Quaternary International 466 (2018) 157–164

Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Taphonomy and the role of pumas (*Puma concolor*) in the formation of the archaeological record

Luis A. Borrero [a, *], Fabiana M. Martin [b], Francisco J. Prevosti [c]

[a] CONICET-IMHICIHU, Saavedra 15, Piso 5, (1083) Buenos Aires, Argentina
[b] Centro de Estudios del Hombre Austral, Universidad de Magallanes, Instituto de la Patagonia, Av. Bulnes 01890, (CP 6200000) Punta Arenas, Chile
[c] CONICET-CRILAR, Entre Ríos y Mendoza s/n, (5301) Anillaco, La Rioja, Argentina

ARTICLE INFO

Article history:
Available online 26 April 2016

Keywords:
Puma
Taphonomy
Den
Archaeology

ABSTRACT

Puma transport of prey remains to dens located in overhangs, rockshelters or caves lead to conditions of potential mixing with archaeofaunas. The evidence for puma use of places which before or after were also selected by humans is reviewed, as well as results of taphonomic studies. These studies include not only naturalistic observations, but also excavations of puma dens, and serve to highlight some of the research areas needed in order to understand the role of pumas as active agents in the accumulations of bone assemblages.

© 2016 Elsevier Ltd and INQUA. All rights reserved.

1. Introduction

Pumas (*Puma concolor)* are highly adaptable felines which are distributed along most of America (Redford and Eisenberg, 1992). They are the largest terrestrial carnivores in Patagonia, with weights over 80–60 kg (Sunquist and Sunquist, 2002: 270). They are mostly solitary, nocturnal hunters that hunt large prey such as guanacos (*Lama guanicoe*) and domestic animals which weight up to 350 kg (Redford and Eisenberg, 1992; Prevosti and Vizcaíno, 2006: 414), although in many areas they live off small prey such as European hares (*Lepus europaeus*), sigmodontine rodents or intermediate size prey such as *Pseudalopex* or *Galictis* (Montalvo et al., 2007; Elbroch and Wittmer, 2013).

As top carnivores of the Patagonian ecosystems, pumas are important agents of bone deposition and, sometimes, bone accumulation. Occasionally, pumas constituted a resource for historic and prehistoric Patagonian peoples who consumed their meat and used their hides (Musters, 1964 [1871]: 105; Greenwood, 2015). Also, pumas sometimes selected the same places chosen by human for their activities, producing an impact in archaeological assemblages, and creating complex palimpsests. It is for this reason that it is important to understand the conditions under which puma bones find their way into archaeological assemblages.

Our knowledge of pumas as depositional agents in Patagonia is very limited, and sometimes it is difficult to separate bones deposited by pumas from those deposited by humans. There are cases -especially in caves-where there is interdigitation between puma and human occupations that complicates interpretation (Borrero, 1981; Martin, 2013). For that reason the interaction between humans, carnivores and their prey is relevant to our understanding of the archaeological record.

Taphonomic studies are one way to increase our knowledge about pumas as agents in the deposition of bones or as disturbing factors of previously deposited remains. Naturalistic observations, including longitudinal studies and excavations of modern puma dens, resulting from our taphonomic research are presented here. We especially use some taphonomic results from our studies at Torres del Paine (Borrero et al., 2005) to discuss aspects of the interaction between free ranging pumas and guanacos. These and other research lines, especially the study of fossil samples, help in the discussion of the importance of pumas in the formation of bone assemblages in general, and archaeofaunas in particular. By using naturalistic observations, including the study of modern sites, we show that under some circumstances pumas use overhangs, rockshelters or dark chambers. This has significant implications for interpretation of deposits in shelters.

2. Antecedents

Most of the few relevant taphonomic studies related with puma behavior were produced in the 1990s, including observations of

* Corresponding author.
E-mail addresses: laborrero2003@yahoo.com (L.A. Borrero), Fabiaana2007@gmail.com (F.M. Martin).

http://dx.doi.org/10.1016/j.quaint.2016.04.011
1040-6182/© 2016 Elsevier Ltd and INQUA. All rights reserved.

marks on sheep bones and the excavation of a puma maternal den (Borrero and Martin, 1996; Martin and Borrero, 1997). A long-term taphonomic project at Torres del Paine National Park -a Biosphere Reserve in South Chile-studied the interaction between pumas and guanacos, with a focus on the material correlates of hunting and feeding episodes. More than 70 guanaco carcasses were studied. Transects and longitudinal observations on carcasses resulting from puma predation were used to understand the spatial distribution of puma activities and its long-term visibility (Borrero, 2001; Borrero et al., 2005). Our work at Torres del Paine took advantage of previous local predator-prey research (Wilson, 1984; Iriarte et al., 1991; Bank and Franklin, 1998; Bank et al., 2002).

Nasti (1996, 2000) published studies of damages produced by pumas on two vicuña skeletons (*Vicugna vicugna*) in the highlands of the Puna in Northwest Argentina. More recently Muñoz et al. (2008) presented a study of one guanaco killed by pumas at the Reserva Laguna del Diamante, Mendoza, Argentina, and Mondini and Muñoz (2007) offered a synthesis of studies involving pumas. Kaufmann (2009) reported the presence of puma marks on nine guanaco carcasses at Cinco Chañares, Río Negro, and discussed their significance.

Scats were also considered in efforts to study the diet of pumas (Yañez et al., 1986; Iriarte, 1988; Iriarte et al., 1991). More specific studies by Gómez (2007), Montalvo et al. (2007) and Labarca et al. (2014) also provided information on the content of puma scats, and used it to discuss their role in archaeological settings.

