

Four Decades of Actualistic Carnivore Taphonomy in the Southern Neotropics: A State of the Art

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Based on a bibliographic survey, this paper reviews the state of the art of actualistic taphonomic information of different autochthonous mammalian carnivores in the southern Neotropics. The characteristics of this corpus of data and its implications for the fossil record are analysed. The paper focuses on identifying and discussing those areas of research that are robustly reflected by existing studies. Synthetic discussion of the results of research on the most studied carnivore taxa, types of bone assemblages, actualistic approaches, and ecological zones in the region are presented. While the field of actualistic taphonomic research is well-developed in the region, there are several gaps that require more attention for the future investigation.

Keywords: CARNIVORES, TAPHONOMY, ACTUALISTIC STUDIES, NEOTROPICS, SOUTHERN SOUTH AMERICA.

Introduction

Actualistic studies of mammalian carnivores are key to the generation of taphonomic principles relevant to the interpretation of the zooarchaeological and palaeontological records (Gifford, 1981). In the Neotropics, research in this field has concentrated mainly in the Southern Cone (Gutiérrez *et al.*, 2007; Mengoni Goñalons, 2010; Mondini & Muñoz, 2011, and bibliography therein). This paper is based on a survey of the

actualistic taphonomic studies of mammalian carnivore carried out in the southern Neotropics with the aim of assessing the current state of the art and the implications for future developments. The survey was carried out by making an exhaustive revision of published material in national and international media –journals, books, and conference proceedings–.

Studies of carnivore taphonomy started to be systematically conducted in the region some forty years ago, and have become

quite rich in the last fifteen years (Mondini & Muñoz, 2011, 2014; Muñoz & Mondini, 2014). In fact, these studies have become the leading branch of taphonomic research in the area. Cumulatively these studies have identified the actions of carnivores under a variety of conditions and contributed to the understanding of the range of taphonomic signals created by these biotic agents that can impact the fossil record. They have generally focused on bone modifications and other traces produced by the redundant behaviour of the different autochthonous Carnivora taxa, in order to characterize them into models applicable to the archaeological record. In this way, these studies have advanced knowledge of the taphonomic signatures and variation created by these actors.

Terrestrial carnivores in south-western South America include a large felid, the puma (*Puma concolor*) of 29-120 kg, and several smaller species of 1-15 kg, including other felids –like *P. yagouaroundi*, *Leopardus colocolo*, *L. geoffroyi*, *L. jacobitus*, *L. guigna*–, canids –*Lycalopex culpaeus*, *L. griseus*, *L. gymnocercus*–, mustelids –like *Galictis cuja*, *Lyncodon patagonicus*, *Lontra longicaudis*, *L. felina*–, mephitids –like *Conepatus humboldtii*, *C. chinga*–, and procyonids –like *Procyon cancrivorus*– (Redford & Eisenberg, 1992; Wilson & Reeder, 2005; Barquez *et al.*, 2006, among others).

In this article, the discussion of these taphonomic studies is organized by most studied carnivore species, the bone assemblages, the actualistic approaches applied, and ecological zones. While the taphonomic signature of the different mammalian carnivores in the Southern Cone is described elsewhere (see Mondini, 2017 and bibliography therein), the state of the art regarding our knowledge on it is

addressed here, and those areas of research that deserve more attention in further rounds of research are identified. The database of the sources cited here is detailed in Appendix 1.

A brief history of carnivore actualistic taphonomy in the region

Carnivore taphonomy has been a relevant issue in southern South America since the 1980s, when Luis Borrero started publishing the results of his actualistic observations and highlighting the relevance of the field (*e.g.*, Borrero, 1988a, 1988b, 1989). It has now been some forty years and these studies and the models derived from them have grown in number and diversity, especially in the new millennium. More than 80 actualistic works on carnivore taphonomy have been conducted over the last four decades (see Appendix 1). While this works out to be an average of about two works per year, the production rate is highly variable through time (Figure 1). Most of the research took place in the last 15 years or so (Figure 2), as did the taphonomic production in the region (Muñoz & Mondini, 2014).

