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Carnivore taphonomy in South America: a review of actualistic studies and their implications in the southern Neotropics

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ABSTRACT

Actualistic studies on mammalian carnivore taphonomy in southern South America are reviewed here, including pumas, small cats, foxes, and other, smaller carnivores. Patterns for different carnivore taxa and their variation are elicited. Also temporal and spatial variability is analysed, and comparisons are made to other carnivores and regions. While generally these Neotropical carnivores produce low damage intensity, stronger modifications and their implications are described as well. These patterns and their variation are put in context by taking into account the particular physical and biotic conditions in the southern Neotropics.

Introduction

Taphonomy is a multidisciplinary field that studies the transition of organic remains from the biosphere into the lithosphere by focusing on the processes that affect these remains after death (Efremov 1940; Gifford 1981; Behrensmeyer & Kidwell 1985; Allison & Briggs 1991; Lyman 1994; Behrensmeyer et al. 2001; Muñoz & Mondini 2010; Domínguez-Rodrigo et al. 2011, among others). Taphonomic research is key to historical biology, archaeology, paleontology, geology, and other disciplines, as it illuminates our capacity to reconstruct past biotas and environments. The taphonomy of mammalian carnivores in particular is germane to fossil faunal records, including zooarchaeological ones, as these agents may accumulate and modify faunal assemblages associated to anthropic remains in contexts such as occupational alternation in preferred loci like rockshelters (Binford 1981; Behrensmeyer et al. 1992; Stiner 1994). Furthermore, faunal accumulations by carnivores in dens are particularly relevant to archaeology as they are the closest paleontological analogue to anthropically accumulated assemblages (Gifford 1981). Carnivore taphonomic activity may not only delete information by biasing faunal accumulations, but also provide relevant palaeoecological information (Behrensmeyer & Kidwell 1985). This activity and its traces, such as the intensity of gnawing damage to bones, are conditioned by ecological factors such as predator competition and prey availability.

Carnivore taphonomy has been developing in southern South America, particularly in Argentina, since the 1980s (e.g. Borrero 1988a; see Mondini & Muñoz 2011 and bibliography therein). The density of regional taphonomic research in the southernmost portion of the continent is outstanding, and a wealth of actualistic studies on carnivore taphonomy has been carried out in the Southern Cone, within the drier Andean-Patagonian subregion

of the Neotropics (Figure 1). A state of the art is presented here, and compared to studies in other regions. The main physical and biotic properties of the continent are considered to contextualize this information, as are the implications for the zooarchaeological record.

While there are several taxa with a carnivorous diet in the region, focus here is on the different Carnivora mammals. Unlike the northern portion of South America, rodents prevail to the south, and the Southern Cone is dominated by rodents, carnivores and, in the southern end, marine mammals (Redford & Eisenberg 1992). Of all the present-day Carnivora species in the world, 29% live in South America. In the south-western regions of the subcontinent, where actualistic taphonomic studies have been carried out, terrestrial carnivores comprise a large felid, the puma (*Puma concolor*); several small felids; small canids, and smaller procyonids, mephitids and mustelids (Table 1). Pumas – the largest carnivores here – and foxes (*Lycalopex* sp.) – the most conspicuous ones – have received most taphonomic attention.

Among the main vertebrate prey of Neotropical carnivores are wild and domestic camelids (*Vicugna vicugna* and *Lama guanicoe*, and *L. glama*, respectively). There are also some deer, a wide array of birds and rodents of variable body size, and introduced vertebrates like leporids and domestic dogs and ungulates (Redford & Eisenberg 1992; Barquez et al. 2006).

Some taphonomic studies have focused on the action of carnivores generally on specific taxa (e.g. Borrero 1989, 1990; Muñoz & Savanti 1998; Belardi 1999; Cruz 1999a, 2000, 2004, 2005, 2007a, 2011; Borella 2004; Martin 2006; Rindel & Belardi 2006; Belardi & Rindel 2008; Massigoge et al. 2015) or in certain locations or the landscape on the whole (e.g. Borrero 1988a, 1988b, 2001a, 2001b, 2007; Borrero & Martin 1996; Cruz 1999b, 2007b, 2008; Belardi & Carballo Marina 2003; Quintana 2004; Martin
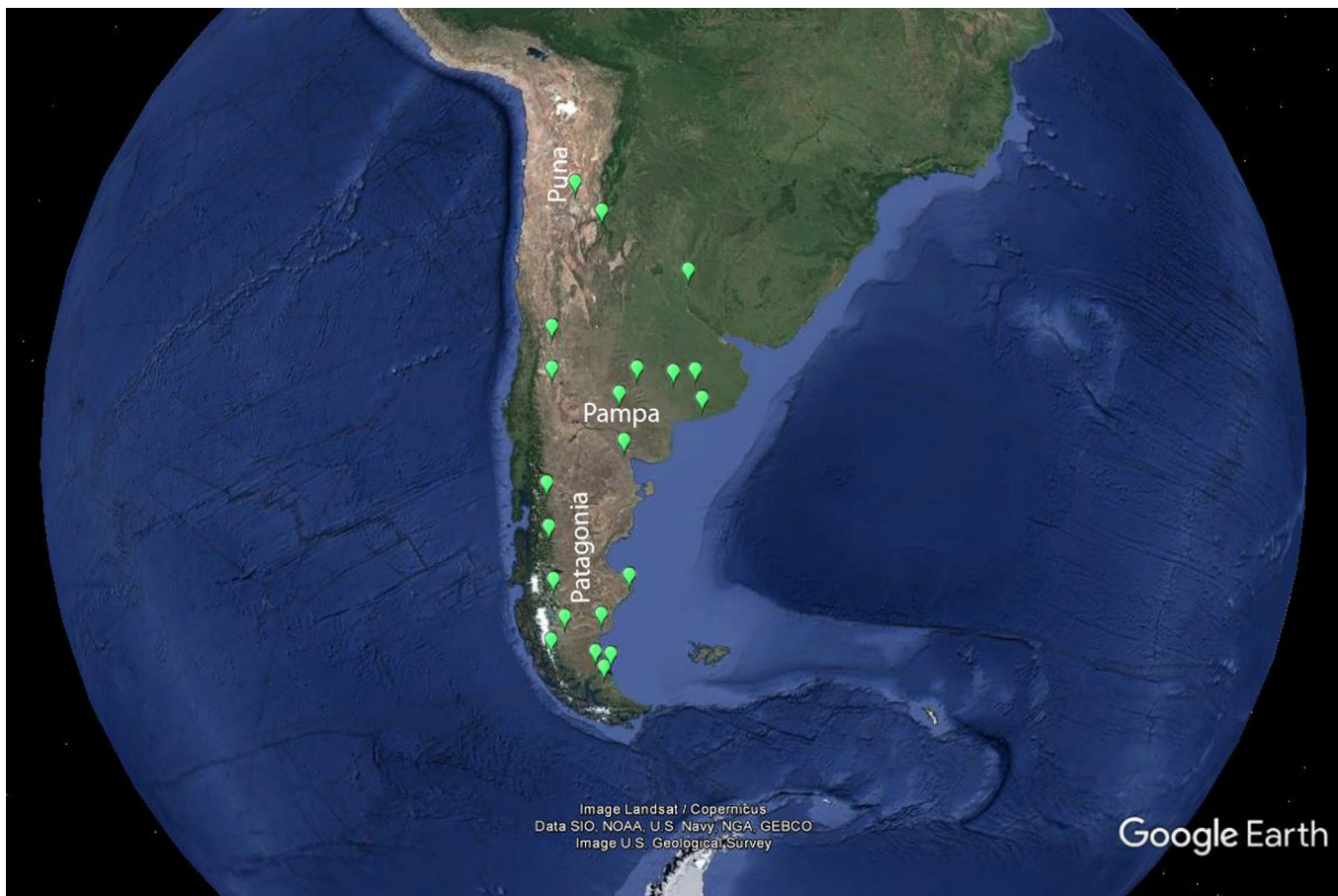
Figure 1. Main locations of actualistic studies on carnivore taphonomy.