On the other hand, an actualistic study by Stiner et al. (2012) in Texas and New Mexico, U.S.A. examined the taphonomic signatures of pumas at prey skeletal remains left at four kill sites and digested bone fragments in scats.

3. Puma characteristics

Pumas are solitary predators that hunt by ambush, jumping and breaking the neck of their prey, with a bite of the skull or the throat (Crawshaw and Quigley, 2002: 230). As a result they produce distinctive marks with their large canines on the cervical vertebrae or the skull.

Pumas have large home ranges and spend most of their time in open terrain. It is generally observed that pumas “do not usually have fixed dens, except during the breeding season” (Guggisberg, 1975: 111), and spend most of their time in the open. Caves are not among their favourite places to live (Shaw, 1989; Hansen, 1991; Cox and Grambo, 1999; Nasti, 2000; Sunquist and Sunquist, 2002), but they use them as maternal dens or under other circumstances, including heightened competition. Sarno et al., (1999: 939) found cases of radio collared infant guanacos (*chulengos*) killed and dragged back to dens by pumas. These dens were probably discontinuously used, but in some cases evidences of redundant use were found (Martin and Borrero, 1997).

There are evidences for puma intra-specific interaction to the point that intraspecies killing is the most important cause of death in pumas beyond human hunting. Males kill and eat cubs for nourishment or to enhance male's fitness (Logan and Sweanor, 2001: 139–140). During our taphonomic study at Torres del Paine we uncovered evidence of puma cubs with punctures that resulted from intraspecies killings (José Vargas, personal communication) (Fig. 1). On the other hand, because of the puma preference for sheep they are hunted systematically in most Patagonian ranches (Greenwood, 2015).

Since Late Pleistocene pumas were probably larger (Prevosti and Martin, 2013), and remembering that “larger pumas tend to kill larger animals” (Logan and Sweanor, 2001: 301), it is possible to maintain that in the past they were able to kill extinct fauna such as *Hippidion saldiasi*, extinct camelids or juveniles of larger prey (Prevosti and Martin, 2013: 80). However, competition with *Panthera onca mesembrina* and *Smilodon* must also be taken into account, although damages produced on the bones should have been comparatively greater.

4. The fossil record of Southern Patagonia

Analysis of archaeological samples suggests that felids visited sites, introducing mesomammal remains and modifying bones (Borrero, 1981; Gutiérrez and Gómez, 2007). The evidence is not abundant, but we believe that this is because the attention was concentrated in the faunas clearly associated with human activities, such as guanacos or pinnipeds. The presence of puma bones at Late Pleistocene archaeological or paleontological sites is minimal and limited to two sites, Cueva del Milodon and Cueva Fell. Reports from collections stored in Europe mention the presence of pumas at Cueva del Milodón (Mol et al., 2003; Barnett and Sylvester, 2009) and some remains of one individual were found at the lower Late Pleistocene layers of Cueva Fell (Poulain-Josien, 1963: 235, 237).

The presence of puma is more important during the Holocene, with at least two sites for the Early Holocene, Cueva de las Manos (Mengoni Goñalons and Silveira, 1976) and Los Toldos 3 (Miotti, 1998). There are several Late Holocene sites with puma remains, such as Cerro Sota (Bird, 1988), Cueva de los Chingues (San Roman et al., 2000), La Martita (Horovitz, 2003), El Ceibo 7 (Miotti, 1998), Alero Cárdenas (Horovitz, 1994), El Rodeo (Aguerre and Pereda, 1994), Don Ariel (Nami, 1993) and Cerro de los Indios (Mengoni Goñalons, 1999). The bones recovered at most of these sites are tarsals, carpals, phalanges and metapodials, in other words, bones that may be transported to habitation sites accompanying puma hides. A phalanx with cut marks was recovered at Los Toldos 3 (Miotti, 1998: 113). The presence of two fragments of tibia and one fragment of femur at El Rodeo (Aguerre and Pereda, 1994) invites a different explanation, perhaps related with subsistence.

At most of these sites only the presence of one or two bones is recorded, and rarely archaeologists were interested in relating them to the rest of the faunas. Junius Bird (1983, 1988) found more than 700 guanaco and horse bone chips and splinters at Cerro Sota, associated with ground sloth and human remains. He assigned all these materials to the Late Pleistocene, and suggested that some of the horse and guanaco splinters were too big and strong to be the result of the action of pumas (Bird, 1983: 63). Since he had no



Fig. 1. Torres del Paine National Park. Femur-innominate of a young puma that was killed and consumed by pumas. Note that the trochanter major of the femur is removed and there is a puncture at the innominate.

taphonomic control at his disposal, this opinion is difficult to maintain today, but what really matters is that he was paying particular attention to pumas as active agents in the formation of bone assemblages. The human bodies recovered at Cerro Sota were dated around 3900 BP, instead of Late Pleistocene as originally thought (Hedges et al., 1992) and it is probable that this is also the maximal date for the puma mandible found at the upper layer. Bird (1983: 63) also mentioned two puma claws in the interior chamber.

In some cases the presence of felids was determined with the aid of zoonotic parasites, as in Cerro Casa de Piedra 5 where they were recorded in the scats from a layer dated 6540 ± 110 BP. Scats whose "shape, colouration and sizes were similar to those of *Puma concolor*" were recovered in that layer (Fugassa et al., 2009: 1178). Partially digested bones and hair were found in the interior of the scats. Their study provided evidence of consumption of viscera of rodents and camelids by felids. This is significant for the health of humans and animals inhabiting that place.