The geographic focus of actualistic carnivore taphonomic studies in the region

Virtually all of the actualistic studies on carnivore taphonomy in southern South America have been done in the drier, Andean-Patagonian subregion of the Neotropics (Figure 3). The great majority have been carried out in Patagonia (62.5%), especially in southern Patagonia, at the meridional end of the continent (Figure 4).

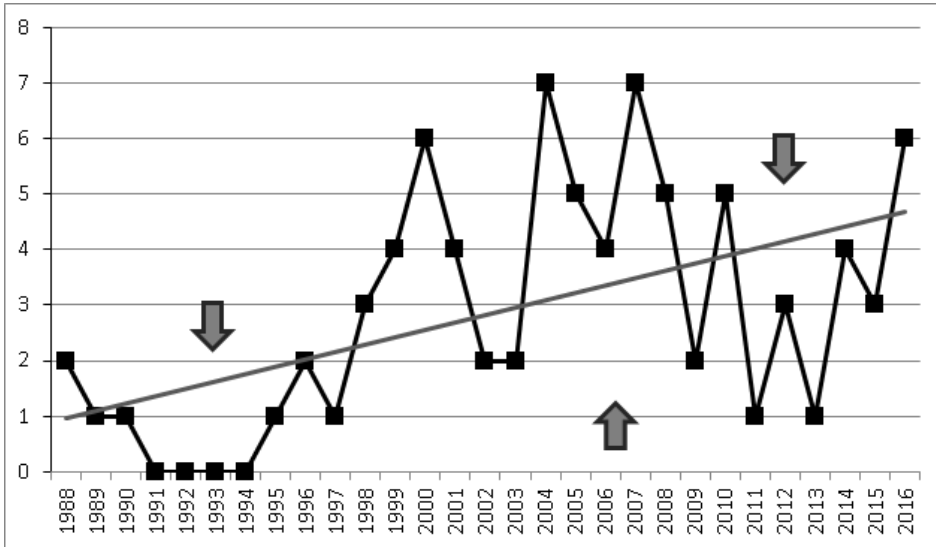


Figure 1. Number of contributions on actualistic carnivore taphonomy per year.

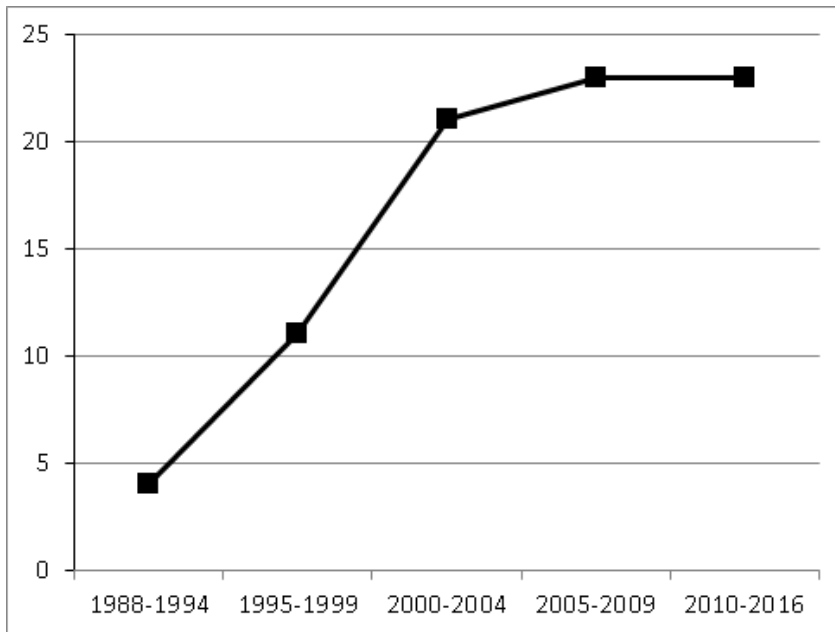


Figure 2. Number of contributions per 5/7-year periods.

