borrero and Martin, 1996; Martin and Borrero, 1997; Elkin and Mondini, 2001; Borrero et al., 2005; Montalvo et al., 2007; Álvarez et al., 2012; Massigoge et al., 2014; Rafuse et al., 2014).

* Corresponding author.
E-mail addresses: ckaufman@soc.unicen.edu.ar (C.A. Kaufmann), drafuse@soc.unicen.edu.ar (D.J. Rafuse), mgonzalez@soc.unicen.edu.ar (M.E. González), malvarez@soc.unicen.edu.ar (M.C. Álvarez), amassigo@soc.unicen.edu.ar (A. Massigoge), nscheifler@soc.unicen.edu.ar (N.A. Scheifler), mgutierr@soc.unicen.edu.ar (M.A. Gutiérrez).

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In South America, the puma has received special attention, as one of the largest extant predators in the continent, and one of the few predators that overlapped in space and prey choice (e.g., guanaco, Patagonian hare, Greater rhea) with hunter–gatherer populations at the end of the Pleistocene and the Holocene (Martínez and Gutiérrez, 2004; Salemme and Miotti, 2008; Borrero, 2013). In southern Patagonia, Borrero and Martin (1996), Borrero et al. (2005) and Martin and Borrero (1997) characterized guanaco and sheep bone assemblages generated by the action of puma for assessing human and carnivore paleoecology, as well as the nature of the association between faunal remains and archaeological materials. Other naturalistic studies on the action of puma in South America were performed by Nasti (2000), Montalvo et al. (2007), and Muñoz et al. (2008). Finally, in North America, Stiner et al. (2012) examined the taphonomic signature of modern free-ranging mountain lion, and Burke (2013) and Delaney-Rivera et al. (2009) performed two feeding experiments with several carnivores, including puma.

The aim of this paper is to provide new data on the bone modification pattern in a modern osteological collection of guanaco (*Lama guanicoe*, Camelidae, Artiodactyla) killed by puma (*Puma concolor*, Felidae, Carnivora). The guanaco was one of the main preys for hunter–gatherer populations in southern South America, during the end of the Pleistocene and the Holocene (Politis, 2002). Remains of this species are commonly found in archaeological sites throughout the Patagonian steppes and Pampean grasslands (Gutiérrez and Martínez, 2008; Salemme and Miotti, 2008). We also studied surface modifications on bones gathered from a puma enclosure at a local zoo in order to compare and discuss patterns of bone damage inflicted by wild and captive pumas.

2. General characteristics of puma and guanaco

The puma (*Puma concolor* Linnaeus, 1771) (also called mountain lion or cougar) has the largest geographic range of any terrestrial mammal in the Western Hemisphere (Culver et al., 2000; Sunquist and Sunquist, 2002). The weight of the puma varies considerably depending on the latitude and habitat (Iriarte et al., 1990). Adult males range from as small as 28 kg in tropical settings, to as large as 120 kg in parts of Canada and southern South America (Iriarte et al., 1990; Sunquist and Sunquist, 2002). Pumas are primarily nocturnal opportunistic and generalist predators (Nowell and Jackson, 1996). Pumas kill and eat prey ranging in size from mice to moose (Sunquist and Sunquist, 2002).

In South America, pumas and jaguars are the largest terrestrial predators and kill large prey including guanacos (primarily young, yearling, and female guanacos), hares, Pampas deer, Marsh deer and rheas (Iriarte et al., 1990; Rau et al., 1995). With declines in some extant mammal populations, pumas now rely on livestock for large game hunting (Novaro and Walker, 2005). Pumas normally launch themselves at the prey, knocking the animal down, and finally killing them by suffocation and biting their throat. They usually leave claw marks on the shoulders and back of their prey, and are capable of dragging and carrying animals for considerable distances, and sometimes up into trees (Sunquist and Sunquist, 2002). They start eating their prey through the ventral part, reaching the ribs and the muscles of the rear limbs (Pitman et al., 2002; Palmeira et al., 2008). Pumas are also known to cover the remains with leaves, grass, sand, or whatever is available and later to return to the carcass (Sunquist and Sunquist, 2002).

The guanaco (*Lama guanicoe* Müller, 1776) is the largest of the wild South American artiodactyls. This species is broadly distributed with an extensive, though discontinuous range from the north of Peru to Navarino Island in southern Chile. For adult individuals, weight averages between 88 and 120 kg, and sexual dimorphism is not significant (Raedeke, 1979; Larrieu et al., 1982). Newly-born young weigh from 8 to 12 kg (Raedeke, 1979; de Lamo and Saba, 1993). Guanacos are characterized by a highly social organization based on a polygamous mating system (Franklin, 1983; Bank et al., 2003). Pumas are the main predator of guanaco; and recent studies have reported occasional attacks on young guanacos by culpeo (*Lycalopex culpaeus*) (Novaro et al., 2009).

3. Materials and methods

3.1. Wild puma sample

The wild puma sample consists of 6 guanaco carcasses from a modern osteological collection of 158 individuals, which were collected during the years 2000 to 2006 as part of an actualistic research study in the province of Río Negro, Argentina (Kaufmann, 2009). These six guanacos, killed by puma, were recovered over an extensive area of dry open landscape with small trees, shrubs and bushes (Fig. 1). There is no information on the guanaco and puma population densities in this area. The killing of the guanacos by pumas was inferred from contextual information gathered in the field, including: large bite marks on the throat, claw marks on the shoulders and backs, and large tooth marks on fractured bones; typical evidence left by a puma attack on large prey (Franklin et al., 1999; Logan and Sweanor, 2001; Nallar et al., 2008; Palmeira et al., 2008). The date of the puma kills is unknown; however, all carcasses contained soft tissue, meaning they were attacked in a time frame of no more than few months before their collection. Other indicators of puma predation were the covering of guanaco carcasses with plant debris and their position near small shrubs (Franklin et al., 1999; Logan and Sweanor, 2001; Nallar et al., 2008; Palmeira et al., 2008). No puma feces were found around or near the guanaco carcasses, however, feces of smaller sized carnivores were identified in the field, suggesting the presence of scavengers after the puma abandoned the carcass.

Skeletons were cleaned in the laboratory using different techniques such as boiling in water (for less than 4 h), maceration or by dermestid action. Sex determination was completed by observation of external genitals during carcass recovery. If there was soft tissue decay or scavenging of the genitals, sex was determined in the laboratory by pelvis and canine shape differentiation (Raedeke, 1979; Cartajena, 2007; Kaufmann et al., 2013). Age determination was established using dental development and wear (Oporto et al., 1979; Kaufmann, 2009).

3.2. Captive puma sample

The captive puma sample was modified by two adult males (older than 5 years) kept in an enclosure at the zoo “Bioparque Municipal La Máxima” (Olavarría, Argentina). The bones correspond to parts of different sized animals. This sample is not the result of a controlled experiment but derived from the regular diet of the pumas accumulated during several months. In general, small vertebrates were offered to the puma as complete carcasses, and larger vertebrates were offered in anatomical segments (in all cases the carcasses were fully fleshed). The bones were gathered in a single recovery event and were cleaned in the laboratory by boiling in water. Bones were identified as mature or immature according to bone fusion. In the captive sample we focused on tooth mark dimensions for characterizing the bone modification pattern produced by the puma. We assume, as other authors do (Gidna et al., 2013), that this variable would not be affected by environmental conditions (i.e., captivity). The most valuable aspect of this sample is that we can assure that the pumas were the only carnivores involved in bone modification.

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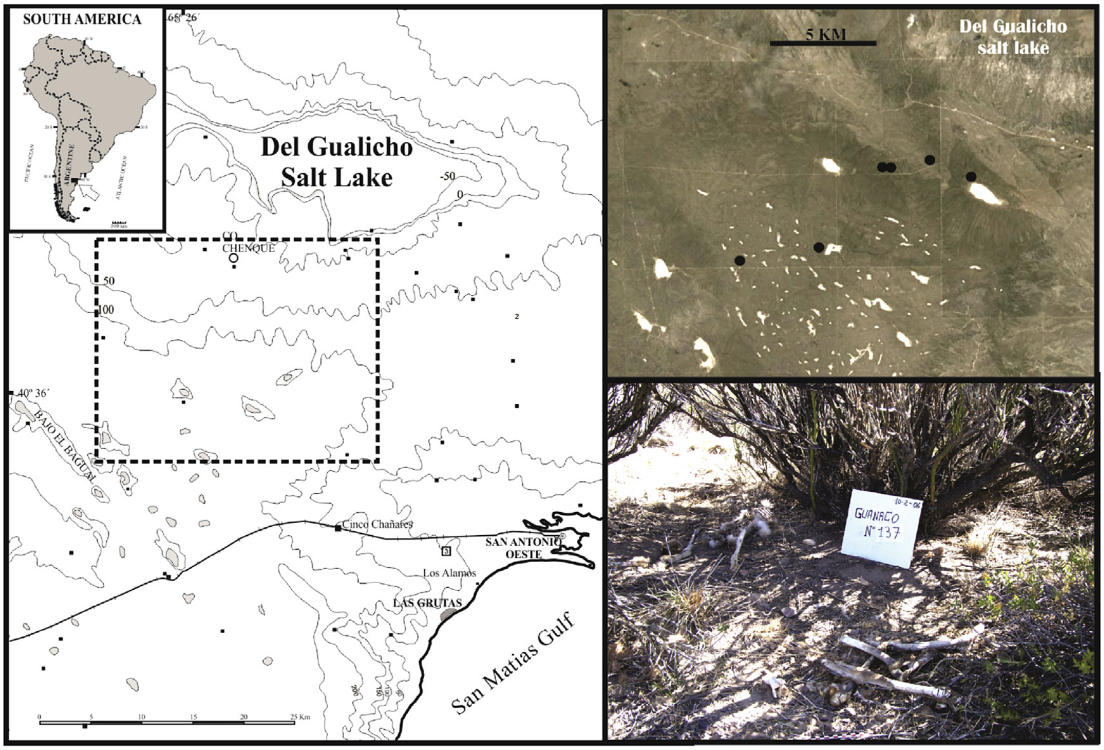

Fig. 1. Actualistic research study area. Left: geographical location of the study area. Upper right: satellite image of the area and location of guanaco individuals. Lower right: Guanaco individual #137 shown next to a European hare.

3.3. Bone damage

For comparative purpose, the total sample was divided according to weight and age of the different taxa. We considered two sizes: 1) small vertebrates [category Ia (2–9 kg) (*sensu* Bunn, 1986),] to specimens of *Lepus europaeus* and *Gallus gallus*; and 2) large vertebrates [category Ib-II (9–113 kg)] to specimens of *Lama guanicoe*, *Lama glama*, *Ovis aries*, *Sus scrofa*, and Artiodactyla order.