Table 1. Main terrestrial carnivores in SW South America.

Taxonomic group	Scientific name	Common name	Body weight (kg)	Food habits and main animal items in diet
Large felids	*Puma concolor*	Puma	29–120	Top predator, carnivorous; preys upon large to small mammals, birds, fish, mollusks
Small felids	*Puma yagouaroundi*	Jaguarundi	4.5–9	Carnivorous; preys upon small mammals, reptiles, birds, frogs, fish, arthropods
	Leopardus colocolo	Colocolo	3–7	Carnivorous; preys upon small mammals, birds, eggs
	Leopardus geoffroyi	Geoffroy's cat	3–5	Carnivorous; preys upon small mammals, birds, fish, amphibians, reptiles
	Leopardus jacobitus	Andean mountain cat	4	Carnivorous; preys upon small mammals, also reptiles, birds
	Leopardus guigna	Guiña	1.5–3	Carnivorous; preys upon small mammals, reptiles, birds, arthropods
Small canids	*Lycalopex culpaeus*	South American red fox	3.4–14	Omnivorous, generalist diet, scavenger; preys upon medium to small mammals, birds, lizards, arthropods
	Lycalopex griseus	South American grey fox	2–4	Omnivorous, generalist diet, scavenger; preys upon small mammals, amphibians, reptiles, birds, eggs, arthropods
	Lycalopex gymnocercus	Pampas fox	4.2–6.5	Omnivorous; preys upon small mammals, birds amphibians, reptiles
Procyonids	*Procyon cancrivorus*	Crab-eating raccoon	3–7	Omnivorous; preys upon amphibians, reptiles, fish eggs, arthropods, marine invertebrates
Mephitids	*Conepatus humboldtii*	Patagonian hog-nosed skunk	1.1-4.5	Carnivorous; primarily eats insects; also birds, small mammals, amphibians, reptiles, fish, eggs, other arthropods
	Conepatus chinga	Andean hog-nosed skunk	2.3–4.5	Omnivorous; eats arthropods; also birds, small mammals, eggs
Mustelids	*Galictis cuja*	Lesser grison	1–2.5	Carnivorous; preys upon small mammals, birds, amphibians, reptiles, eggs, arthropods
	Lyncodon patagonicus	Patagonian weasel	2.25	Carnivorous; preys upon small mammals
	Lontra longicaudis	Neotropical otter	5–15	Carnivorous; opportunistic; feeds mainly on fish, crustaceans and molluscs; also insects, reptiles, birds, small mammals
	Lontra felina	Marine otter	3–5	Carnivorous; eats mainly invertebrates (including crustaceans and molluscs), fish; also birds, small mammals

Notes: After Redford and Eisenberg (1992), Wilson and Reeder (2005), Barquez et al. (2006), among others. Common and scientific names applied to these carnivores vary across the studies; Wilson and Reeder (2005) are followed here so as to provide a uniform source.

& Borrero 2010; Otaola 2014; Gutiérrez et al. 2016; Otaola & Tripaldi 2016). Other studies, summarized below, have centred on the action of specific carnivores. As diverse variables have been considered in the studies carried out over the last forty years, with different aims and varying methodologies, comparisons are made here at a gross scale and at the most inclusive level, and a few more detailed examples are provided by way of illustration.

Taphonomic action by pumas

Pumas are top predators (Redford & Eisenberg 1992). They have a carnivorous diet ranging ungulates and smaller vertebrates, livestock, and other carnivores including co-specifics. They typically hunt by stalking and then biting the prey's neck. Pumas eat just some of each large prey and may cache them by dragging them and covering them with leaves and debris or, as has been recently acknowledged, accumulating them in protected rockshelters.