Again, this tracks the trend of taphonomic research in general (Muñoz & Mondini, 2014).

The environmental variability addressed by these actualistic studies is unevenly represented (Figures 5 and 6). The Patagonian steppe –including the Atlantic coast– is by and large the most thoroughly studied ecoregion, followed by the Patagonian forests, the Pampas –including the Atlantic coast and riverine settings–, the Andean Puna, and other ecoregions. Several important ecological zones, including the wet and dry Chaco, grasslands and savannahs, several wetlands, rain forests, and oceanic ecoregions, have not been subjected to taphonomic studies on carnivores.

The taphonomic approaches

A vast majority (82.22%) of actualistic studies on Neotropical carnivores in the region are naturalistic (*sensu* Marean, 1995), while 17.78% –mostly fairly recent ones– are experimental. In fact, nearly half of the actualistic works are naturalistic studies specifically focused in carnivores, while about one third are more general naturalistic studies including carnivores as one of several agents (Figure 7).

Some 70.49% of these studies focused on non-ingested bones, while 29.51% deal with digested, scat-derived specimens. If we further subdivide the former into the studies dealing with residual *versus* transported assemblages (*sensu* Binford, 1981) –that is, those dealing with the opposite ends of the food procurement, consumption and transport circuit–, more than half addressed residual assemblages, a quarter transported assemblages from dens, and the proportion of ingested assemblages drops to about 23%

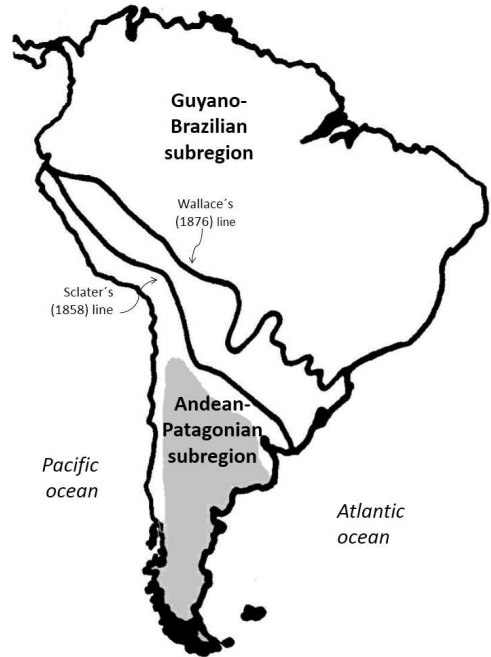


Figure 3. Main distribution of carnivore taphonomic studies in the southern Neotropics (shaded area). Neotropical subregions after Rapoport (1968).

(Figure 8). Within the latter, nearly all of the studies deal with ingested bone, generally just the identifiable portion, and few address the other tissues and remains ingested by the carnivores (*e.g.*, Mondini & Rodríguez, 2006).

The best known Neotropical carnivores

Most taphonomic studies (57.69%) have focused on pumas (*Puma concolor*) –the largest sized carnivore– and South American foxes (*Lycalopex sp.*) –the most ubiquitous ones–, either altogether or in