Quantification of the wild and captive puma samples was performed, including NISP (number of identified specimens), MNI (minimum number of individuals), MNE (minimum number of skeletal elements) and MAU (minimum number of anatomical units) (Binford, 1978; Grayson, 1984; Klein and Cruz-Uribe, 1984; Lyman, 1994).

Tooth marks on bone surfaces were classified into pits, punctures, furrowing, scores, and crenulated edges (Haynes, 1980a, 1980b, 1983; Binford, 1981; Lyman, 1994). According to previous studies, punctures are among the most typical bone modification produced by puma (Borrero and Martin, 1996; Nasti, 2000; Muñoz et al., 2008). For this reason, we focused on the location and size of these marks. Following Delaney-Rivera et al. (2009), measurements were taken using digital photographs and open source software for image analysis. Punctures were photographed using a Dino-Lite digital microscope (AnMo Electronics Corporation), and measured using ImageJ software (Rasband, 2014). The maximum length of individual punctures was calculated based on a best fit ellipse for the outlined mark generated by the software. Only tooth marks with sharp outlines and those located along the edges of intact or broken bone which presented >1/3 of the estimated original circumferences were measured.

The tooth mark sample was stratified on different bone portions according to the distribution of cancellous and cortical bone (e.g., Andrews and Fernandez Jalvo, 1997; Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Saladié et al., 2013). For long bones (femur, tibia, humerus, radius, ulna, and metapodial), three bone portions were considered: cancellous bone (from epiphyseal sections), thinning cortical bone (from metadiaphyseal sections) and dense cortical bone (from diaphyseal sections). For flat bones (skull, mandible, scapula, ribs, and pelvis), and irregular bones (vertebrae, and sternebrae), two bone portions were taken into account: cancellous bone and thinning cortical bone. To avoid variability in tooth mark size related to differences in dental morphology, we only considered circular to oval punctures resembling the shape of canines in the metric analysis. In order to discuss guanaco utilization by puma, the long bones were examined following the method described by Haynes (1981, 1982) and modified by Sala et al. (2014:128) that include five stages of consumption, from low to heavy modification.

4. Results

4.1. Wild puma sample

4.1.1. Individual # FCS.CC.13 (collected: April 23, 2000)

Category 1b, 9–23 kg (*sensu* Bunn, 1986). This individual was found near a shrub, where it was possibly hidden by a puma after the attack. At five meters from this shrub, guanaco fibers were recorded, which could indicate the kill site. Bones were scattered in a range of 20 m, but three main accumulations were identified. The first accumulation was composed of parts of the vertebral column and three limbs joined by the skin. The second accumulation contained the forelimb, and the third accumulation was composed of the skull and some cervical vertebrae (Fig. 2). The mandible and a cervical vertebra were found isolated near the shrub. We also recorded the presence of feces that were assigned to Pampean fox (*Lycalopex gymnocercus*). This small canid could have scattered, modified, and transported some of the bones away from the kill site. Considering the development and tooth wear, the age of this individual was

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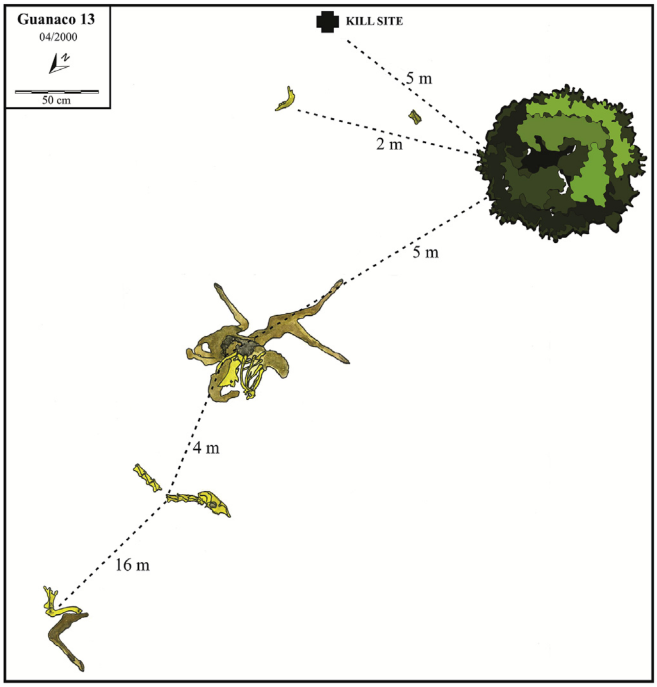

Fig. 2. Skeletal distribution map of guanaco individual #13.

estimated at three to six months old. The sex could not be determined. The relative time of death would have been short considering that there was skin and flesh in the lower limbs, and all the specimens were un-weathered. Most of the bone elements were present. Nevertheless, several ribs, some vertebrae, and the sacrum were absent; some tarsals and carpals were also missing (Table 1).

There are 19 specimens (18%; Table 2) with tooth marks, mainly from the axial skeleton, including the skull, some sternebrae and vertebrae, and the innominate, as well as part of the limbs, such as femora, tibiae, calcaneum, scapulae, and humeri. The average number of marks per specimen is 2.5. The scores are the most abundant type of mark, followed by pits and punctures (Table 2). Punctures are located in the cervical, thoracic and lumbar vertebrae (both in the body and in the processes), the innominate (around the acetabulum), the scapula blade, the proximal metaphysis of the femur, and the proximal epiphysis of the tibia. Punctures show large difference in maximum length, from 1.96 to 9.68 mm; and the mean value is 3.68 mm (Table 3).

In this individual, no carnivore breakage was recorded, but 10 (9.52%) of the specimens are incomplete, and 90% of those present marks. In both scapulae, the medial border is missing. In the right femur, the proximal epiphysis is gone. In the innominates, the iliac crest and part of the ischium are absent. In four of the lumbar vertebrae, the body is present but some processes and the spine are absent. In one of the thoracic vertebrae, part of the spine is missing.

4.1.2. *Individual # FCS.CC.14 (collected: April 3, 2000)*

Category 2, 23–113 kg (*sensu* Bunn, 1986). This individual was found in a low area, 100 m from a shallow body of water. The guanaco was almost completely articulated. The carcass was divided into two portions separated at the dorsal-lumbar region, and a disarticulated forelimb was found 78 cm from the rest of the skeleton (Fig. 3). Some isolated bones were found around the main accumulation, such as three thoracic vertebrae and several ribs. There was some skin around the lower limbs and the neck. The age of this guanaco was estimated at 30–36 months old and the sex was determined as male. Most elements are present, with the exception of a few carpals and tarsals and half of the ribs (Table 1).

Table 1
Anatomical representation and carnivore marks proportions in the wild puma sample.

Anatomical unit	Individual						Total NISP	SM	
	#13	#137	#58	#66	#14	#65			
	NISP	NISP	NISP	NISP	NISP	NISP		N	%
Cranium	1	–	1	–	1	1	4	2	50
Mandible	1	–	1	–	1	1	4	1	25
Atlas	1	1	–	–	1	1	4	–	–
Axis	1	–	–	1	1	1	4	2	50
Cervical vertebrae	3	2	4	5	5	5	24	7	29.2
Thoracic vertebrae	3	–	–	8	12	12	35	5	14.3
Lumbar vertebrae	4	4	3	7	7	7	32	18	56.2
Caudal vertebrae	9	–	–	–	3	–	12	–	–
Sacrum	–	1	–	1	1	1	4	1	25
Rib	9	2	–	16	12	24	63	17	27
Sternebra	5	–	–	–	6	1	12	2	16.7
Scapula	2	2	2	1	2	2	11	8	72.7
Humerus	2	1	2	1	2	2	10	8	80
Radio-Ulna	2	1	2	1	2	2	10	5	62.5
Metacarpal	2	2	–	1	2	2	9	2	22.2
Innominate	2	2	–	2	2	2	10	7	77.8
Patella	2	–	–	1	2	1	6	–	–
Femur	2	2	1	2	2	2	11	7	63.6
Tibia	2	2	–	2	2	2	10	3	30
Metatarsal	2	2	–	2	2	1	9	2	22.2
Astragalus	2	2	–	2	2	1	9	–	–
Calcaneum	2	2	–	2	2	1	9	1	11.1
Tarsal	9	10	–	8	10	4	41	1	2.4
Carpal	13	7	–	6	13	12	51	–	–
1st Phalanx	8	6	–	6	8	4	32	4	12.5
2nd Phalanx	8	6	–	4	8	3	29	1	3.5
3rd Phalanx	8	6	–	3	8	2	27	–	–
Total	105	63	16	82	119	97	482	104	21.8

References: number of identified specimens (NISP); specimens with carnivore marks (SM).

Table 2
Frequency of specimens with carnivore marks and frequency of marks per individual in the wild puma sample.

	Individual												Total	
	#13		#137		#14		#58		#65		#66			
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Frequency of specimens with marks														
Presence	19	18.1	15	23.81	27	22.7	16	100	14	14.4	13	15.8	104	21.8
Punctures	13	68.4	9	60	2	7.4	16	100	6	42.9	4	30.8	50	48.1
Pits	7	36.8	7	46.7	2	7.4	12	75	8	57.1	8	61.5	44	42.3
Scores	15	78.9	15	100	22	81.5	14	87.5	12	85.7	8	61.5	86	82.7
Furrows	5	26.3	4	26.7	1	3.7	12	75	4	28.6	2	15.4	28	26.9
Crenulated edges	8	42.1	10	66.7	1	3.7	10	62.5	2	14.3	4	30.7	35	33.6
Scooping out	–	–	–	–	–	–	1	6.2	–	–	–	–	1	1
Frequency of marks														
Punctures	27	23.3	16	12.8	14	7	58	34.3	27	16.1	7	8.33	149	17.3
Pits	31	26.7	25	20	13	6.5	32	18.9	50	29.8	52	61.9	203	23.6
Scores	58	50	84	67.2	172	86.4	79	46.7	91	54.2	25	29.8	509	59.1
Total	116	100	125	100	199	100	169	100	168	100	84	100	861	100

Reference: percentage (%) was calculated considering the total number of specimens (Total NISP, Table 1) and the total number of specimens with marks (N).

