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

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ABSTRACT

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).

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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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