There are other deposits which are not characterized by archaeological components but offer useful information about pumas. Cueva del Puma, located at the Pali-Aike Volcanic Field, is an endogenous dark cave, with difficult access. It offers actualistic evidence for puma transport of bones and/or carcasses. Moreover, there are evidences of intensive use of the cave by pumas, and the skeletons of at least four pumas were found concentrated on a small isolated and difficult to access chamber (Fig. 2), including a small juvenile (Martin et al., 2004). They were probably trapped in the caves by ranchers, a usual tactic employed to kill pumas (Greenwood, 2015). Around 10% of the modern bone assemblage recovered at Cueva del Puma presented carnivore marks (Fig. 3). These carcasses were processed by pumas in their usual pattern in which plenty of meat remains adhered to the bones. These bones were still fresh and partially complete at the time of the first visit in 1999, and at the start of our work in 2002 several segments were still articulated (Fig. 4). Puma bones and faeces were recorded in several areas of the cave. Puma fibers were found at the roof of the lava tube attesting to their circulation between chambers. The largest chambers are full of modern prey remains including *Pteroocnemia*, guanaco and introduced species such as sheep, which are averaged in a surface bone assemblage with late Pleistocene species, such as *Mylodon*, Camelidae, cf. *Lama gracilis*, *Hippidion saldiasi*, *Dusicyon avus*, *Panthera onca mesembrina* and *Arctotherium*. A puma humerus from the surface of Cueva del Puma was dated as "modern" 98.4 ± 0.4 (Ua-21034) (Martin, 2013: 303), while the extinct faunas have dates that start around 30,000 BP in a context



Fig. 3. Cueva del Puma, Pali-Aike. A surface bone assemblage at the main chamber averaging the remains of both modern and extinct faunas.

that suggest that it was a *Panthera onca mesembrina* den (Martin et al., 2004). Evidence of prey consumption of modern species by pumas also exists outside of caves, mostly partially consumed sheep carcasses.

Several Felidae remains were recovered interdigited with human occupations at Cueva de los Chingues (San Roman et al., 2000), including a third phalanx, a fragment of a lower jaw, a canine tooth and two claws, one assigned to puma and another to a large felid (Martin, 2013: 189). The presence of a puma cub is important because it points toward a maternal den. A puma left humerus was dated 3510 ± 45 AP (Ua-24683). Extinct felines were contributing and modifying bones during the Late Pleistocene, between



Fig. 2. Cueva del Puma, Pali-Aike. Skulls of two modern pumas recovered in a lava tube.



Fig. 4. Cueva del Puma, Pali-Aike. Accumulation of bones, feathers and soft tissues of modern animals by pumas.

12,165 ± 80 and 10,650 ± 50 BP. The modern taphonomic assemblages recovered from the surface near the shelter produced additional evidence of pumas transporting prey or bones to caves.

Places selected for a den are sometimes too exposed to permit the long-term preservation of bone assemblages, as in La Porfía, which is an open and exposed overhang (Martin and Borrero, 1997). Several bedding places were recorded under the overhang, associated with partially articulated sheep carcasses, sheep bones and puma scats. Our studies suggest that it was a lair, probably a sleeping place, where several consumption episodes involving the feeding of cubs took place. The superposition of bedding areas attests to recurrent utilization of the overhang, as expected for territorial carnivores (Hansen, 1991).

Locations for dens are varied. We have evidences of use of fissures in the tufa deposits of Lago Sarmiento, at Torres del Paine National Park (Fig. 5), and in the badlands located at the northeast of lago Argentino, Argentina. The deposits found at these places, probably generated in the context of competition, usually consist of prey bones and some flattening of the surface. Bones preserved at maternal dens, on the other hand, are sometimes associated with plant bedding.

Other modern localities at the Pali-Aike Volcanic Field show how pumas used lava tubes and dark chambers, such as Orejas de Burro 13 and 14, where herbivore bones with punctures were recovered (Figs. 6 and 7). In this case sheep and *Pterocnemia* carcasses were found partially complete, indicating the transport capacity of prey above 50 kg by pumas. There are also observations of pumas entering some of the tubes (Martin and Borrero, 2010).

5. Discussion

5.1. Chulengos

Observations made by several authors indicate that young animals, in contrast with adult prey, are intensively consumed by pumas (Borrero et al., 2005; Kaufmann, 2009; Skewes et al., 2012; Stiner et al., 2012). It was observed that the combined activities of pumas and scavengers swiftly destroy the skeletons of *chulengos*, sometimes in days. As Stiner and collaborators emphasized, pumas "quickly remove the carcasses of very young prey from the pool of potentially scavengeable resources", biasing against the representation of young individuals due to differential bone destruction. Since recent studies by Massigoge et al. (2010) showed that young guanacos are differentially affected by weathering it is fair to propose that they are equally affected by other processes. Our observations at Torres del Paine confirm the swift removal of skeletal remains of *chulengos*, which probably result from a combination of intensive gnawing and consequent bone destruction by pumas and activities of scavengers such as condors (*Vultur gryphus*) or foxes (*Lycalopex*).



Fig. 5. Lago Sarmiento. Torres del Paine. Puma den in the tufa deposits of the lake's coast.



Fig. 6. Orejas de Burro 13, Pali-Aike. Sheep carcass and isolated bones transported by pumas to a dark chamber.