Table 3
Puncture measurements in the wild and captive puma samples.

	n	Mean	IC − 95%	IC + 95%	SD	Min	Max	*p*-value*
All bone portions								
Guanaco #13	18	3.68	3.07	4.76	1.70	1.96	9.68	**0.000**
Guanaco #14	8	5.07	4.03	6.72	1.61	3.81	8.77	
Guanaco #58	33	4.03	3.60	4.73	1.59	1.77	8.39	
Guanaco #65	25	2.92	2.63	3.24	0.74	1.55	4.37	
Guanaco #66	5	2.77	2.03	3.53	0.60	2.12	3.46	
Guanaco #137	9	5.00	3.36	7.29	2.55	1.94	11.01	
Epiphyses								
Guanaco	12	3.88	3.00	5.11	1.66	1.94	7.91	0.238
Large vertebrate	9	5.27	3.54	7.35	2.48	2.30	9.81	
Small vertebrate	10	3.52	2.45	5.36	2.04	2.49	8.45	
Metaphyses								
Guanaco	17	4.91	3.99	6.27	2.22	2.54	11.01	0.491
Large vertebrate	22	4.81	4.31	5.51	1.36	2.61	8.30	
Small vertebrate	17	4.30	3.51	5.43	1.87	2.09	9.34	
Diaphyses								
Small vertebrate	4	4.29	3.63	5.50	0.59	4.24	5.45	
Axial bones_Cancellous								
Guanaco	25	3.40	3.01	3.78	0.93	1.77	4.97	**0.010**
Large vertebrate	21	4.51	3.89	5.61	1.89	2.12	9.53	
Axial bones_Thin cortical								
Guanaco	44	3.54	3.25	4.26	1.67	1.55	9.68	0.325
Large vertebrate	6	4.30	3.51	5.43	1.87	2.36	6.77	

Dimension (maximum length in millimeters) of punctures on different bone samples. Descriptive statistics include mean values, 95% confidence interval, standard deviation and minimum and maximum values. **p*-values for Kruskal Wallis test and Mann–Whitney U statistic. Values in bold are significant at $p < 0.05$.

This individual was lying on its left side; and accordingly, presented most of the carnivore modifications on the right side. The relative time of death was short and all the specimens are un-weathered.

There are 27 (22.68%; Table 2) specimens with tooth marks: lumbar, thoracic, cervical and axis vertebrae, innominates, ribs, scapula, humerus, radio-ulna, femur, tibia, metatarsal, and navicular. The scores are overrepresented in the sample in relation with the punctures and the pits (Table 2). All the punctures are present on the proximal metaphysis of the right femur and on the right ischium body. The mean value of the maximum length is 5.07 mm, and the minimum and maximum values are 3.81 and 8.77 mm (Table 3).

In this individual, no carnivore fractures were recorded, but 7 specimens (5.83%) with carnivore marks are incomplete. In one of the ribs, a small portion of the medial diaphysis is gone. In the right femur, the greater trochanter is absent. In the right innominate, the iliac crest and part of the ischium is missing. In four of the lumbar vertebrae, the right transverse process is gone. It is worth mentioning that the fifth cervical vertebrae had fissures in the anterior apophysis (Fig. 4c). These marks could be related to the puma-kill, as this felid often attack their prey with a bite to the neck or throat (Nallar et al., 2008).

4.1.3. Individual # FCS.CC.58 (collected: July 13, 2002)

Category 1b, 9–23 kg (*sensu* Bunn, 1986). This individual was found in the margin of a shallow body of water and was highly disarticulated. The vertebrae, ribs, and some fragments of the skull were scattered on the ground. The elements reached a maximum dispersion of 61 m. The age of this individual was calculated at three to six months old, and the sex could not be determined. Several bones were absent, including the atlas, axis, and thoracic vertebrae, sacrum, ribs, sternebrae, innominates, metarcarpal, patella, tibiae, metatarsal, phalanges, and some tarsals and carpals. Other bones were underrepresented, such as the cervical and lumbar vertebrae and femora (Table 1). The relative time of death was short and 15 of the specimens were un-weathered (93.75%), while only one (6.25%) was at weathering stage 1.

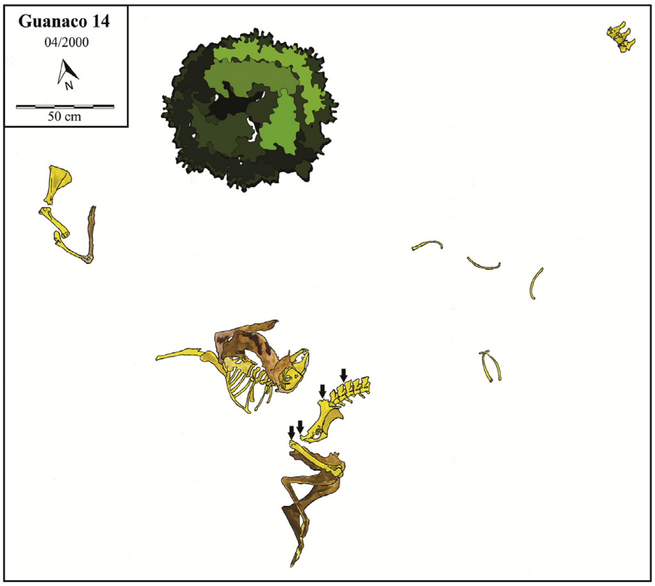

Fig. 3. Skeletal distribution map of guanaco individual #14. Arrows point to carnivore marks.

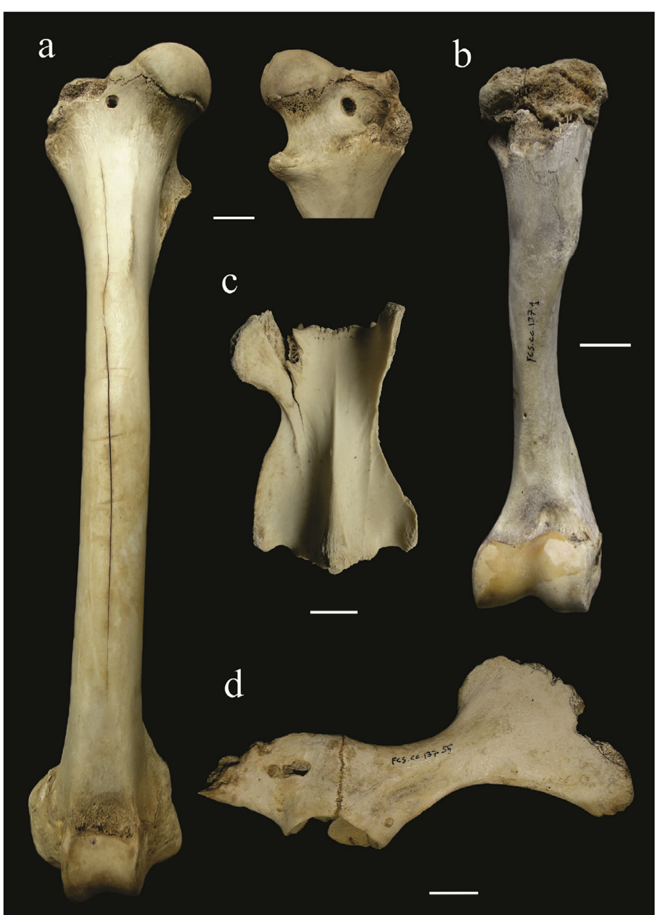

Fig. 4. Examples of damage inflicted by wild puma on guanaco bones: (a) Femur with furrowing and puncture on greater trochanter; (b) Humerus with furrowing on proximal epiphysis; (c) Cervical vertebra with fissure on transverse process; (d) Innominate with crenelation on iliac crest and puncture on ischium body. Scale = 2 cm.

All of the specimens present tooth marks (Table 2). The scores are the most abundant type. Punctures are well represented, and pits are not frequent. This individual shows the highest frequency of punctures, located mainly on the cervical vertebrae (body and arch) and humerus (proximal and distal epiphyses and metaphyses). Other elements which present punctures are the lumbar vertebrae (body and arch), radio-ulna (olecranon), femur (proximal metaphysis), scapula (acromion and blade), and mandible (angle). Punctures show large difference in size, from 1.77 to 8.39 mm; and the mean value is 4.03 mm (Table 3).

In this individual, 15 specimens (93.75%) were incomplete and four of them presented fractures (Table 2). In the two ribs, the proximal and distal epiphyses are gone. In the right humerus, part of the distal epicondyles is absent and the proximal epiphysis is missing. This specimen presents a fresh fracture along the proximal diaphysis. In the left humerus, the proximal epiphysis is gone. In the skull, only the maxillas and parts of the parietals are present. In the mandible, the condyles and coronoid processes are gone. In the scapulae, the tubercles and the medial border are missing. The great trochanter in the right femur and the olecranon in the right radio-ulna are gone. The four cervical vertebrae were incomplete. These elements present loss of bone tissue and fractures in the body. In two of the lumbar vertebrae, the left transverse processes and the spine are absent, and a third vertebrae is missing both the transverse processes and the arch.

4.1.4. Individuals # FCS.CC.65 and # FCS.CC.66 (collected: January 19, 2003)

Adult: Category 2, 23–113 kg (*sensu* Bunn, 1986). Unborn: Category 1b, 9–23 kg (*sensu* Bunn, 1986). These two individuals correspond to a female guanaco and its unborn fetus. They were found in a low area under a shrub. The adult animal was 60–72 months, and the unborn was between 10 and 11 months of gestation (the sex could not be determined). In reference to the adult female, the axial skeleton was articulated while the limbs were scattered with some bone portions articulated and others separated, such as the femora and other long bones. The elements reached a maximum dispersion of 29 m. All the anatomical elements are present but the sternebrae, ribs, innominates, patellae, metatarsal, and astragalus are underrepresented. In the case of the unborn individual, the skull, mandible, atlas, and sternebrae are absent; and the thoracic vertebrae, ribs, scapulae, humeri, radio-ulnae, metacarpal, patellae, tarsal, carpal, and phalanges are underrepresented (Table 1). The relative time of death was short; with 72 of the adult specimens (75%) un-weathered, and 24 in weathering stage 1 (25%). All the specimens of the unborn individual (82) were in stage 0.

Fourteen specimens (15%; Table 2) of the adult individual show tooth marks, which include the ribs, tibiae, humeri, radio-ulnae, sternebrae, thoracic vertebrae, and innominates. In the case of the unborn individual, 13 specimens (14.43%; Table 2) present tooth marks, including the axis, lumbar vertebrae, ribs, innominates, radio-ulnae, femora, metatarsal, and the first and second phalanges. For the adult, the scores prevail, followed by pits and punctures. In the case of the unborn, the pits are abundant, followed by scores and punctures. The adult individual presents abundant punctures, all of them located on the sternebra and on the distal portion of a few ribs. On average, punctures are 2.92 mm in maximum length; and the minimum and maximum values are 1.55 and 4.37 mm (Table 3). A considerably lower number of punctures are observed in the unborn individual, though they are present in various elements, including one distal metatarsal, one proximal phalange, one distal epiphysis of the radio, and one proximal rib. Marks are between 2.12 and 3.46 mm in maximum length, and the mean value is 2.77 mm (Table 3).