In southern South America, camelid and sheep (*Ovis aries*) are typically the main items in puma diet. On being predated by pumas, the carcasses of these ungulates remain basically complete for months or even years (Borrero & Martin 1996; Nasti 1996, 2000; Borrero 2001b; Borrero et al. 2005, Forthcoming; Kaufmann 2009; Kaufmann et al. Forthcoming). In fact they often hunt several prey individuals and only consume just a small part of them. Bone modifications produced by pumas are usually present in 30% specimens at the most – although almost as twice can be gnawed in captivity (Kaufmann et al. Forthcoming). Gnawing damage is mainly related to the killing episode, like bite marks on the neck and head bones, with incidental bone damage while dismembering and defleshing prey, in areas like the rib cage, scapula, pelvis and upper limbs. In spite of pumas bite force (Christiansen & Wroe 2007), a low proportion of fractured bones has been reported.

Scorings, punctures and pitting are the most common gnawing damage, and crenulated edges and furrows are frequently reported as well, the latter being typical of these larger felids (Borrero & Martin 1996; Nasti 1996, 2000; Martin & Borrero 1997; Borrero 2001b; Borrero et al. 2005, Forthcoming; Muñoz et al. 2008; Kaufmann 2009; Kaufmann et al. Forthcoming). High proportions of isolated punctures are also characteristic of the puma, as they are of other large felids. Distinctive punctures of a relatively large size are described in several studies, averaging >3 to >5 mm, with a great deal of size variation, and a smaller average size in maternal dens (cf. Martin & Borrero 1997). Marks by young puma cubs might in fact be difficult to distinguish from those by scavengers (Borrero et al. Forthcoming). Some other much larger perforations have been reported, which in several cases are in fact 'tooth impressions' (sensu Andrews & Fernández-Jalvo 1997) caused by multi-cusped teeth (Figure 2). Actually, pumas are the only carnivores in southern South America to cause these tooth impressions.

Carcass consumption by pumas tends to be minimal, although ungulate offspring – which are the preferred prey if available – and smaller vertebrates are more thoroughly consumed, as carcasses generally when pumas are in captivity (Borrero & Martin 1996; Nasti 1996, 2000; San Román et al. 2000; Borrero 2001b; Martin et al. 2004; Borrero et al. 2005, Forthcoming; Kaufmann


Figure 2. Tooth impression attributed to puma on guanaco bone in the Andes of Central Argentina (Muñoz et al. 2008) (bar = 1 cm).

2009; Kaufmann et al. Forthcoming). Similar patterns have been observed in North America (Stiner et al. 2012). Sheep are easier to hunt than guanacos and are not as intensively consumed. Generally these carcass consumption and modification levels by pumas, produced at the beginning of the cycle of carnivore exploitation, are described as light (sensu Haynes 1981, 1982; Sala et al. 2014; see Mondini & Muñoz 2008; Borrero et al. Forthcoming). This renders many carcasses bearing minimal differences with animals that died of causes other than predation, and increases scavenging opportunities in the landscape.

Yet, a couple of exceptions to this light pattern have been reported (see Mondini & Muñoz 2008). One consists of a number of native huemul deer (*Hippocamelus bisulcus*) kills on a lake coast in the Patagonian forest, where full utilization of these carcasses is inferred (Fernández & Forlano 2009). A minimum number of 8 carcasses, including one juvenile and two offspring, with an anatomical survival of about half in average, bear carnivore gnawing marks in 3–43% bones. All of the skulls, innominates and upper limbs have tooth marks, as do, to a lesser extent, other long bones. Punctures and soft bone tissue removal are common, and some bones are fractured. The intensive exploitation of several anatomical units denotes the consumption of not just flesh but also intra-bone and intra-skull-case grease. Another exceptional case is in the high Andes of Central Argentina, where a couple of guanacos inferred to have been hunted in the warm season, perhaps by mothers with offspring, were heavily consumed. One of them was studied in detail, and 36% specimens showed tooth marks (Muñoz et al. 2008). Significant levels of modification were inferred in some anatomical units, including a very heavy degree in the skull – broken through to access the brain – and a full degree in upper limb bones (Figure 3). A case of carnivore stress is suspected here. Both case studies rely on naturalistic observations, and thus imply less control than in experimental studies. Nevertheless, the possibility of intensive exploitation of large carcasses by pumas under some circumstances must be further explored in future.

Pumas can transport away carcasses or parts of them of more than 50 kg, like partially complete sheep and lesser rhea (*Rhea pennata*) (Martin & Borrero 1997, 2010; Borrero et al. 2005, Forthcoming; Martin & San Román 2010). Recent studies in southern Patagonia show that, if available, pumas regularly use caves as maternal dens or as secluded places to consume their prey (Martin & Borrero 1997; Martin et al. 2004; Borrero et al. Forthcoming).