5.2. Pumas and caves

It is possible that pumas avoided caves during the Late Pleistocene due to competition with panthers (Martin, 2013). It is known



Fig. 7. Orejas de Burro 14, Pali-Aike. Entry of a basalt chamber used by pumas.

that jaguars hunt pumas today, and also that the latter avoid areas inhabited by jaguars (Iriarte et al., 1990; Hoogesteijn and Mondolfi, 1992: 19, 60; Crawshaw and Quigley, 2002: 229) and perhaps that was also the case at the end of the Pleistocene. However, today and through the Holocene the puma is the dominant carnivore in Patagonia, but still it is not well represented in the Holocene deposits. After reviewing the cases of Porfía, Cueva del Puma, Cueva de los Chingues and other caves and fissures, it is clear that under some conditions pumas can transport bones to protected places under a rock roof (Martin and Borrero, 1997; Martin et al., 2004; Martin, 2013). Then, the explanation for pumas not extensively using caves during the Holocene is probably more related with displacement produced by humans.

The study at Torres del Paine study illustrates that there are few conditions under which puma prey remains can be preserved in open air situations. The behavior of covering the skeletal remains with plants provides short-term protection from weathering. In some habitats the skeletons remain basically complete for months or even years (Fig. 8), with foxes and other small scavengers dispersing the bones (Borrero, 1990; Kaufmann, 2009), particularly at dry high altitude Puna environments (Nasti, 2000). Anyway, in little more than two decades most of the exposed bones in Patagonian environments are recycled by weathering, except those buried (Fig. 9). On the other hand, the conditions are different at dark chambers such as Cueva del Puma, where long-term preservation occurs (Figs. 3 and 4).

In some cases the puma bones recovered at archaeological sites were transported by humans or other agents. Some of them could have been exploited for their hides, and a few perhaps for their meat. On the other hand, most of the recent paleobiological sites appear to be the result of pumas dying at caves or fissures. However, the mode of deposition is ambiguous at several cases.

5.3. Marks

The guanaco studied by Muñoz et al. was represented by 128 specimens, some still articulated. Several bones were fragmented. When the guanaco carcass was studied there were no soft tissues and the bones were already distributed along some 30 m. This wide distribution indicates that other agents beyond the puma probably acted on the bones. Work by Nasti with vicuñas, which are smaller than guanacos, showed that “primary access by the puma affects the integrity of carcasses less than secondary access by the fox”



Fig. 9. Lagunas Mellizas, Torres del Paine. Semiburied guanaco bones resulting from a puma kill.

(Nasti, 2000: 291). Scavengers also have time to contribute marks, which sometimes are difficult to distinguish from those of young puma cubs. There are furrows, fractures and other damages that could not be attributed to a known agent (Muñoz et al., 2008: 126).

Borrero et al., 2005 observed abundant damages in the skull, innominate, atlas-axis and proximal femur in that order, while the sternum was heavily gnawed. Thin bones such as the scapulas are regularly punctured and quickly destroyed (Fig. 10). In a ranking of body parts presenting damages Muñoz et al. observed a concentration of marks on the innominate, skull, femur, sacrum, humerus, cervical vertebrae and radio-ulna (Muñoz et al., 2008). Kaufmann (2009) found abundant marks on pelvic bones, but also in lumbar vertebrae, in the blade of the scapula, femur (trochanter major) and humerus. Stiner et al. (2012) recorded important damages at the skull, axis vertebrae and innominate.

A different pattern was observed by Nasti, who found a predominance of marks on axial skeletons of vicuñas (Nasti, 1996: 267), basically damages resulting from the early access to the thoracic cavity. Cases of *chulengos* with their spine severed were also observed at Torres del Paine (Borrero et al., 2005:102). Some of the bones of the axial skeleton from puma kills in the park are highly destroyed, especially the cervical vertebrae, the skull and the



Fig. 8. Lago Cisnes, Torres del Paine. Guanaco carcass after approximately six months on the surface. The guanaco was killed by a puma.



Fig. 10. Lagunas Mellizas, Torres del Paine. Guanaco scapula with punctures.

pelvic girdle (Figs. 11 and 12). Similar observations were made at dens such as Cueva del Puma (Fig. 13).

29.8% of the 590 elements examined by Kaufmann (2009) and 34% of the 94 elements recovered by Muñoz et al. (2008) displayed marks. Nasti described marks 3–5 mm, with punctures more than 5 mm in diameter that produce small radial fissures (Nasti, 2000: 280). Muñoz et al. (2008) report punctures between 1.7 and 21 mm, with a continuous distribution and an average 5.51 mm. The upper limit of this range is certainly large in comparison with other cases. Punctures recorded by Kaufmann measure ca. 5 mm (Kaufmann, 2009: 191). During our work at Sarmiento lake, in the guanacos summer range at Torres del Paine, we measured 146 punctures, with an average of 4.2 mm. Martin and Borrero (1997) reported one puncture of 7 mm on a sheep temporal that went through the bone, but the average for 26 punctures was 3.4 mm. The recovery context in a maternal den may explain these smaller sizes. These are places where the mother brings bones and meat for her young (Young and Goldman, 1946: 112; Guggisberg, 1975: 122). Values recorded by Muñoz et al. may be at the upper end of the puncture's size, damages too large to think that they resulted from the activities of cubs. If environmental stress is the explanation for the intensity of processing as suggested by Muñoz et al., these sizes make more sense. Anyway, our observations at Torres del Paine indicated that pumas biting prey skulls in the same locations of previous punctures systematically enlarge them. Also, the production of punctures is often associated with fissure lines that break bones.