In the adult individual, no breaks were recorded but 7 of the specimens (8.54%) are incomplete. Four of those specimens present carnivore marks. In six of the ribs, some portions of the distal end are gone. In the sternebra, the ends are missing. In the unborn individual, 5 specimens (6%; all of them with carnivore marks) were incomplete and two were fractured. These correspond to two of the first phalanges, in which the distal epiphysis is absent. In the left scapula, a portion of the medial border is gone. In the axis, part of the proximal arch is absent, and in one of the lumbar vertebrae both transverse processes are gone.

4.1.5. Individual # FCS.CC.137 (collected: February 10, 2006)

Category 2, 23–113 kg (*sensu* Bunn, 1986). This individual was found under a shrub, along with a fresh hare carcass (see Fig. 1). The age of this animal was estimated at six to nine months old and the sex could not be determined. Few bone elements are present (Table 1). The skull, mandible, axis, thoracic vertebrae, sternebrae, and the patella are absent. The cervical and lumbar vertebrae, ribs, humeri, radio-ulnae, tarsals, carpals, and phalanges are underrepresented. The relative time of death was likely short, and most of the specimens are un-weathered (n = 60; 95%). However, two specimens (3%; metatarsal and radio-ulna) are in weathering stage 1 and one specimen (2%; tibia) in stage 2 (*sensu* Behrensmeyer, 1978).

The specimens with tooth marks (n = 15, 24%; Table 2) include the humeri, metacarpal, scapulae, femora, innominates, sacrum, lumbar vertebrae, and ribs. The scores are the most abundant type of tooth marks in the sample, followed by pits and punctures (Table 2). The punctures are located mainly on the innominate (in the ischium and ilium body), and the femur (proximal metaphysis); though they are also observed on the lumbar vertebrae processes, humerus (tuberosity), and the scapula (neck). Punctures size range from 1.94 to 11.01 mm; and the mean value is 5.00 mm (Table 3).

In this individual, no carnivore breakage was recorded, but 13 specimens (20.63%) with carnivore marks are incomplete. In the two ribs, the proximal and distal epiphyses are gone. In both scapulae, the medial border and tubercles are absent, and the glenoid cavity of the right scapulae is missing. In the right femur, the proximal epiphysis is gone. In the innominate, the iliac crest and part of the ischium are absent. In the left humerus, part of the head and greater tubercle and proximal diaphysis are missing. In four of the lumbar vertebrae, the body is present but some processes are gone. In the sacrum, the spinous process is missing.

4.1.6. Synthesis of the wild puma sample

Our results indicate a low modification in the guanaco carcasses (Table 4). If we compare the age classes, the young individuals present a greater frequency of damage. In the affected bones, the majority are within stage I, followed by stages II and IV (Table 4). The adult individuals present a high percentage of long bones without modifications; and those with damage, only reach a stage I.

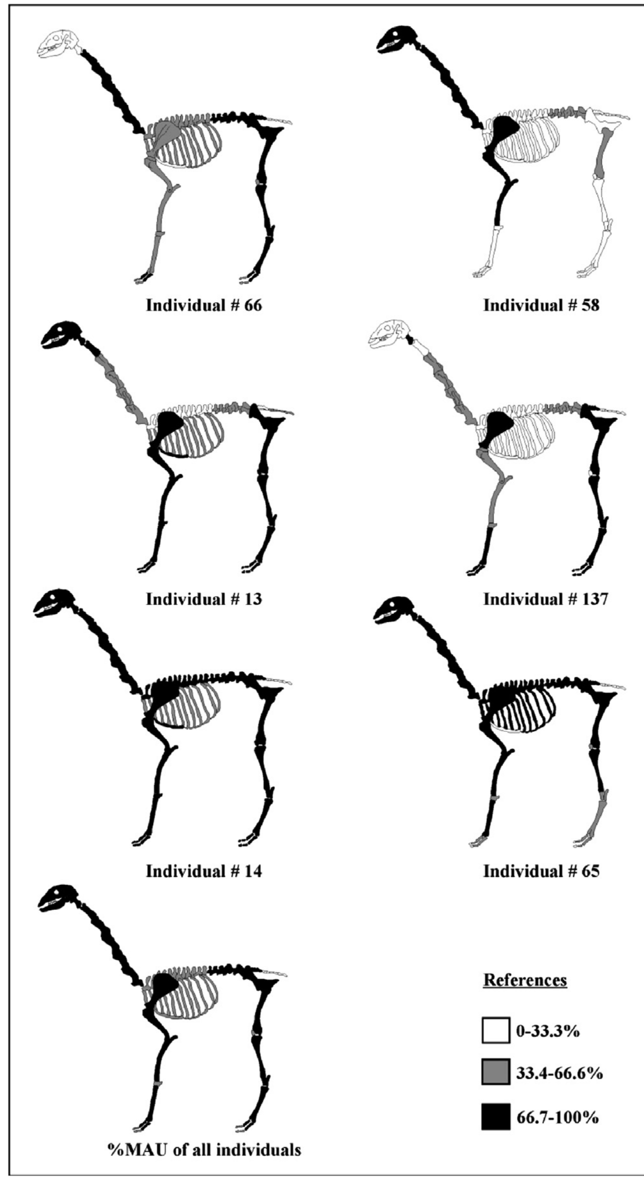

Fig. 5. Skeletal representation (%MAU) of guanaco.

In the six guanaco individuals, variability in the grade of completeness is observed (Fig. 5). Considering the age of the individuals, there is a greater destruction of the rib cage as well as the skull and the primary cervical vertebrae in the unborn and newborn. For these individuals, 16.16% (n = 43) of the bones are

Table 4
Quantitative data of the bone modification stages (*sensu* Haynes, 1981, 1982; Sala et al., 2014) in long bones of guanaco consumed by wild puma.

	NULL			Low			Moderate						Heavy						NR		
				I			II			III			IV			V					
	Y	A	T	Y	A	T	Y	A	T	Y	A	T	Y	A	T	Y	A	T	Y	A	T
Femur	3	3	6	–	1	1	–	–	–	2	–	2	2	–	2	–	–	–	7	4	11
Tibia	6	4	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	4	10
Humerus	2	4	6	1	–	1	1	–	1	–	–	–	2	–	2	–	–	–	6	4	10
Radius–Ulna	6	4	10	–	–	–	2	–	2	–	–	–	–	–	–	–	–	–	8	4	12
Metapodial	7	6	13	4	1	5	–	–	–	–	–	–	–	–	–	–	–	–	11	7	18
%	63.2	91.3	73.8	13.1	8.7	11.5	7.9	–	4.9	5.3	–	3.3	10.5	–	6.5	–	–	–	38	23	61

References: young (Y): individuals 13, 137, 58 and 66; adult (A): individuals 14 and 65; total (T); number of remains (NR).

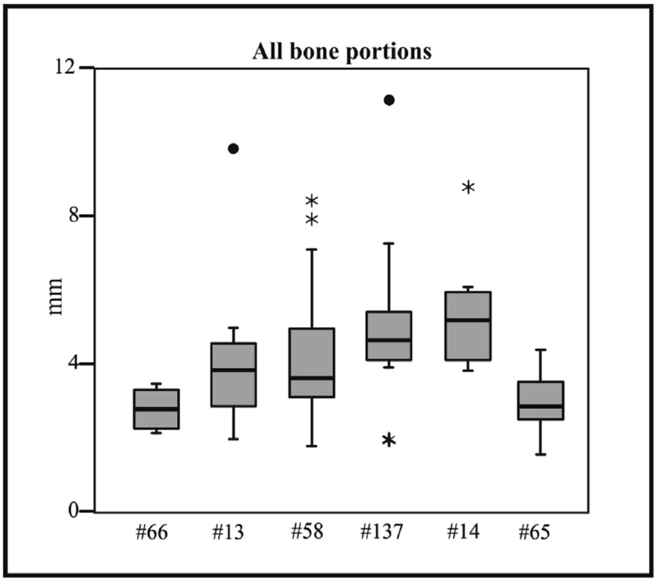

Fig. 6. Box plots showing the range of variation in maximum length of the punctures from the guanaco bone sample, by individual.

incomplete. In regards to the sub-adult and adult individuals, there is a greater completeness of the carcasses and bone elements, with only 6.48% (n = 14) of the bones incomplete.

Among the bone specimens registered with carnivore marks, the most affected are the humerus, followed by the innominate, scapula, femur, radius–ulna, axis, and skull (see Table 1). In reference to the frequency of specimens with marks and the average number of marks per specimen, the most affected elements are the sternebra, followed by the skull, innominate, femur, scapula, and ribs. In particular, punctures are more frequent on the innominate (three individuals) and on the proximal portion of the femur (4 individuals). This type of tooth mark shows significant differences in size, with a mean value of 3.76 mm for the total sample of guanaco bones. A Kruskal Wallis test shows that there is a significant difference when comparing the maximum length of punctures from different individuals (p = 0.000). On average, the size of punctures increases in a direct relationship with age (Table 3; Fig. 6). In general, the difference in puncture size is significant when individuals are distant in age (Table 5). Contrary to this trend, no statistical difference is observed between the youngest and oldest individuals, corresponding to the female and its unborn fetus (Individuals #65 and #66, respectively). Besides the circular to oval punctures included in the metric analysis, seven marks possibly made by multi-cusped teeth are present in the guanaco bones (Fig. 7A). Two of these marks are very large: one is 15.42 mm in maximum length and 4.89 mm in maximum breadth, and the other is 14.13 mm in maximum length and 6.39 mm in maximum breadth.

Table 5
The Mann–Whitney U-tests (p-values) for differences in the dimension (maximum length in millimeters) of punctures from different guanaco individuals.

Individual	#13	#58	#137	#14	#65
#66	0.062	0.036	**0.020**	**0.003**	0.636
#13		0.554	0.054	**0.012**	**0.016**
#58			0.129	0.031	**0.001**
#137				0.773	**0.001**
#14					**0.000**

Values in bold are significant at $p < 0.05$.