The digested bones found in puma scats in Patagonia include abundant remains of sheep, hare (*Lepus* sp.), and small rodent bones (Martin & Borrero 1997; Labarca Encina et al. 2014;
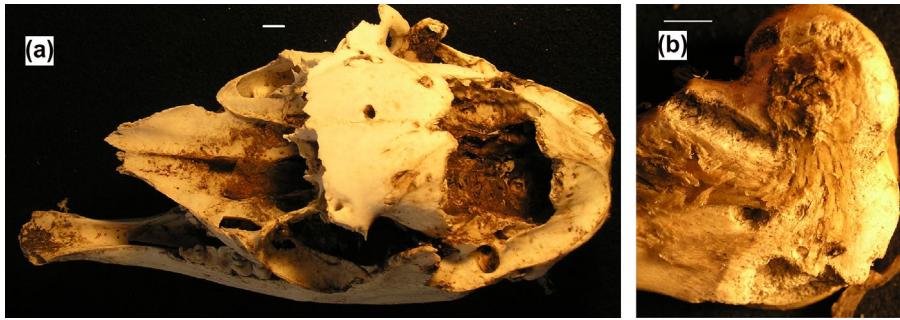
Figure 3. Carnivore damage attributed to puma on guanaco skull (a) and limb bone (b) in the Andes of Central Argentina (Muñoz et al. 2008) (bar = 1 cm).
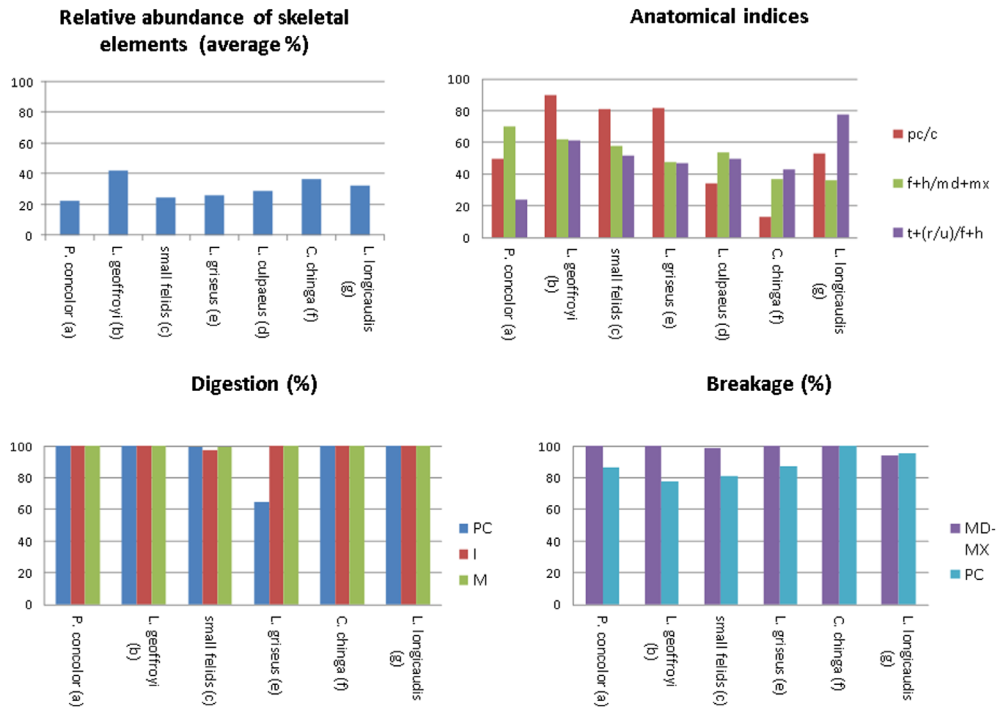
Figure 4. Digestion bone modifications in small mammals in the region.

Notes: Indices after Andrews (1990), Fernández-Jalvo and Andrews (1992); also see Fernández-Jalvo et al. (2016). Abbreviations: pc = postcranial; c = cranial; f = femur; h = humerus; md = mandible; mx = maxilla; t = tibia; r = radio; u = ulna; i = incisor; m = molar. References: (a) Montalvo et al. (2007), (b) Montalvo et al. (2012), (c) López et al. (2016), (d) Gómez and Kaufmann (2007), (e) Cruz et al. (2010), (f) Montalvo et al. (2008), (g) Montalvo et al. (2015).

Borrero et al. Forthcoming). In the Pampas they also contain abundant mammal remains, especially rodents, and also carnivores, artiodactyls, dasypodids, and lagomorphs (Montalvo et al. 2007). The larger the prey, the lower the proportion of identifiable bones, in agreement with the incomplete use of large mammal carcasses pumas make and also with their strong masticatory power. Often only hair of the largest mammals can be identified to species. Bones of up to 44 mm long were found, including some articulated elements preserved by the retention of soft tissues – like autopodials, vertebrae, and dasypodid scutes. Anatomical integrity was greater in smaller prey, suggesting that they were swallowed without much chewing (Figure 4). While good preservation of cranial elements is similar to those produced by other felids (cf. Andrews 1990), small mammal limbs and vertebrae are less represented here. Digestion modifications are generally strong (sensu Andrews 1990), although this is highly variable in small mammals. Similar patterns generally were observed in pumas from North America (Stiner et al. 2012). In an experiment with a captive puma, a low relative abundance

of mice was obtained, as well as extreme modification (Gómez 2007). It should be noted that these categories have recently been revised taking into account the particularities of South American ingested prey, namely Ctenomydae, producing an adapted categorization (Fernández et al. 2017), which needs to considered in further studies.

Taphonomic action by small felids

Small felids, particularly Geoffroy's cat (*Leopardus geoffroyi*), have recently been studied as well. These studies have emphasized digested bones accumulations and modifications. Scatological assemblages tend to be deposited near trees and sometimes in rockshelters (Borrero & Martin 1996; Quintana 2004; Montalvo et al. 2012).

In an experiment with two Geoffroy's cats fed with rabbits (*Oryctolagus cuniculus*), about 40% of the bones survived in the non-ingested assemblage, particularly those of the rear limbs, the innominate and the cranium, in agreement with their higher

bone density (Álvarez et al. 2012; Rafuse et al. 2014; Massigoge et al. 2014). Most were complete and some 19% had tooth marks, mainly pitting, followed by scorings and, to a lesser extent, punctures. These results imply greater bone survival than in experiments with European foxes (*Vulpes* sp.) fed with rabbits (Lloveras et al. 2011).