Our evidence supports the identifiability of felids proposed by Haynes based on "the rough and irregular marking left by biting on or through cancellous bone of epiphyses. These marks are wide, deep, and countable" (Haynes, 1985: 54). This is also consistent with observations made by other researchers such as Nasti (2000) or Stiner et al. (2012). Even when pumas have the power to destroy bones, Stiner et al. informed that, "lions swallowed very little bone from the adult deer carcasses" (Stiner et al., 2012: 905). In fact the high proportion of isolated punctures appears to be a pattern produced by pumas, similar t those produced by other large felids (Haynes, 1983).

5.4. Bedding

One of the modifications regularly produced by pumas at kill or sleeping sites is to flatten grass near the areas where they kill and consume their prey (Bank and Franklin, 1998). They also cover their kill with a mound of "leaves, moss, sticks, and dirt" (Guggisberg, 1975: 117), and produce oval depressions ca. 2 m in diameter sometimes covered with grass and sticks (Martin and Borrero, 1997). The visibility of these areas only lasts for a few weeks and rarely will produce a fossil record (Borrero et al., 2005; Kaufmann, 2009: 178). Other transformations have more long-term visibility. Excavations at La Porfía identified several changes introduced by pumas at overhangs, such as leveling of the grass, by repeatedly using the same places and bedding using uprooted grass. Similar arrangements were noted at Torres del Paine at places not too far away from a puma kill (Yañez et al., 1986; Borrero et al., 2005).

Three stratigraphically segregated plant layers were found at La Porfía, with scattered gnawed sheep bones and puma scats. Bones and scats were also recovered between bedding layers. This pattern is similar to that found at archaeological sites, such as Alero de los Sauces in Neuquén, only that in this case there were archaeological occupations alternating with puma evidences (Borrero, 1981).

Beddings similar to those created by pumas are regularly found at Patagonian archaeological sites, in some cases associated with puma scats (Gradín et al., 1979; Borrero, 1981). Since archaeological bedding is not always characterized by the abundance of tools, the distinction could be difficult to make. The fact is that pumas and



Fig. 12. Laguna Mellizas, Torres del Paine. Guanaco lumbar vertebrae displaying puma punctures.



Fig. 11. Lagunas Mellizas, Torres del Paine. Guanaco lumbar vertebrae with lateral apophysis gnawed and the innominate crenulated by pumas.



Fig. 13. Cueva del Puma. Guanaco cervical vertebrae heavily punctured by pumas.

humans select similar places, sometimes alternated in time, producing palimpsests which are difficult to disentangle. These beddings not only sometimes include puma faeces, but also carnivore marked bones (San Roman et al., 2000; Martin, 2013). Beddings can be the result of activities of agents other than humans.

Other more subtle archaeological correlates of the presence of pumas are bones from disintegrated scats. They are usually found at latrines, dens, or marking their home ranges. It was observed that recognition of bone remains in scats decreases as prey size increases (Montalvo et al., 2007), which of course implicates mature individuals of large prey (Stiner et al., 2012: 905). Even when they are difficult to assign taxonomically, bones recovered from puma scats are recognizable, since signs of digestive corrosion are usually present, with polished surfaces and rounded edges (Gómez, 2007; Montalvo et al., 2007; Stiner et al., 2012). Their presence at archaeological sites, such as Cueva de los Chingues, is another marker of puma presence at the site (Martin, 2013).

Mule deer bones up to 38,9 mm long were recovered in scats by Stiner et al. (2012: 900), while Montalvo et al. (2007) recovered bones up to 44 mm long. Polished bone fragments recovered at several archaeological deposits could result from the disintegration of puma scats. Given that destructive digestive erosion over bones can be the product of many animals, intensive work with bone fragments resulting from raptor regurgitations (Pardiñas, 1998; Gómez, 2007), fox scats (Mondini, 2000; Mondini and Rodríguez, 2006; Gómez and Kaufmann, 2007) and small carnivores scats (Montalvo et al., 2012) are also required to distinguish puma related bones.

6. Conclusions

We are just beginning to understand some of the consequences of puma behavior for the formation of bone assemblages. Pumas produce identifiable marks and regularly use caves as maternal dens or as secluded places to consume their prey. This behavior creates the conditions for the contamination of archaeological sites with bones deposited by pumas. As Fugassa et al. (2009: 1179) remarked "The utilization of the caves inhabited by big felines and by other mammals was probably not simultaneous with the human occupations, but it could be contemporary and alternative". These are the conditions under which bones resulting from human and puma activities are averaged. Moreover, pumas sometimes transform the interior of the places that they use as dens creating plant beddings which are similar to those produced by humans. It is not unusual that few tools are deposited inside human plant beddings, so that difficulties in the interpretation of archaeological places exist. It was also suggested that open air conditions are sometimes adequate to contaminate archaeological sites with bones from puma kills (Muñoz et al., 2008).

Most published studies show that pumas are active agents interacting with the local fauna in different pampean and patagonian regions. They hunt guanacos of varied ages (Kaufmann, 2009), but they significantly destroy the skeletal remains of the young. As observed by Stiner et al. (2012: 906), the resulting bias in the representation of prey of different ages "is unlikely to result in a false indication of prime-dominant mortality", since older juveniles "are much less affected than infants".