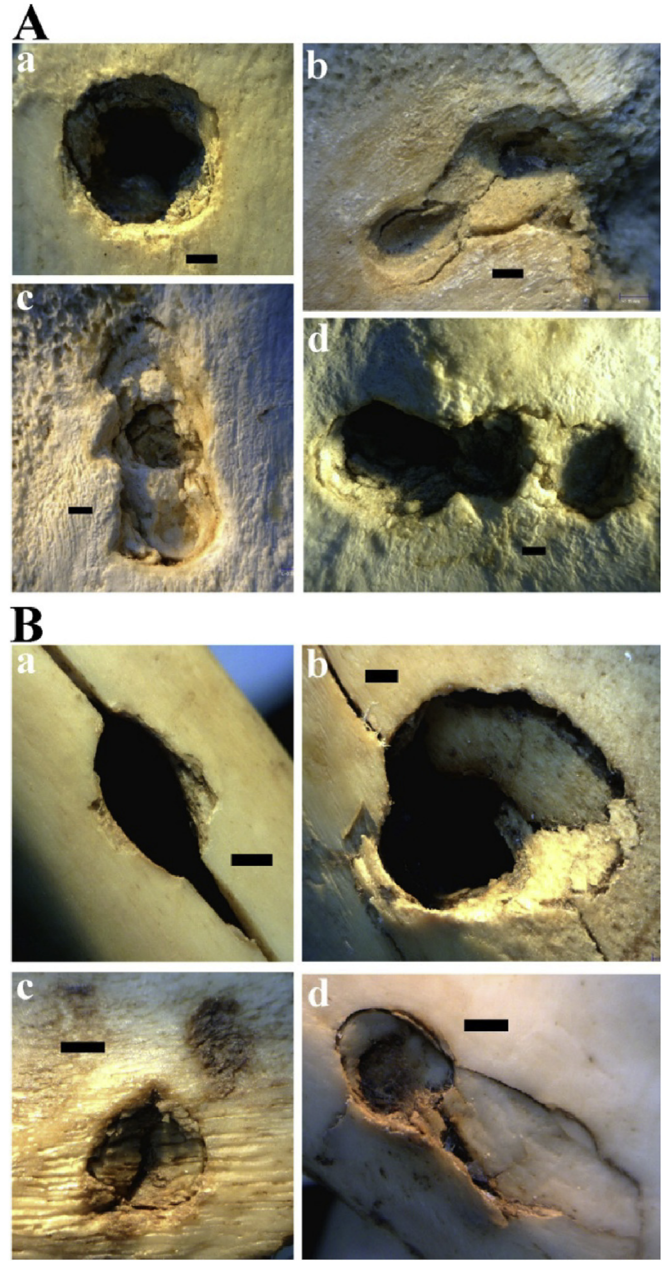

Fig. 7. A. Detail of punctures on guanaco bones from the wild puma sample. (a) circular puncture; (b–d) irregular punctures. B. Detail of punctures on guanaco bones from the captive puma sample. (a–c) circular punctures; (d) irregular puncture. Scale = 1 mm.

4.2. Captive puma sample

A total of 145 bone remains were recovered from the puma enclosure, 136 of which were identified taxonomically and anatomically. A total of 113 specimens were assigned to large vertebrates distributed as followed: *Sus scrofa* (NISP = 74), *Ovis aries* (NISP = 4), *Lama glama* (NISP = 4), Artiodactyla (NISP = 5), and undetermined mammalian (NISP = 26). Twenty-three bone specimens were determined as small vertebrates: *Lepus europaeus* (NISP = 14), and *Gallus gallus* (NISP = 9). With the exception of domestic pig (MNI = 2) and European hare (MNI = 4), the rest of the taxa have a minimum number of one individual

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Fig. 8. Examples of damage inflicted by captive puma: (a) Domestic pig innominate with crenelation, scoring, punctures and pitting; (b) Femur of domestic pig with furrowing, scoring, pitting and punctures on proximal and distal epiphyses; (c) Lumbar vertebra of domestic pig with punctured lateral process and body; (d) Thoracic vertebra of Artiodactyla with broken dorsal spine; (e) Tibia of European hare with puncture on proximal epiphysis; (f–g) Ribs of large mammal (f) and llama (g) with crenulated edge on the sternal extremity and lower edge. Scale = 2 cm.

(Supplementary Table 1). The analysis of the total sample indicates that 68% of the bone specimens are fractured and that 56.5% presents some carnivore damage (Fig. 8). A greater proportion of specimens with carnivore marks were observed in the small vertebrate sample (Fig. 7B). In both vertebrate classes, pits, punctures, and scores are the most abundant tooth marks (Table 6, Fig. 7B). Puncture size distribution is very similar in both samples: in the large vertebrates, the mean value of the puncture maximum length is 4.75 mm, and the minimum and maximum values are 2.12 mm and 9.81 mm; in the small vertebrates, the mean value is 4.11 mm, and the minimum and maximum values are 2.09 mm and 9.34 mm. Additionally, six irregular punctures not included in the metric analysis were present (Fig. 7B(d)). Two of them, particularly large, were possibly created by a multi-cuspid tooth. One of them was observed in a proximal femur of domestic pig (10.9 × 7.1 mm) and the other in a tibia diaphysis of European hare (12.9 × 6.6 mm).

We estimated the damage produced in the captive puma sample for *Sus scrofa*. This is the better represented taxa in this sample and is similar in body size to the guanaco. The modification generated by puma can be categorized as light (Table 7).

5. Discussion

Different lines of evidence registered in the field, such as feces, footprints, and direct observations of the animals suggest the intervention of the Pampas fox (*Lycalopex gymnocercus*) in the guanaco carcasses after the puma kill. In previous studies using the same guanaco collection; the disarticulation and movement of anatomical units generated by fox on individuals of different ages and causes of death were studied (Kaufmann and Messineo, 2002). Additionally, bone remains found in fox feces were collected and analyzed (Gómez and Kaufmann, 2007). Consequently, some of the properties of the guanaco bone assemblage analyzed here cannot be solely the result of the action of the puma, especially the pattern of anatomical representation. Nevertheless, the studies of South American foxes inform that the modifications from these small sized carnivores are generally restricted to gnawing on bony portions like processes, scapula blades, trochanters, apophysis, ilium, ischium, and distal epiphysis of ribs. This action produces small punctures, pits, and scores; producing light damage in the carcass of medium sized prey (Borrero, 1990; Fernández et al., 2010; Mondini, 2012).

We consider that the guanaco bone assemblages reflect ecological interactions common in nature where more than one agent is responsible for carcass modification. The scavenging of the carcasses by small sized carnivores in the puma-kill sites is frequently mentioned in other naturalistic studies (Martin and Borrero, 1997; Nasti, 2000; Logan and Sweanor, 2001; Borrero et al., 2005; Stiner et al., 2012). These combined actions create averaged assemblages expected in the fossil assemblage. This argument highlights the importance of complementing naturalistic studies with controlled experiments which together can provide useful information to discuss the interaction between the different agents that integrate ecosystems. Thus, we consider that our results of the captive puma sample, where there is unequivocal relationship between predator and prey, are of vital importance to strengthen the pattern of bone modifications generated in the naturalistic context.

After the guanaco bones were disarticulated by the puma, anatomical parts such as ribs, thoracic vertebrae and some appendicular elements were dispersed by fox. In the six guanacos, we observed an important variability in the degree of skeletal completeness. When considering age, the unborn and young individuals have a higher absence of the rib cage, skull, and the first cervical vertebra. In the case of the sub-adult and adult individuals, there is a greater integrity of the carcasses and skeletal elements.

Despite the complex origin of the analyzed sample, we can extract useful information to characterize the bone modification patterns produced by puma on medium sized ungulates. In natural settings, the percentage of affected bones reflects the intensity of carcass utilization by carnivores, which depends on several ecological factors such as the abundance and vulnerability of prey in the environment and the degree of competition between predators; among other factors (Iriarte, 1988; Sunquist and Sunquist, 1989; Rau et al., 1991). Furthermore, studies of samples collected in different contexts indicate that the frequency of damage is greater in the carnivore den than at the kill site (Haynes, 1980a). In the puma-kill sites studied here, 22% of the bones present some type of modification assigned to carnivores. This data is similar to those registered by Nasti (2000) in vicuñas (23%) from the Puna region of Argentina, and lower to those registered by Muñoz et al. (2008) in guanaco (34%) from the Central Andes. If we consider the age of the individuals, the sub-adults and adults present 19% of their bones with carnivore marks, and the young and unborn present 24%. As expected, higher percentages were observed in the zoo

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Table 6
Frequency of specimens with carnivore marks and frequency of marks per individual in the captive puma sample.

	Large vertebrate >10 kg												Small vertebrate <10 kg					
	Sus scrofa		*Ovis aries*		*Lama glama*		Artiodactyla		Mammal		Total		*Lepus europaeus*		*Gallus gallus*		Total	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Specimens with marks																		
Presence	33	44.6	3	75	4	100	3	60	17	61.5	60	53.1	10	71.4	9	100	19	82.6
Punctures	18	54.5	2	66.7	3	75	2	66.7	8	47.1	33	55	7	77.8	5	55.6	12	63.2
Pits	19	57.6	2	66.7	4	100	3	100	8	47.1	36	60	10	100	8	88.9	18	94.7
Furrowing	8	24.2	–	–	–	–	–	–	4	23.5	12	20	–	–	–	–	–	–
Scores	19	57.6	2	66.7	4	100	1	33.3	7	41.2	26	43.3	7	70	5	55.6	12	63.4
Crenulated edges	4	12.2	–	–	2	50	1	33.3	6	35.3	13	21.6	1	10	–	–	1	5.3
Notch	–	–	–	–	–	–	–	–	–	–	–	–	3	30	2	22.2	3	15.8
Indeterminate	1	3	–	–	1	25	–	–	–	–	2	3.3	2	20	–	–	2	10.5
Frequency of marks																		
Punctures	68	29.7	4	36.4	9	10.7	3	23.1	16	17.8	100	23.4	26	25.7	14	29.2	40	26.9
Pits	59	25.8	4	36.4	45	53.6	9	69.2	48	53.3	165	38.6	40	39.6	25	51.1	65	43.6
Scores	102	44.5	3	27.2	30	35.7	1	7.7	26	28.9	162	37.9	35	34.7	9	18.8	44	29.5
Total	229	100	11	100	84	100	13	100	90	100	427	100	101	100	48	100	149	100

Table 7
Quantitative data of the bone modification stage in domestic pig long bones consumed by captive puma.

	NULL	Low	Moderate		Heavy		NR
		I	II	III	IV	V	
Femur	–	–	1	–	1	–	2
Tibia	–	2	–	1	–	–	3
Humerus	–	–	–	–	1	–	1
Metapodial	4	2	–	1	–	–	7
%	30.8	30.8	7.6	15.4	15.4	–	13

References: number of remains (NR).

sample, with carnivore marks in 53% of the bones in large vertebrates, and 83% in small vertebrates.