Within scats, the more abundant rabbit parts were those less represented in the residual assemblage (sensu Binford 1981), and only 1.6% had tooth marks (Álvarez et al. 2012). An analysis of a couple of scats of Geoffroy's cats from the Pampas showed a low relative abundance of prey and strong to moderate digestion (Gómez 2007). A larger naturalistic study in the region showed similar results on rodent prey from Geoffroy's cat scats, but a greater survival rate, with high relative abundance and up to 7 individuals per scat (Montalvo et al. 2012). This differs from previous studies reporting much higher bone destruction in felids (e.g. Andrews 1990), although similar results were found in African cats (Matthews 2006). Larger rodents were more fragmented and less identifiable than smaller ones, although no tooth marks were found (Figure 4). This study assigned the predator to the heavy modification category (Montalvo et al. 2012). Relatively lower levels of fragmentation and digestion damage in the cold season may indicate a faster going through the digestive system related to higher seasonal prey availability.

A captive jaguarundi (*Puma yagouaroundi*) was also fed with mice and, although a higher relative abundance was inferred in the scatological assemblage, bone material is scarce, and it was also included in the extreme category (Gómez 2007). Naturalistic observations on colocolo (*Leopardus colocolo*) scats in the Pampas showed highly fragmented bones (Quintana 2004). Scatological assemblages in a monte environment by small felids – potentially involving Geoffory's cat, jaguarundi and specially colocolo – were recently studied by López et al. (Forthcoming). They display great bone loss and high levels of breakage and digestive corrosion (Figure 4), and have been assigned to the category of extreme modification.

Taphonomic action by foxes

South American foxes, as opportunistic scavengers, often have a secondary access to carcasses. They feed upon a wide array of animals, including humans (Borrero 1988a, 1988b, 1989, 1990, 2001b, 2007; Mameli & Estévez 1999–2000; Borrero & Martin 1996; Nasti 1996, 2000; Martin 1998, 2006; Cruz 1999a, 2000, 2007b; Estévez Escalera & Mameli 2000; Kaufmann & Messineo 2002; Jensen et al. 2004; Borrero et al. 2005; Rindel & Belardi 2006; Belardi & Rindel 2008; Kaufmann 2009, 2016). Foxes may disarticulate ungulates during consumption, and accelerate disarticulation when started by pumas, by separating the head, limbs and some ribs and vertebrae. Yet, they leave a minimal amount of marks – e.g. in 12% of the skeletal elements in the case of a large guanaco sample in Patagonia (Kaufmann 2009) –, and their consumption and destruction levels have been characterized as light damage (Borrero 1990, among others). Nonetheless, a wider range of bones as compared to the puma are usually gnawed, including both axial and appendicular elements. Frequently missing are ribs and vertebrae, as well as some distal limb segments. Once anatomical segments are disarticulated, dispersal by these scavengers often implies a large area.

In ungulate carcasses scavenged by foxes there are commonly pittings and punctures – the latter of about 2.5 mm average –, and a few thin scorings (Borrero 1988a, 1988b, 1989, 1990, 2001a, 2001b, 2007; Borrero & Martin 1996; Nasti 1996, 2000; Martin 1998, 2005, 2006; Mameli & Estévez 1999–2000; Jensen et al. 2004; Borrero et al. 2005; Kaufmann 2009). As foxes consume intra-bone nutrients more intensively than felids, they gnaw bones accordingly, although their gnawing power is not as strong as in larger carnivores. Long bones usually bear gnawing marks just in the shafts. Fractures are rare and they affect mainly ribs and vertebrae apophyses. Even when carcasses have been depleted of most soft tissues, foxes may keep returning even after a long time to feed upon the bones and skin. Smaller vertebrates like hares are more intensively consumed *in situ* (e.g. Gutiérrez et al. 2016). Avian resources are variably consumed according to the type of bird – e.g. while most flying birds are easily destroyed by foxes and other carnivores in Patagonia, and the few surviving bones bearing gnawing damage are an artefact of their total destruction, lesser rheas are hardly destroyed and display even higher levels of gnawing damage than mammals (Belardi 1999; Cruz 1999b, 2000, 2004, 2005, 2007b, 2008, 2011, 2015; Belardi & Carballo Marina 2003) – and also according to their abundance – e.g. low to null levels of fox damage have been observed in penguin colonies (Cruz 1999a, 2007a) while elsewhere these birds present higher levels of carnivore modifications (Massigoge et al. 2015).

Similar patterns of bone modification were obtained in experimental studies (Elkin & Mondini 2001; Massigoge et al. 2014; Rafuse et al. 2014). In an experimental study with a captive pampas fox (*Lycalopex gymnocercus*) fed with rabbits, half the bones survived, especially long bones, innominate, skull and mandible (Rafuse et al. 2014; Massigoge et al. 2014). While less bones (13%) were gnawed as compared to those fed upon by Geoffroy's cats, more marks were found on each gnawed bone. Marks were quite similar to those of cats; pitting was more common, followed by scorings and, in a lower proportion, punctures.

Foxes actively transport bones away from carcasses, dens being their final destination (Mondini 1995, 1998, 2002, 2004a, 2005b, 2012; Martin 1998; Cruz 2000; Quintana 2004; Fernández & Cruz 2010; Fernández et al. 2010; Kaufmann 2016). Little rock-shelters are preferred. Smaller carcasses are more often and more completely transported if available. Factors like carrion availability and competition play a role. Leporid carcasses transported to dens in Patagonia can be fairly complete or else dominated by limbs, and may include relatively abundant ribs and few autopodials, unlike residual assemblages (Martin 1998; Fernández et al. 2010). More than 20% hare bones have been observed to be gnawed, especially disarticulated parts (Fernández & Cruz 2010; Fernández et al. 2010). Unlike the experiment mentioned above, punctures prevail in this context, including very small ones that suggest a reproductive den with cubs. A fox den – also used by other small carnivores – in a Pampean environment had plenty of lagomorphs and even more dasypodids, the main transported prey here (Kaufmann 2016). Both bore medium to low survival. While hares are dominated by limbs, as in other fox dens, the scutes protecting dasypodids and associated bones are most frequent. This also impacted in the proportion of gnawed bones (8% vs. 15.6% in hares). Here pitting prevails, followed by scoring and punctures.