Several authors commented on the low levels of prey consumption by pumas, which implied that they construct potential scavenging niches (Borrero et al., 2005; Prevosti and Vizcaíno, 2006; Stiner et al., 2012), although it was considered that this potential was low for some regions (Muñoz et al., 2007). This wasteful behavior by pumas was recorded in the guanacos winter and summer ranges at the Parque Nacional Torres del Paine, suggesting that scavenging puma kills could have been a useful tactic for humans during the Late Pleistocene winters (Borrero et al., 2005; Martin, 2005). In fact, scavenging is recorded in prehistoric and historic times (Martin, 2012; Tomassini et al., 2014; Chancellor and Wyhe, 2009: 257) and surely was a useful tactic for the southern Late Pleistocene winters during the Antarctic Cold Reversal.

The lack of taphonomic studies prevents disentangling human from nonhuman bone deposition at archaeological sites in Patagonia. Activities by pumas constitute just one of the many active depositional agents. Junius Bird already recognized in the 1930s their importance as potential formational agents at archaeological sites, so it is time that we came to a full realization of how necessary these studies are.

Acknowledgements

Thanks to Guillermo Santana Macías and Park rangers from CONAF, particularly José Vargas for their help at Torres del Paine. We are also grateful to Mike Bank, Carlos Barría, Gonzalo Cisternas, Anibal Cufré,.Agustín Iriarte, Hugo Mercado España, Flavia Morello, Juan José Romero Morano, Manuel San Román, Alejandra Silva and Ron Sarno.

References

Aguerre, A.M., Pereda, I., 1994. Restos óseos de fauna del enterratorio Puesto El Rodeo. In: Aguerre, A.M. (Ed.), Arqueología y paleoambiente en la Patagonia santacruceña argentina. Nuevo Offset, Buenos Aires, pp. 333–342.

Bank, M.S., Franklin, W.L., 1998. Puma (*Puma concolor*) feeding observations and attacks on guanacos (*Lama guanicoe*). Mammalia 62 (4), 599–605.

Bank, M.S., Sarno, R.J., Campbell, N.K., Franklin, W.L., 2002. Predation on guanaco (*Lama guanicoe*) by southernmost mountain lions (*Puma concolor*) during a historically severe winter in Torres del Paine National Park, Chile. Journal of Zoology 258, 215–222.

Barnett, R., Sylvester, S., 2009. Does the ground sloth, *Mylodon darwinii*, still survive in South America? Deposits Magazine 23, 8–11.

Bird, J., 1983. Enterratorios paleo-indios con cremación en las cuevas de Palli-Aike y cerro Sota en Chile Meridional. Anales del Instituto de la Patagonia 14, 55–66.

Bird, J., 1988. Travels and Archaeology in South Chile. University of Iowa Press, Iowa City.

Borrero, L.A., 1981. La economía prehistórica de los habitantes del Alero de los Sauces. Trabajos de Prehistoria 1, 111–124.

Borrero, L.A., 1990. Taphonomy of guanaco bones in Tierra del Fuego. Quaternary Research 34, 361–371.

Borrero, L.A., 2001. Regional taphonomy: background noise and the integrity of the archaeological record. In: Kuznar, L. (Ed.), Ethnoarchaeology of Andean South America. Contributions to Archaeological Method and Theory. International Monographs in Prehistory, Ann Arbor, pp. 243–254.

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

Borrero, L.A., Martin, F.M., Vargas, J., 2005. Tafonomia de la interaccion entre pumas y guanacos en el Parque Nacional Torres del Paine, Chile. Magallania 33 (1), 95–114.

Chancellor, G., Wyhe, J. v, 2009. Charles Darwin's Notebooks from the Voyage of the Beagle. Cambridge University Press, Cambridge.

Cox, D.J., Grambo, R.L., 1999. Mountain Lion. Chronicle Books, San Francisco.

Crawshaw, P.G.J., Quigley, H.B., 2002. In: Medellín, R.A., Equihua, C., Chetkiewicz Jr., P.G.C., Rabinowitz, A., Redford, K.H., Robinson, J.G., Sanderson, E.W., Taber, A.B. (Eds.), Hábitos alimentarios del jaguar y el puma en el Pantanal, Brasil, con implicaciones para su manejo y conservación, en El jaguar en el nuevo milenio. Universidad Nacional Autónoma de México, Wildlife Conservation Society, México D. F, pp. 223–235.

Elbroch, L.M., Wittmer, H.U., 2013. The effects of puma prey selection and specialization on less abundant prey in Patagonia. Journal of Mammalogy 94 (2), 259–268.

Fugassa, M.H., Beltrame, M.O., Bayer, M.S., Sardella, N.H., 2009. Zoonotic parasites associated with felines from the Patagonian Holocene. Memorias Instituto Oswaldo Cruz 104 (8), 1177–1180.

Gómez, G.N., 2007. Predators categorization base don taphonomic analysis of micromammal bones: a comparison to proposed models. In: Gutierrez, M., Miotti, L., Barrientos, G., Mengoni Goñalons, G., Salemme, M. (Eds.), Taphonomy and Zooarchaeology in Argentina. BAR International Series 1601, Oxford, pp. 89–103.

Gómez, G.N., Kaufmann, C.A., 2007. Taphonomic analysis of *Pseudalopex griseus* (Gray, 1837) scat assemblages and their archaeological implications. Journal of Taphonomy 5 (2), 59–70.