With respect to the stages of carcass utilization (*sensu* Haynes, 1981, 1982; Sala et al., 2014) the modification pattern in both age classes of the guanaco is light. However, the young individuals have a higher frequency of bone damage. A light modification pattern was also recorded in the domestic pig sample recovered from the zoo. Yet, the frequencies of specimens with bone modifications from the pig sample were considerably higher than the guanaco bones found in the wild. The increased use of carcasses in captivity has been suggested for other carnivores like wolves and lions (Gidna et al., 2013; Sala et al., 2014). The greater degree of damage in situations of captivity is a response to the animals' stereotypic behaviors, such as “boredom chewing” on bones, and that carnivores have been removed from the pressure of selective factors of their original ecological habitats. These behaviors produce artificially high bone modification patterns, not commonly documented in the wild (Carlstead, 1996). Nevertheless, we believe that the information derived from captive environments provides valuable evidence related to the type and size of the marks, as demonstrated in this work.

In general, our results from the wild puma sample, in terms of the intensity in the use of carcasses, are consistent with those obtained in other puma studies (Nasti, 2000; Borrero et al., 2005; Stiner et al., 2012). Previous authors mention a light intensity in the utilization of the carcasses and a high survival of all the skeletal parts. An exception to these observations is found in the taphonomic study of an adult guanaco from the Laguna del Diamante Reserve in Mendoza, Argentina. This particular case shows an intensive use of the carcass, including the breakage of the skull to access the brain tissue (Mondini and Muñoz, 2008; Muñoz et al., 2008). While this case greatly contributes to understand the variability in the intensity of the use of carcasses by puma, it should be kept in mind that this is a single example where it records such significant consumption intensity.

The bones with a higher frequency of damage are the humerus, pelvis, scapula, femur, ulna, radius, lumbar vertebra, axis and skull. As with other studies with similar sized prey consumed by puma (Borrero and Martin, 1996; Nasti, 2000; Borrero et al., 2005; Stiner et al., 2012), there are very few fractured elements. For the young individuals, fractures were observed on the proximal end of two humeri, on the distal end of two ribs, and on the proximal metaphysis of two phalanxes. Furthermore, fissures and other types of damage were observed on the cervical vertebra of a sub-adult. The modifications to guanaco elements are linked to the kill technique and feeding behavior of the puma (Nallar et al., 2008; Palmeira et al., 2008; Canedi, 2011). The modifications found on the cervical vertebra and the skull could be the result of suffocation and biting to the throat during the puma kill. Other modifications would be related to the feeding habits, which provoke greater damage to the scapula, the upper forelimb, the pelvis, and upper

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hindquarter and rib cage. This anatomical pattern of damage is consistent with those mentioned in other naturalistic studies (Borrero and Martin, 1996; Nasti, 2000; Muñoz et al., 2008; Stiner et al., 2012).

The type of modification with greater frequency in the wild puma sample is scores, followed by similar proportions of punctures and pits. This modification pattern is comparable to those registered by Muñoz et al. (2008); however, it differs in the frequency and proportion at which each is present in the sample. There is a notable difference in the frequency of scores with respect to punctures and pits in our study. The other types of modifications, such as furrows and crenulated edges present moderate values and we only registered evidence of scooping out in one individual.

Through the traces left on the bones in the naturalistic sample analyzed here, it is difficult to identify which teeth were responsible for the marks. As observed in other prey hunted by puma (Martin and Borrero, 1997; Muñoz et al., 2008; Stiner et al., 2012), the punctures were commonly found on the body of the ilium and ischium, and around the femoral head. Punctures show a great variability in size and on average are 3.8 mm. A maximum length of 11 mm was recorded in the sample of sub-circular punctures. We consider that most of these marks were created by the puma with their canines during the kill, dismembering and defleshing of their prey. The presence of large punctures could be diagnostic of the puma, helping to differentiate the action of this felid from other South American carnivores, such as foxes. Although detailed metric analyses of tooth marks produced by foxes on guanaco or similar preys are lacking, preliminary data on this smaller carnivore indicate a mean value of 2 mm for punctures (Nasti, 2000).

Additionally, larger punctures (14–15 mm) with irregular shapes are present [referred as “tooth impressions” by Andrews and Fernandez Jalvo (1997)]. These particular tooth marks were made by multi-cusped check teeth. This interpretation is supported by a feeding experiment conducted by Burke (2013) with mountain lions and bobcats which demonstrated that these felids do not utilize their paws for leverage to remove flesh, but use almost every tooth in their dental arcade to remove soft tissue, with the exception of the smallest molars. Likewise, Muñoz et al. (2008) observed the presence of a large tooth mark (18.4 mm) in a guanaco killed by a puma. The authors attributed this large mark as produced by a carnassial tooth.

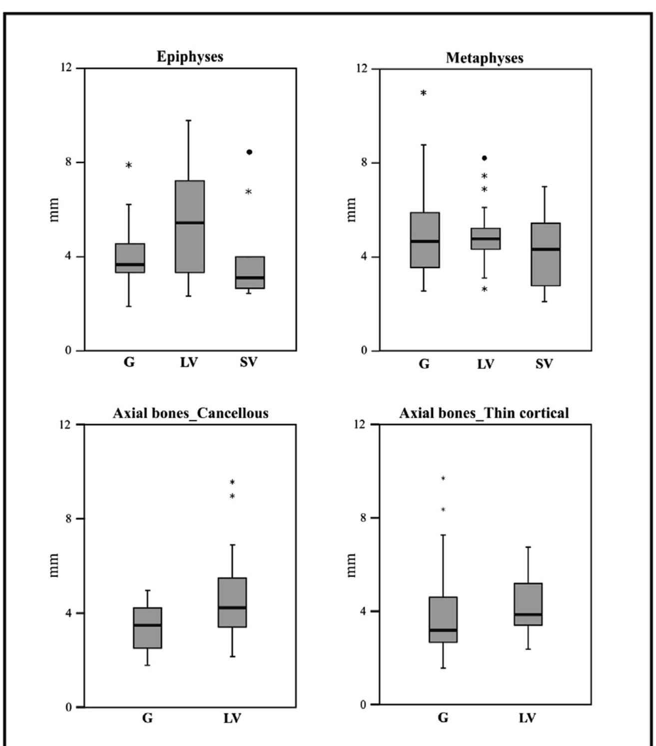

Fig. 9. Box plots showing the range of variation in maximum length of the punctures from the guanaco (G), large vertebrates (LV) and small vertebrates (SV) samples, stratified by bone portions.

With respect to the captive puma sample, we observed that the most common types of modifications are the same as those observed in the wild puma sample, although the frequencies of marks are different. In the large vertebrate sample, the most abundant marks are pits, followed by punctures and scores. In the sample of small vertebrates, the pits continue to be abundant, followed by similar proportions of punctures and scores. The size distribution of punctures in large and small vertebrates (from approx. 2 to 10 mm) is similar to the guanaco sample, although slightly higher mean values were recorded in the zoo samples. Fig. 9 shows a substantial overlap in the maximum length of punctures when the sample is stratified by bone regions. Only a significant difference was observed when comparing the length of punctures on cancellous bone from axial elements in the guanaco and large vertebrate samples (see Table 3). This minor difference in puncture size between the captive and wild puma sample could be the result of the inclusion of some punctures produced by foxes. Despite this confounding factor, we believe that the distribution of puncture sizes from both samples (in combination with other types of damage and contextual information) can be used as a frame of reference to identify puma predation in fossil assemblages.

6. Conclusions

Since the initial peopling of America, pumas and humans have preyed on the same species and have occupied the same places in the landscape. Our results constitute a valuable contribution to characterize puma action and thus identify the participation of this agent in the formation of the fossil record. The data presented here confirm that this predator is characterized by its partial consumption of their prey, thus providing potential resources for scavenging by other agents such as foxes. As some authors have suggested, during moments of the initial settlement of South America, carcasses with minimal consumption by the puma would have offered an alternative food supply for human populations (Borrero et al., 2005:111; Martin, 2013:348–350). The close interaction between carnivores and humans in rock shelters and caves of this region has been recognized and discussed in detail by other researchers (Borrero et al., 1988, 2005; Mondini, 2002; Martin, 2012, 2013).

Although the naturalistic sample analyzed here is small, a tendency towards the selection of the most vulnerable individuals in the population (young individuals) is observed. These observations are sustained by wildlife conservation studies which inform of pumas predominantly preying on calves (Palmeira et al., 2008). This expected mortality profile, dominated by young individuals, constitutes a complementary line of evidence that would help to infer the role of large felids in the fossil record. As we mentioned, the puma generates a light modification in their prey, characterized by a low number of fractured and damaged bones which are concentrated on the upper part of the front and hind limbs, rib cage, scapula, and pelvis. The most frequent type of damage corresponds to scores, pits, and punctures. In agreement with previous published work (Martin and Borrero, 1997; Muñoz et al., 2008), the metric analysis in the present study indicates that punctures by puma are generally 3.5–5 mm; although larger tooth marks

(>10 mm) should be expected; some of them possibly made by multi-cusped check teeth such as the carnassial.

While none of the variables analyzed in this work is independently a defining criterion to infer the role of the big cats in the formation of the fossil assemblage, combining them under a naturalistic and experimental approach offers a heuristic model to apply to past contexts. The long standing contributions of Gary Haynes to archaeological interpretations from an actualistic taphonomy approach constitute a baseline for understanding the paleoecological interactions between carnivores and humans. In Argentina, his proposals have inspired the development of research programs that generate a growing body of knowledge available to taphonomic archeology.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2016.03.003.

References

Álvarez, M.C., Kaufmann, C.A., Massigoge, A., Gutiérrez, M.A., Rafuse, D.J., Scheifler, N.A., González, M.E., 2012. Bone modification and destruction patterns of leporid carcasses by Geoffroy's cat (Leopardus geoffroyi): an experimental study. Quaternary International 278, 71–80. http://dx.doi.org/10.1016/j.quaint.2011.11.029.

Andrés, M., Gidna, A.O., Yravedra, J., Domínguez-Rodrigo, M., 2012. A study of dimensional differences of tooth marks (pits and scores) on bones modified by small and large carnivores. Archaeological and Anthropological Sciences 4, 209–219. http://dx.doi.org/10.1007/s12520-012-0093-4.

Andrews, P., Fernandez Jalvo, Y., 1997. Surface modifications of the Sima de los Huesos fossil humans. Journal of Human Evolution 33, 191–217. http://dx.doi.org/10.1006/jhev.1997.0137.