Besides small mammals and birds, other transported prey include caprines, and to a lesser degree camelids (Mondini 1995, 2012; Martin 1998, among others). In the Puna, carnivore dens used mainly by foxes contained only some 40 bones each average (Mondini 1995, 1998, 2001, 2003, 2004a, 2005a, Mondini 2007, 2012). The main transported prey were juvenile-adult medium to large mammals – especially caprines and to a lesser extent wild and domestic camelids; there were also some birds, and small mammals were the least abundant taxa. Caprines, which are easier to hunt and to transport, were fairly complete, while camelids showed a limb-dominated anatomical pattern. About half the bones in these dens are broken, and long bone shafts prevail over ends. Tooth marks are present in <30% bones, camelids being more frequently damaged. Pitting and scoring are more common, and no fractures were attributed to carnivores. The integrity of these transported ungulate bones differs from carnivore dens in other regions of the world, where vertebrate carcasses are commonly more intensively depleted (e.g. Stiner 1991). Nevertheless, differential destruction affects smaller taxa here, which are more abundant in scats. Predator:prey and scavenger: carcass body size relationship has proved to be very relevant to account for these study cases.

Fox scats in Patagonia – both from around consumed carcasses and from dens – contain leporids, small rodents, birds, sometimes larger mammals, and also unidentified bones, frequently in high proportions, besides invertebrates (Martin 1998; Gómez & Kaufmann 2007; Cruz et al. 2010). The ingested anatomical pattern is complementary to the transported one (Figure 4). High levels of fragmentation are described, especially in the larger prey, and few tooth marks were identified. Digestion affects all bones and has been characterized as strong to extreme. In the dens in the Puna and a lower Andean valley, scatological assemblages mostly corresponding to foxes – although other carnivores are also involved to a lesser degree – were sampled (Mondini 2000, 2012; Mondini & Rodríguez 2006; Mondini et al. 2006). The nearly 2900 bones contained are highly comminuted, with an average maximum size of 4–5 mm, significantly less than reported elsewhere for canids (e.g. Schmitt & Juell 1994). Few specimens are identifiable, and small vertebrates, namely rodents, are dominant. Long bones prevail, followed by teeth, vertebrae and phalanges. The larger the prey, the higher the destruction levels that were observed. In an experiment a pampas fox was fed with mice and produced a low relative abundance, with few cranial parts and no femora or humeri surviving (Gómez 2007).

Taphonomic action by other carnivores

Mustelids and mephitids have been subjected to a few taphonomic studies. In a naturalistic study of scats of Andean hog-nosed skunk (*Conepatus chinga*), various taxa were found – including amphibians, reptiles, birds, and rodents being the only mammals (Montalvo et al. 2008). A low relative abundance was inferred, especially in the larger rodents, suggesting differential destruction according to prey size (Figure 4). Unlike previous observations of small mustelids, which apparently did not feed on prey heads (Andrews & Nesbit-Evans 1983), here isolated incisors are abundant, suggesting that heads are eaten but destroyed by chewing. Few elements protected by skin were articulated, and severe destruction of bone remains is inferred,

mainly by chewing, although only one specimen had tooth damage. Extreme modification prevails. In the zoo experiment with mice, a skunk was also included and the highest relative abundance of all predators was obtained, with a higher postcranial abundance than the other taxa considered (Gómez 2007). Anyway, like them, this carnivore is included in the extreme category.

A study of Neotropical otter (*Lontra longicaudis*) scats in a riverine Pampean area showed a much higher survival rate than in the skunk (Montalvo et al. 2015). Intense bone breakage was observed, but not as high as in the skunk (Figure 4). It is attributed mainly to chewing, although only a couple of bones had tooth marks. Digestion modifications are quite abundant and intense, and this predator was also assigned to the extreme modification category. All of these results are generally in agreement with previous studies on mustelids and viverrids (Andrews 1990, among others).

Discussion

Prey consumption, temporal variation and spatial patterning

While there are some taxon-specific patterns, as shown above, several studies suggest that bone modification properties overlap to some degree among different carnivores – even humans –, hampering actor identification in the fossil record (e.g. Elkin & Mondini 2001; Massigoge et al. 2014; Borrero et al. Forthcoming). Nonetheless, some important lessons can be drawn from naturalistic studies taking the mammalian carnivore community as a whole. They show, as expected, that smaller carcasses are more fully consumed than larger ones (e.g. Borrero & Martin 1996; Borella 2004; Cruz 2011; Mondini 2012; Massigoge et al. 2015; Borrero et al. Forthcoming). Hares, for instance, had a relative abundance of only 29% in a Pampean landscape, with up to 40% bones displaying gnawing marks in some areas (Gutiérrez et al. 2016). And as shown above, carnivore activity is the main factor of destruction and modification of avian remains in Patagonia, and thus a lower proportion of carnivore bone modifications as compared to mammals – with the exception of lesser rheas, even more commonly gnawed – only reflects the higher rates of destruction of the birds (Cruz 1999b, 2008, among others).

The degree of carcass consumption is varied both temporally and spatially, not just with the carnivore and prey taxa involved (e.g. Borrero & Martin 1996; Muñoz & Savanti 1998; Borrero 2001b; Belardi & Carballo Marina 2003; Cruz 2008; Gutiérrez et al. 2016; Otaola & Tripaldi 2016). Among other reasons, more gnawing and disarticulation are produced under higher carnivore:herbivore rates (Borrero & Martin 1996; Borrero 2001b; among others). In the Puna, camelid carcasses often remain with minimal alterations for months (e.g. Nasti 2000), while in other regions they are consumed at a faster rate. Carcass modification in the cold season – when hunting is easier and foxes can profit from the abundant natural deaths of ungulates – has been observed to be lower in Patagonia, while in summer – when pumas hunt with their cubs – prey are more fully exploited (Borrero 1990; Borrero & Martin 1996; Borrero et al. 2005, Forthcoming; among others).