Gradín, C.J., Aschero, C.A., Aguerre, A.M., 1979. Arqueología del área río Pinturas. Relaciones de la Sociedad Argentina de Antropología 13, 183–227.
Greenwood, W.H., 2015. Patagonia wild and free. In: Campbell, D.S., Grace-Paz, G. (Eds.), Memories of William H. Greenwood. Salesianos Impresores, S.A., Santiago.
Guggisberg, C.A.W., 1975. Wild Cats of the World. David & Charles, Newton Abbot, London.
Gutiérrez, M.A., Gómez, G.N., 2007. Taphonomic analysis of micro y mesomammals from Tres Reyes 1 archaeological site (Pampean region, Argentina). In: Gutierrez, M., Miotti, L., Barrientos, G., Mengoni Goñalons, G., Salemme, M. (Eds.), Taphonomy and Zooarchaeology in Argentina, BAR International Series 1601. Oxford, pp. 105–119.
Hansen, K., 1991. Cougar. The American Lion. Northland Publishing, San Francisco.
Haynes, G., 1983. A guide for differentiating mammalian carnivore taxa responsible for gnaw damage in herbivore limb bones. Paleobiology 9, 164–172.
Haynes, G., 1985. On watering holes, mineral licks, death, and predation. In: Mead, J., Meltzer, D. (Eds.), Environments and Extinction: man in Late Glacial North America. Center for the Study of Early Man, Orono, pp. 53–71.
Hedges, R.E.M., Housley, R.A., Bronk, C.R., van Klinken, G.J., 1992. Radiocarbon dates from the Oxford AMS system: archaeometry datelist 15. Archaeometry 34, 337–357.
Hoogesteijn, R., Mondolfi, E., 1992. The Jaguar. Armitano Publishers, Caracas.
Horovitz, I., 1994. Restos faunísticos no guanaco del Alero Cárdenas. In: Gradía, C.J., Aguerre, A.M. (Eds.), Contribución a la arqueología del río Pinturas. Provincia de Santa Cruz, pp. 63–72. Búsqueda de Ayllu, Concepción del Uruguay.
Horovitz, I., 2003. Restos faunísticos de La Martita y nuevo registro biogeográfico de Lestodelphys halli (Didelphida, Mammalia). In: Aguerre, A.M. (Ed.), Arqueología y paleoambiente en la Patagonia santacruceña argentina. Nuevo Offset, Buenos Aires, pp. 87–91.
Iriarte, J.A., 1988. Feeding Ecology of the Patagonia puma (Felis concolor patagonica) in Torres del Paine National Park, Chile. University of Florida, Gainesville, U.S.A. M.A. Thesis.
Iriarte, J.A., Franklin, W.L., Johnson, W.E., Redford, K.H., 1990. Biogeographic variation of food habits and body size of the America puma. Oecologia 85, 185–190.
Iriarte, J.A., Johnson, W.E., Franklin, W.L., 1991. Feeding ecology of the Patagonia puma in Southernmost Chile. Revista Chilena de Historia Natural 64, 145–156.
Kaufmann, C., 2009. Estructura de edad y sexo en guanaco. Estudios actualísticos y arqueológicos en Pampa y Patagonia. Sociedad Argentina de Antropología, Buenos Aires.
Labarca, R., Prieto, A., Villalobos, R., 2014. Taphonomy of bones contained in *Puma concolor* (Linnaeus) scats: its potential to interpret archaeofaunal contexts with large herbivore. In: Libro de resúmenes – Abstracts. 12da Conferencia Internacional ICAZ. Universidad Nacional de Córdoba, San Rafael, pp. 90–91. Córdoba.
Logan, K.A., Sweanor, L.L., 2001. Desert Puma. Evolutionary Ecology and Conservation of an Enduring Carnivore. Hornocker Wildlife Institute, Island Press, Washington.
Martin, F.M., 2005. Frozen storage. Journal of Taphonomy 3, 55–56.
Martin, F.M., 2012. Human-carnivore interaction at the end of the Pleistocene in Southern Patagonia, Chile. Journal of Taphonomy 10 (3–4), 561–574.
Martin, F.M., 2013. Tafonomía de la Transición Pleistoceno- Holoceno en Fuego-Patagonia. Interacción entre humanos y carnívoros y su importancia como agentes en la formación del registro fósil. Ediciones de la Universidad de Magallanes, Punta Arenas.
Martin, F.M., Borrero, L.A., 1997. A puma lair in southern Patagonia: implications for the archaeological record. Current Anthropology 38 (3), 453–461.
Martin, F.M., Borrero, L.A., 2010. Mundo Subterráneo: tafonomía regional en el Campo Volcánico Pali-Aike, Santa Cruz, Argentina. In: Borrero, L.A., Charlin, J.E. (Eds.), Arqueología de Pali Aike y Cabo Vírgenes (Santa Cruz, Argentina). CONICET-IMHICIHU, Buenos Aires, pp. 55–80.
Martin, F.M., Prieto, A., Román, M.S., Morello, F., Prevosti, F., Cárdenas, P., Borrero, L.A., 2004. Late Pleistocene Megafauna at Cueva del Puma, Pali-Aike Lava Field, Chile. Current Research in the Pleistocene 21, 101–103.
Massigoge, A., González, M., Kaufmann, C., Gutiérrez, M.A., 2010. Observaciones actualísticas sobre meteorización ósea en restos esqueletales de guanaco. In: Berón, M., Luna, L., Bonomo, M., Montalvo, C., Aranda, C., Carrera Aizpitarte, M. (Eds.), Mamül Mapu: pasado y presente desde la arqueología pampeana. Editorial Libros del Espinillo, Ayacucho, pp. 215–228.