Bank, M.S., Sarno, R.J., Franklin, W.L., 2003. Spatial distribution of guanaco mating sites in southern Chile: conservation implications. Biological Conservation 112, 427–434. http://dx.doi.org/10.1016/S0006-3207(02)00342-7.

Behrensmeyer, A.K., 1978. Taphonomic and ecological information from bone weathering. Paleobiology 4, 150–162.

Binford, L.R., 1978. Nunamiut Ethnoarchaeology. Academic Press, New York, United States.

Binford, L.R., 1981. Bones: Ancient Men and Modern Myths. Academic Press, New York, United States.

Blumenschine, R.J., 1986. Early Hominid Scavenging Opportunities; Implications of Carcass Availability in the Serengeti and Ngorongoro Ecosystems. BAR International, Oxford.

Borrero, L., 1990. Taphonomy of guanaco bones in Tierra del Fuego. Quaternary Research 34, 361–371. http://dx.doi.org/10.1016/0033-5894(90)90047-O.

Borrero, L.A., 2013. Estrategias de Caza en Fuego-Patagonia. Comechingonia. Revista de Arqueología 17, 11–26.

Borrero, L.A., Lanata, J.L., Borella, F., 1988. Reestudiando huesos: nuevas consideraciones sobre sitios de Última Esperanza. Anales del Instituto de la Patagonia (Serie de Ciencias Sociales) 18, 133–155.

Borrero, L.A., Martin, F.M., 1996. Tafonomía de carnívoros: un enfoque regional. In: Otero, G. (Ed.), Arqueología. Sólo Patagonia. CENPAT-CONICET, Puerto Madryn, pp. 189–198.

Borrero, L.A., Martin, F.M., Vargas, J., 2005. Tafonomía de la Interacción entre Pumas y Guanacos en el Parque Nacional Torres del Paine, Chile. Magallania (Punta Arenas) 33, 95–114.

Brain, C.K., 1981. The Hunters or the Hunted. University of Chicago Press, Chicago.

Bunn, H.T., 1986. Patterns of skeletal representation and hominid subsistence activities at Olduvai Gorge, Tanzania, and Koobi Fora, Kenya. Journal of Human Evolution 15, 673–690. http://dx.doi.org/10.1016/S0047-2484(86)80004-5.

Burke, C.C., 2013. Neotaphonomic analysis of the feeding behaviors and modification marks produced by North American carnivores. Journal of Taphonomy 11, 1–20.

Canedi, A., 2011. Gatos Salvajes, Félidos Neotropicales de la provincia de Jujuy. Universidad Nacional de Jujuy, Jujuy, Argentina.

Carlstead, K., 1996. Effects of captivity on the behavior of wild mammals. In: Kleiman, D.G., Allen, M.E., Thompson, K.V., Lumpkin, S. (Eds.), Wild Mammals in Captivity: Principles and Techniques. University of Chicago Press, Chicago, pp. 317–333.

Cartajena, I., 2007. Una propuesta metodológica para la estandarización de medidas en huesos cortos de camélidos y para la determinación de sexo. Werken 10, 49–62.

Cohen, B.F., Kibii, J.M., 2015. Experimental study of bone modification by captive caracal (Caracal caracal); a model for fossil assemblage analysis. Journal of Archaeological Science 62, 92–104. http://dx.doi.org/10.1016/j.jas.2015.07.008.

Culver, M., Johnson, W.E., Pecon-Slattery, J., O'Brien, S.J., 2000. Genomic ancestry of the American puma (Puma concolor). The Journal of Heredity 91, 186–197. http://dx.doi.org/10.1093/jhered/91.3.186.

de Lamo, D.A., Saba, S., 1993. Características del parto normal en el guanaco (Lama guanicoe). Veterinaria Argentina X, 33–37.

de Ruiter, D.J., Berger, L.R., 2000. Leopards as taphonomic agents in dolomitic caves — implications for bone accumulations in the hominid-bearing deposits of South Africa. Journal of Archaeological Science 27, 665–684. http://dx.doi.org/10.1006/jasc.1999.0470.

Delaney-Rivera, C., Plummer, T.W., Hodgson, J.A., Forrest, F., Hertel, F., Oliver, J.S., 2009. Pits and pitfalls: taxonomic variability and patterning in tooth mark dimensions. Journal of Archaeological Science 36, 2597–2608. http://dx.doi.org/10.1016/j.jas.2009.08.001.

Domınguez-Rodrigo, M., 1999. Flesh availability and bone modifications in carcasses consumed by lions: palaeoecological relevance in hominid foraging patterns. Palaeogeography, Palaeoclimatology, Palaeoecology 149, 373–388. http://dx.doi.org/10.1016/S0031-0182(98)00213-2.

Domínguez-Rodrigo, M., Pickering, T.R., Bunn, H.T., 2010. Configurational approach to identifying the earliest hominin butchers. Proceedings of the National Academy of Sciences of the United States of America 107, 20929–20934. http://dx.doi.org/10.1073/pnas.1013711107.

Domínguez-Rodrigo, M., Piqueras, A., 2003. The use of tooth pits to identify carnivore taxa in tooth-marked archaeofaunas and their relevance to reconstruct hominid carcass processing behaviours. Journal of Archaeological Science 30, 1385–1391. http://dx.doi.org/10.1016/S0305-4403(03)00027-X.

Elkin, D., Mondini, M., 2001. Human and small carnivore gnawing damage on bones - an exploratory study and its archeological implications. In: Kuznar, L.A. (Ed.), Ethnoarchaeology of Andean South America: Contributions to Archaeological Method and Theory, International Monographs in Prehistory, Ethnoarchaeological Series, Ann Arbor, vol. 4, pp. 255–265.

Fernández, P.M., Cruz, I., Forlano, A., 2010. Sitio 37: una madriguera de carnívoro en el norte de la Patagonia Andina (Cholila, Provincia de Chubut, Argentina). In: Gutiérrez, M.A., De Nigris, M., Fernández, P.M., Giardina, M., Gil, A.F., Izeta, A., Neme, G., Yacobaccio, H.D. (Eds.), Zooarqueología a Principios Del Siglo XXI: Aportes Teóricos, Metodológicos Y Casos de Estudio. Libros del Espinillo, Buenos Aires, pp. 409–417.

Franklin, W.L., 1983. Contrasting socioecologies of South America's wild camelids: the vicuña and the guanaco. In: Eisemberg, J.F., Kleiman, D.G. (Eds.), Advances in the Study of Mammalian Behavior. American Soc. of Mammalogists. Special Pub. No 7.

Franklin, W.L., Johnson, W.E., Sarno, R.J., Iriarte, J.A., 1999. Ecology of the Patagonia puma Felis concolor patagonica in southern Chile. Biological Conservation 90, 33–40. http://dx.doi.org/10.1016/S0006-3207(99)00008-7.

Gidna, A., Yravedra, J., Domínguez-Rodrigo, M., 2013. A cautionary note on the use of captive carnivores to model wild predator behavior: a comparison of bone modification patterns on long bones by captive and wild lions. Journal of Archaeological Science 40, 1903–1910. http://dx.doi.org/10.1016/j.jas.2012.11.023.

Gómez, G.N., Kaufmann, C.A., 2007. Taphonomic analysis of Pseudalopex griseus (Gray, 1837) scat assemblages and their archaeological implications. Journal of Taphonomy 5, 59–70.

Grayson, D.K., 1984. Quantitative Zooarchaeology: Topics in the Analysis of Archaeological Faunas. Academic Press, Orlando.

Gutiérrez, M.A., Martínez, G.A., 2008. Trends in the faunal human exploitation during the late Pleistocene and early Holocene in the Pampean region (Argentina). Quaternary International 191, 53–68. http://dx.doi.org/10.1016/j.quaint.2007.09.024.

Haynes, G., 1980a. Evidence of carnivore gnawing on Pleistocene and recent mammalian bones. Paleobiology 6, 341–351.

Haynes, G., 1980b. Prey bones and predators. Potential ecologic information from analysis bones of bone site. OSSA 7, 75–97.

Haynes, G., 1981. Bone Modifications and Skeletal Disturbances by Natural Agencies: Studies in North America (unpublished Ph.D thesis). The Catholic University of America, Washington, D.C.

Haynes, G., 1982. Utilization and skeletal disturbances of North American prey carcasses. Arctic 35, 266–281.

Haynes, G., 1983. A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones. Paleobiology 9, 164–172.