From a spatial perspective, patterned variation is also perceived (Borrero 1988a, 2001b; Borrero & Martin 1996; Mondini

2005b, among others). In the Pampas, for instance, carnivore traces on hares tend to increment near rocky hills and to decrease near the sea coast (Gutiérrez et al. 2016). In Patagonia, a much lower carnivore signal on birds is found on the coast, where they abound, than in the interior steppe and forests (Cruz 2008, among others). Up to 50% of each ungulate carcass is exploited by pumas and scavengers altogether in some Patagonian areas, while this proportion was found to be lower or higher under varying conditions in the region (Borrero & Martin 1996; Borrero 2001b), and some cases of strong to extreme modification attributed to pumas have been described elsewhere (Muñoz et al. 2008; Fernández & Forlano 2009). These patterns in the spatial expression of carnivore trace intensity probably reflect changes in predatory intensity in most cases, although they should not be assumed to be isomorphic, and other factors such as differential destruction of bones as that highlighted by Cruz (1999b, 2008) should be considered.

At a smaller spatial scale, bone movement by carnivores is receiving increasing attention (e.g. Kaufmann & Messineo 2002; Otaola 2014). It has been noticed that within an assemblage, carnivores move bones laterally and vertically when they dig for buried anatomical units. They also do so when they move sediments to bury their scats, as do skunks (Montalvo et al. 2008). As noted, carnivores regularly disperse residual assemblages and delete bones by taking them to final destinations in dens or to intermediate caches. When prey are abundant, foxes do not disperse bones that much (Borrero 1990, among others). While this all has long been known, new information is shedding light on the magnitude of these movements in the region – which can reach hundreds of metres – and of prey size and amounts of bones, quite large in the case of puma dens.

One single species may leave differential traces depending if it is the ingested or the non-ingested part of its diet that has been sampled – or both –, and if it is in the residual or in the transported end of the trajectory of food consumption – or somewhere in between this continuum. Pumas tend to hunt in places appropriate for stalking, and their residual carcasses are usually found on those spots (Borrero & Martin 1996, among others). This partly depends on prey size, and sheep are hunted at more random places than guanacos. At predictable killing areas, scavenging sources can be anticipated. Pumas sometimes hide their prey under plants and can even transport them up to 30 m to protected places like rockshelters (e.g. Martin & Borrero 1997). Foxes are the most common agents of bone deposition and modification in the region, and they have proved to leave a highly variable record, which is unevenly distributed in the landscape. Foxes tend to transport their food to dens in rocky outcrops if available, or otherwise protected places (Martin 1998; Mondini 2012, among others). In the Puna, water availability and closeness to human settlements are important location factors in reproductive dens (Mondini 2005b). So the location of transported assemblages can often be predicted as well, rockshelters being the spots with more chances that carnivore and human occupations overlap. This varies in fact according to the characteristics of the shelters, carnivores preferring smaller ones if available. Scatological assemblages tend to concentrate in protected places as well when used as latrines, and are also found in predictable spots for territory marking places (Martin 1998; Mondini 2012, among others). Dens are in fact the only loci where unconsumed

prey remains – usually of large- and medium-sized taxa –, faeces contents – usually small vertebrates – and sometimes remains of the carnivores themselves may overlap. And when dens are in rockshelters, this record has higher chances to be preserved (Borrero & Martin 1996; Martin 1998; Borrero 2001b; Mondini 2012). As we take all of this variation in carnivore taphonomic landscapes into consideration, and extrapolating from Thomas and Mayer's (1983) concept of 'monitoring perspective', awareness of the 'taphonomic monitoring perspective' is thus crucial.

Digestion modifications and beyond

Generally, carnivore digested assemblages are dominated by small vertebrate bones and teeth – namely rodents and, where available, introduced hares – (Martin 1998; Mondini 2000, 2012; Quintana 2004; Gómez & Kaufmann 2007; Montalvo et al. 2008, 2012, 2015; Cruz et al. 2010), although puma scats include more larger prey (Martin & Borrero 1997; Montalvo et al. 2007; Labarca Encina et al. 2014). Taking these studies as well as experimental ones (Gómez 2007; Álvarez et al. 2012) altogether, the lowest survival rates are recorded in pumas and foxes (also see Fernández et al. 2017). These taxa also tend to present the lowest representation of the postcranial skeleton, particularly of the distal limbs. Yet, damage levels and other variables make carnivore taxonomic distinction very difficult (e.g. Álvarez et al. 2012). Another quite common trend in scatological assemblages is an increment in bone destruction directly correlated to an increment in prey size (e.g. Mondini 2000; Montalvo et al. 2007, 2008). Smaller carcasses are more fully consumed than larger ones, and animals in this size-range will be disproportionately represented in scatological assemblages relative to their actual frequency in carnivore diet. Yet, the fact that anatomical units like the autopodium are ingested without much mastication in the smaller prey preserves these bones, as the keratin from nails and hair acts as an efficient protection against digestive acids. As has been recognized elsewhere, some variation is also related to prey morphology and some to seasonal changes in prey availability as well (e.g. Montalvo et al. 2012).

The low abundance of larger prey in scats relates not only to destruction during mastication, but also to the low rates of bone damage and consumption usually produced in ungulate carcasses. As they cannot be identified, large amounts of unrecognizable bone fragments in fox and puma scats, probably derived from ungulates, have received less attention. Yet, being these minute fragments often dominant, they may well be the only scatological bones to enter the fossil record and be sampled in an archaeological excavation (Mondini 2000; Borrero et al. Forthcoming, among others). Thus, their full description is as necessary as the more traditional indices on identified specimens.