Mengoni Goñalons, G.L., Silveira, M.J., 1976. Análisis e interpretación de los restos faunísticos de la cueva de las Manos, estancia Alto Río Pinturas (provincia de Santa Cruz). Relaciones de la Sociedad Argentina de Antropología 10, 261–270.
Mengoni Goñalons, G., 1999. Cazadores de guanaco de la estepa patagónica. Sociedad Argentina de Antropología, Buenos Aires.
Miotti, L., 1998. Zooarqueología de la Meseta Central y costa de Santa Cruz. Un enfoque de las estrategias adaptativas aborígenes y los paleoambientes. Museo Municipal de Historia Natural, San Rafael.
Mol, D., Bree, P.J.H.V., McDonald, G.H., 2003. De Amsterdamse collectie fossielen uit de Grot van Ultima Esperanza (Patagonië, Zuid-Chili). Grondboor & Hamer 2, 26–36.
Mondini, M., 2000. Tafonomía de abrigos rocosos de la Puna. Formación de conjuntos escatológicos por zorros y sus implicancias arqueológicas. Archaeofauna 9, 151–164.
Mondini, M., Muñoz, A.S., 2007. Pumas as taphonomic agents: a comparative analysis of actualistic studies in the Neotropics. Quaternary International 180, 52–62.
Mondini, M., Rodríguez, M.F., 2006. Taphonomic analysis of plant remains contained in carnivore scats in Andean South America. Journal of Taphonomy 4 (4), 223–235.
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.
Montalvo, C.I., Bisceglia, S., Kin, M., Sosa, R.A., 2012. Taphonomic analysis of rodent bone accumulations produced by Geoffroy's cat (*Leopardus geoffroyi, Carnivora, Felidae*) in Central Argentina. Journal of Archaeological Science 39, 1933–1941.
Muñoz, A.S., Mondini, M., Durán, V., Gasco, A., 2008. Pumas (*Puma concolor*) as taphonomic agents. Actualistic analysis of a kill site in the Andes of Mendoza, Argentina. Geobios 41, 123–131.
Musters, G.C., 1964. Vida entre los Patagones [1871]. Solar-Hachette, Buenos Aires.
Nami, H.G., 1993. Arqueología en la localidad arqueológica de Pali Aike, cuenca del río Chico. Praehistoria 3, 189–218.
Nasti, A., 1996. Predadores, carroñeros y huesos: la acción del puma y el zorro como agentes modificadores de esqueletos de ungulados en la Puna meridional, Argentina. In: Meléndez Hevia, G., Blasco Sancho, M.F., Pérez Urresti, I. (Eds.), II Reunión de Tafonomía y Fosilización. Institución "Fernando el Católico", Zaragoza, pp. 265–269.
Nasti, A., 2000. Modification of vicuña carcasses in high-altitude deserts. Current Anthropology 41, 279–283.
Pardiñas, U.F.J., 1998. Roedores holocénicos del sitio Cerro Casa de Piedra 5 (Santa Cruz, Argentina): tafonomía y paleoambientes. Palimpsesto 5, 66–90.
Poulain-Josien, T., 1963. La Grotte Fell. Ètude de la faune. Journal de la Société des Américanistes 52, 230–254.
Prevosti, F., Vizcaíno, S.F., 2006. Paleoecology of the large carnivore guild from the late Pleistocene of Argentina. Acta Paleontologica Polonica 51 (3), 407–422.
Redford, K.H., Eisenberg, J.F., 1992. Mammals of the Neotropics. The Southern Cone. In: Chile, Argentina, Uruguay, Paraguay, vol. 2. The University of Chicago Press, Chicago.
San Roman, M., Morello, F., Prieto, A., 2000. Cueva de los Chingues (Parque Nacional Pali Aike), Magallanes, Chile. Historia natural y cultural I. Anales Instituto Patagonia 28, 125–146.
Sarno, R.J., Clark, W.R., Bank, M.S., Prexl, W.S., Behl, M.J., Johnson, W.E., Franklin, W.L., 1999. Juvenile guanaco survival: management and conservation implications. Journal of Applied Ecology 36, 937–945.
Shaw, H., 1989. Soul among the Lions. The Cougar as Peaceful Adversary. Johnson Books, Boulder.
Skewes, O., Moraga, C.A., Arriagada, P., Rau, J.R., 2012. El jabalí europeo (*Sus scrofa*): un invasor biológico como presa reciente del puma (*Puma concolor*) en el sur de Chile. Revista Chilena de Historia Natural 85, 227–232.
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.
Sunquist, M., Sunquist, F., 2002. Wild Cats of the World. The University of Chicago Press. Chicago and London.
Tomassini, R.L., Frontini, R., Bayón, C., 2014. Taphonomic analysis of an assemblage of *Lama guanicoe* (artiodactyla, Camelidae) from the late Holocene (Pampean region, Argentina. Palaios 29, 570–577.
Wilson, P., 1984. Puma predation on guanaco in Torres del Paine National Park, Chile. Mammalia 48, 515–522.
Yañez, J., Cárdenas, J.C., Gazelle, P., Jaksic, F.D.M., 1986. Food habits of the southernmost mountain lions (*Felis concolor*) in South America: natural versus livestocked range. Journal of Mammalogy 67, 604–606.
Young, S.P., Goldman, E.A., 1946. The Puma, Mysterious American Cat. The American Wildlife Institute, Washington, D.C.