Iriarte, J.A., 1988. Feeding Ecology of the Patagonia puma (Felis concolor patagonica) in Torres del Paine National Park, Chile (unpublished M.A. thesis, Gainesville).
Iriarte, J.A., Franklin, W., Johnson, W., Redford, K., 1990. Biogeographic variation of food habits and body size of the America puma. Oecologia 85, 185–190. http://dx.doi.org/10.1007/BF00319400.
Jackson, D., Jackson, D., 1999. Tafonomía de zorros: preservación diferencial e implicancias para el registro arqueológico de la provincia de Choapa. Conserva, pp. 99–113.
Kaufmann, C.A., 2009. Estructura de edad y sexo en guanaco. Estudios actualísticos y aruqeológicos en Pampa y Patagonia. Sociedad Argentina de Antropología, Buenos Aires.
Kaufmann, C.A., Álvarez, M.C., L'Heureux, L.G., Gutiérrez, M. a, 2013. Dimorfismo sexual en la pelvis de Lama guanicoe (Artiodactyla, Camelidae): Un caso de aplicación en el sitio Paso Otero 1, Buenos Aires, Argentina. Mastozoologia Neotropical 20, 47–59.
Kaufmann, C.A., Messineo, P.G., 2002. Los desplazamientos óseos de guanaco producto de la acción de zorros en un caso actual y sus implicaciones arqueológicas. In: Mazzanti, D.L., Berón, M.A., Oliva, F. (Eds.), Del Mar a Los Salitrales. Diez Mil Años de Historia Pampeana En El Umbral Del Tercer Milenio. Universidad Nacional de Mar del Plata, Facultad de Humanidades, Mar del Plata, Argentina, pp. 419–429.
Klein, R., Cruz-Uribe, K., 1984. The Analysis of Animal Bones from Archaeological Sites. The University of Chicago Press, Chicago.
Larrieu, E., Bigatti, R., Oporto, N., 1982. Somatometría en guanacos de Río Negro. Anatomía en Borrador 3, 8–13.
Lloveras, L., Moreno-García, M., Nadal, J., 2012. Feeding the foxes: an experimental study to assess their taphonomic signature on leporid remains. International Journal of Osteoarchaeology 22, 577–590. http://dx.doi.org/10.1002/oa.1280.
Logan, K., Sweanor, L., 2001. Desert Puma: Evolutionary Ecology and Conservation of an Enduring Carnivore. Island Press, Washington.
Lyman, R.L., 1994. Vertebrate Taphonomy. Cambridge University Press, Cambridge.
Marean, C.W., Spencer, L.M., 1991. Impact of carnivore ravaging on zooarchaeological measures of element abundance. American Antiquity 56, 645–658.
Martin, F.M., 2012. Human-carnivore interaction at the end of the Pleistocene in southern Patagonia, Chile. Journal of Taphonomy 10, 561–574.
Martin, F.M., 2013. Tafonomía y paleoecología de la Transición Pleistoceno-Holoceno en Fuego-Patagonia: Interacción entre humanos y carnívoros y su importancia como agentes en la formación del registro fósil. Universidad de Magallanes, Punta Arenas, Chile.
Martin, F.M., Borrero, L.A., 1997. A Puma Lair in southern Patagonia: implications for the archaeological record. Current Anthropology 38, 453–461.
Martínez, G.A., Gutiérrez, M.A., 2004. Tendencias en la Explotación Humana de la Fauna durante el Pleistoceno Final-Holoceno en la Región Pampeana (Argentina). In: Mengoni Goñalons, G. (Ed.), Zooarchaeology of South America, British Archaeological Research International Series, Oxford, UK, vol. 1298, pp. 81–98.
Massigoge, A., Gutiérrez, M.A., Álvarez, M.C., Kaufmann, C.A., Rafuse, D.J., González, M.E., 2014. Estudio Comparativo de las Marcas de Dientes Producidas por Dos Pequeños Carnívoros Sudamericanos. Revista Chilena de Antropología 30, 42–49.
Mondini, M., 1995. Artiodactyl prey transport by foxes in Puna rock shelters. Current Archaeology 36, 520–524. http://dx.doi.org/10.1086/204391.
Mondini, M., 2002. Carnivore taphonomy and the early human occupations in the Andes. Journal of Archaeological Science 29, 791–801. http://dx.doi.org/10.1006/jasc.2001.0780.
Mondini, M., 2003. Modificaciones óseas por carnívoros en la Puna argentina, Una mirada desde el presente a la formación del registro arqueofaunístico. Mundo de Antes 3, 87–108.
Mondini, M., 2012. Tafonomía de carnívoros en los andes centro-sur. Madrigueras actuales y sus implicaciones para el registro arqueofaunístico. In: Acosta, A., Loponte, D., Mucciolo, L. (Eds.), Temas de Arqueología: Estudios Tafonómicos Y Zooarqueológicos (II), pp. 67–105.
Mondini, M., Muñoz, A.S., 2008. Pumas as taphonomic agents: a comparative analysis of actualistic studies in the Neotropics. Quaternary International 180, 52–62. http://dx.doi.org/10.1016/j.quaint.2007.08.013.
Montalvo, C.I., Pessino, M.E.M., González, V.H., 2007. Taphonomic analysis of remains of mammals eaten by pumas (Puma concolor Carnivora, Felidae) in central Argentina. Journal of Archaeological Science 34, 2151–2160. http://dx.doi.org/10.1016/j.jas.2007.02.012.
Muñoz, A.S., Mondini, M., Durán, V., Gasco, A., 2008. Los pumas (Puma concolor) como agentes tafonómicos. Análisis actualístico de un sitio de matanza en los Andes de Mendoza, Argentina. Geobios 41, 123–131. http://dx.doi.org/10.1016/j.geobios.2006.11.010.
Nallar, R., Morales, A., Gómez, H., 2008. Manual para la identificación y reconocimento de eventos de depredación del ganado doméstico por carnívoros altoandinos. Wildlife Conservation Society (WCS), La Paz, Bolivia. http://dx.doi.org/10.1017/CBO9781107415324.004.
Nasti, A., 2000. Modification of vicuña carcasses in high-altitudes deserts. Current Anthropology 41, 279–283. http://dx.doi.org/10.1086/300133.
Njau, J.K., Blumenschine, R.J., 2006. A diagnosis of crocodile feeding traces on larger mammal bone, with fossil examples from the Plio-Pleistocene Olduvai Basin, Tanzania. Journal of Human Evolution 50, 142–162. http://dx.doi.org/10.1016/j.jhevol.2005.08.008.
Novaro, A.J., Moraga, C. a., Briceño, C., Funes, M.C., Marino, A., 2009. First records of culpeo (Lycalopex culpaeus) attacks and cooperative defense by guanacos (Lama guanicoe). Mammalia 73, 148–150. http://dx.doi.org/10.1515/MAMM.2009.016.
Novaro, A.J.A.J., Walker, R.S.S., 2005. Human-induced changes in the effect of top carnivores on biodiversity in the Patagonian Steppe. In: Ray, J.C., Redford, K.H., Steneck, R.S., Berger, J. (Eds.), Large Carnivores and Biodiversity Conservation. Island Press, Washington, pp. 268–288.
Nowell, K., Jackson, P., 1996. Wild Cats: Status Survey and Conservation Action Plan, Iucn/Ssc Action Plans for the Conservation of Biological Diversity. World Conservation Union, Gland, Switzerland.
Oporto, N., Bigatti, R., Larrieu, E., 1979. Determinación de edades en guanaco (Lama guanicoe) en base a su dentición. Revista Argentina de producción animal 4, 965–983.
Palmeira, F.B.L., Crawshaw, P.G., Haddad, C.M., Ferraz, K.M.B., Verdade, L.M., 2008. Cattle depredation by puma (Puma concolor) and jaguar (Panthera onca) in central-western Brazil. Biological Conservation 141, 118–125. http://dx.doi.org/10.1016/j.biocon.2007.09.015.
Pitman, M.R.P.L., Oliveira, T.G., Paula, R.C., Indrusiak, C., 2002. Manual de identificação, prevenção e controle de predação por carnívoros. Edições IBAMA, Brasília, Brazil.
Pobiner, B.L., DeSilva, J., Sanders, W.J., Mitani, J.C., 2007. Taphonomic analysis of skeletal remains from chimpanzee hunts at Ngogo, Kibale National Park, Uganda. Journal of Human Evolution 52, 614–636. http://dx.doi.org/10.1016/j.jhevol.2006.11.007.
Politis, G.G., 2002. South America: in the garden of forking paths. In: Cunliffe, B.W., Davies, W., Renfrew, C. (Eds.), Archaeology: the Widening Debate. Oxford University Press, Oxford, pp. 193–244.
Raedeke, K., 1979. Population Dynamics and Sociology of the Guanaco (Lama guanicoe) of Magallanes. University of Washington.
Rafuse, D.J., González, M.E., Kaufmann, C.A., Álvarez, M.C., Gutiérrez, M.A., Massigoge, A., 2014. Análisis Comparativo de los Patrones de Modificaciones Óseas de Dos Carnívoros Sudamericanos: El Gato Montés (Leopardus Geoffroyi) y el Zorro Pampeano (Lycalopex Gymnocercus). Aportes para la Identificación de la Acción de Pequeños Carnívoros en el Registro Arqueológico. Magallania (Punta Arenas) 42, 165–184.
Rasband, W.S., 2014. ImageJ. U. S. National Institutes of Health Bethesda, Maryland, USA. http://imagej.nih.gov/ij/.
Rau, J.R., Martínez, D.R., Muñoz-Pedreros, A., 1995. Trophic ecology of pumas in southern South America. In: Bissonette, J.A., Krausman, P.R. (Eds.), Integrating People and Wildlife for a Sustainable Future. The Wildlife Society, Bethesda, MD, pp. 602–604.
Rau, J.R., Tilleria, M.S., Martinez, D.R., Munoz, A.H., 1991. Dieta de Felis concolor (Carnivora: Felidae) en areas silvestres protegidas del sur de Chile. Revista Chilena de Historia Natural 64, 139–144.
Sala, N., Arsuaga, J.L., Haynes, G., 2014. Taphonomic comparison of bone modifications caused by wild and captive wolves (Canis lupus). Quaternary International 330, 126–135. http://dx.doi.org/10.1016/j.quaint.2013.08.017.
Saladié, P., Huguet, R., Díez, C., Rodríguez-Hidalgo, A., Carbonell, E., 2013. Taphonomic modifications produced by modern brown bears (Ursus arctos). International Journal of Osteoarchaeology 23, 13–33. http://dx.doi.org/10.1002/oa.1237.
Salemme, M., Miotti, L.L., 2008. Archaeological hunter-gatherer landscapes since the latest Pleistocene in Fuego-Patagonia. In: Rabassa, J. (Ed.), The Late Cenozoic of Patagonia and Tierra Del Fuego. Elsevier, New York, pp. 437–483.
Selvaggio, M.M., Wilder, J., 2001. Identifying the involvement of multiple carnivore taxa with archaeological bone assemblages. Journal of Archaeological Science 28, 465–470. http://dx.doi.org/10.1006/jasc.2000.0557.
Stiner, M.C., Munro, N.D., Sanz, M., 2012. Carcass damage and digested bone from mountain lions (Felis concolor): implications for carcass persistence on landscapes as a function of prey age. Journal of Archaeological Science 39, 896–907. http://dx.doi.org/10.1016/j.jas.2011.10.020.
Sunquist, M.E., Sunquist, F.C., 1989. Ecological constraints on predation by large felids. In: Gittleman, J.L. (Ed.), Carnivore Behaviour, Ecology and Evolution. Chapman and Hall, London, pp. 283–301.
Sunquist, M.E., Sunquist, F.C., 2002. Wild Cats of the World. The University of Chicago Press, Chicago.
Sutcliffe, A., 1970. Spotted hyaena: crusher, gnawer, digester and collector of bones. Nature 227, 1110–1113. http://dx.doi.org/10.1038/2271110a0.
Westaway, M.C., Thompson, J.C., Wood, W.B., Njau, J., 2011. Crocodile ecology and the taphonomy of early Australasian sites. Environmental Archaeology 16, 124–136. http://dx.doi.org/10.1179/174963111X13110803260930.
Young, A., Stillman, R., Smith, M.J., Korstjens, A.H., 2015. Scavenger species-typical alteration to bone: using bite mark dimensions to identify scavengers. Journal of Forensic Sciences. http://dx.doi.org/10.1111/1556-4029.12839 n/a–n/a.
Yravedra, J., Lagos, L., Barcena, F., 2011. A taphonomic study of wild wolf (Canis lupus) modification of horse bones in northwestern Spain. Journal of Taphonomy 9, 37–65.

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