Ungulate soft tissues can also be preserved in scatological assemblages. Hair is particularly durable and identifiable (Mondini 2000; Mondini et al. 2006; Gómez & Kaufmann 2007, Montalvo et al. 2007; among others), although its scatological origin cannot be identified once out of the matrix. Besides prey, carnivore hair derived of grooming has helped determine scat taxonomy in the Puna (Mondini et al. 2006; Mondini 2012). Plant remains from these scats were also analysed, and these grasses were barely affected by digestion (Mondini et al. 2006; Mondini & Rodríguez 2006). Plant micro-remains are being studied as

well, as they also have good chances of preservation. Arthropods are abundant in scats from some areas, particularly in the warm season, and chitin can be quite durable too (e.g. Montalvo et al. 2008). Parasites have also been successfully identified even in some fossil samples (e.g. Beltrame et al. Forthcoming). Thus, several kinds of organic remains may enter the fossil record out of carnivore scats.

Neotropical carnivore taphonomy in context

Generally, on comparing this taphonomic scenario to other parts of the globe, scatological assemblages represent some variations, but in the main they are not that different. Carnivore ingestion and digestion appear to be conditioned by evolutionary factors that are relatively invariable at an ecological scale – like anatomical constraints such as body size, masticatory apparatus and digestive acids of different linages –, and by the type and size of prey rather than specific taxa. Instead, residual and transported assemblages seem to be more directly affected by biogeographical and ecological factors that are more variable in space and time, affecting both the carnivores themselves – like competition – and their prey – like the relative saturation of large mammals. It is in these assemblages that southern Neotropical carnivores differ the most from their relatives elsewhere.

Considering the environmental particularities of southern South America thus implies not just projecting the models elicited in other contexts, but reconsidering them, and formulating brand new ones in the light of the specific physical and biotic conditions in the region (Mondini & Muñoz 2011).

One such condition is the shape of the South American landmass – a peninsula narrowing southwards within the oceanic hemisphere –, which prompts gradients such as that of ecological and morphostructural systems becoming simpler as latitude increases (Morello 1984). Available landmass decreases with latitude, and becomes more limiting a factor with it. It is oceanity that increases with latitude here, instead of continentality, as in northern continents. Besides, the subcontinent is linked to North America only by the Panama isthmus, which acts like a filter to the flow of organisms (Rapoport 1982). The Andes cordillera is the most prominent physical feature, and there are no other large orographic barriers in South America (Morello 1984). It runs north-south along the western flank, and stops the westerly winds. The arrangement of ecosystems into latitudinal bands is thus dimmed due to the combined effects of oceanity, the Andes configuration and the impact of marine currents (Morello 1984). This all lessens the latitudinal gradient in biotic communities that promotes less species and larger ranges as latitude increases. The Southern Cone, spreading over a wide latitudinal range, entails in fact quite an even stretch of land.

In post-glacial temperate South America, many ecological niches are only partially occupied by mammals as compared to North America (Redford & Eisenberg 1992). This has to do with the long history of isolation of the subcontinent and the extinction of Pleistocene faunas. At present, even when mammal body sizes are similar, there are generally fewer species per feeding niche here. Consequently, a low saturation of large mammals prevails, not only as regards species richness but also demography, precluding keen competition (Keast 1972; Franklin 1982; Berta

1988). Ungulates have a low representation in the continent, and they comprise one of the best examples of unsaturation. Camelids have been the ecologically dominant large herbivores since Pleistocene extinctions. In southern South America, carnivores are part of the dominant faunas. Most of them have generalized omnivorous dentitions and flexible feeding habits (Berta 1987, 1988; Marshall & Cifelli 1990; Prevosti & Pereira 2014). Larger species with a more carnivorous diet were the most impacted by Pleistocene extinctions. The diversity of small-sized predators, instead, has kept fairly constant throughout the Pleistocene and Holocene. One implication of unsaturated environments such as this is that competition among predators – including humans – is not as intense. Further, solitary carnivores are a distinct feature in the region, unlike others where social carnivores are more common. Even though higher levels of competition are inferred for the Southern Cone in Pleistocene times (Martin 2013; Prevosti & Martin 2013; and bibliography therein), the overlap of human feeding niche with others would have been restricted mainly to large felids, which on the other hand would also have provided opportunities for a scavenging niche (Borrero et al. 2005; Martin 2013). With the exception of southern Patagonia, where the fossil record of large felids and humans often coincides (Martin 2013), a 'dilution effect' is common in the Southern Cone, whereby carnivore fossil record is weakly represented relative to the denser anthropic one (Mondini 2005a). This suggests that interspecific competition between mammalian predators and humans – the latest immigrants into the continent – has been low or intermittent in the region, especially after the extinction of Pleistocene megacarnivores (Muñoz & Mondini 2007, 2008, among others). On the other hand, generalized symbiotic interactions such as commensalism would have been important in this context (Mondini 2004b; Stahl 2012, among others).

In this context, carnivore taphonomic signals and their biasing of human-produced assemblages can be expected to be of low intensity in average situations. Exceptions should be expected as informed by palaeoecolgcial studies and also under particular present-day conditions, which can be identified via actualistic research. In this regard, while there is a lot of information on Patagonian and Pampean plains and surrounding areas, other environments have not been sampled in detail yet, and this is necessary to better define how 'exceptional' some reported cases are and how diverse carnivore taphonomic traces can be under varying circumstances. Also, even in the modal cases of light carcass modification, specific biases may be introduced by carnivores in the archaeological record. And no matter how subtle their taphonomic signature, it is informative of the past predatory community and the role of humans within it. To elicit this information, integral diagnoses need to be made, which call for multiple, independent lines of evidence, including not just bone modifications but also considering all the biotic, spatial and environmental evidence generally.

As discussed here, unique physical and biotic conditions prevail in southern South America that affect the taphonomic action of mammalian carnivores. Thus, as has often been appealed for, specific models are required to generate taphonomic principles that are germane to this specific context. On the other hand, this particular arena represents an instance of the whole spectrum of variation that can be expected in carnivore activity worldwide,

and one that we can learn from in order to deeply understand the circumstances under which such variation occurs through space and time.

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