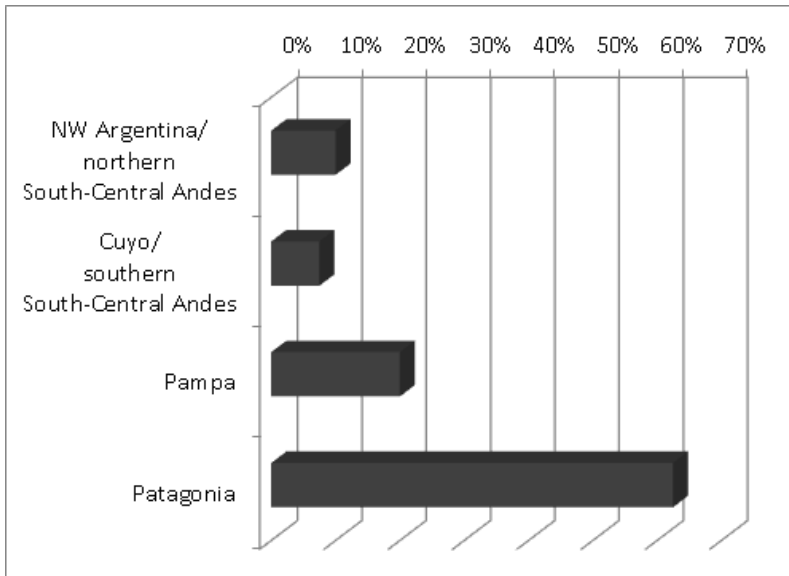


Figure 4. Carnivore taphonomic studies (%) by regions.

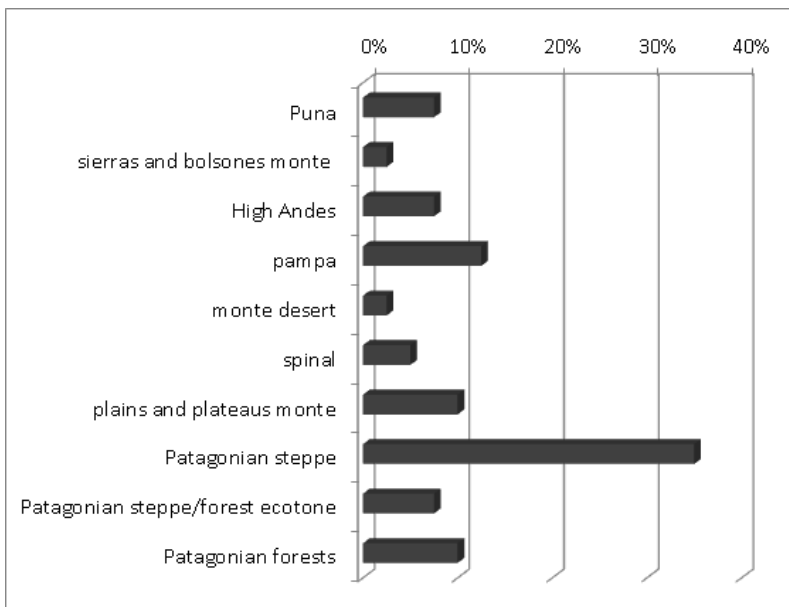


Figure 5. Carnivore taphonomic studies (%) by ecoregions.

Actualistic carnivore taphonomy in the southern neotropics



Figure 6. Distribution of carnivore taphonomic studies across southern Neotropical ecoregions. Actualistic carnivore taphonomic studies concentrate to the SW of the bold line. The oval surrounds the areas where most actualistic studies on pumas have been undertaken; the arrows point to “exceptionally” strong puma action. Ecoregions after Griffith et al. (1998, http://ecologicalregions.info/htm/sa_eco.htm).

about equal parts (Figure 9). The studies of these taxa are followed in frequency by research on smaller cats and, to a lower extent, mephitids (*Conepatus chinga*) and mustelids (*Lontra longicaudis*). Over 23% deal with multiple taxa. Among canids, most studies deal with multiple and/or indeterminate species (Figure 10). Among wild smaller felids, studies on *Leopardus geoffroyi* are well represented (Figure 11). Other carnivores in the region have not yet been studied from a taphonomic viewpoint.

Broadly speaking, the taphonomic signatures of these carnivores are characterized by their low intensity (see Mondini, 2017; Appendix 1). These animals tend to produce low –although variable– levels of biasing, in the sense of loss of information. Yet the degree of carcass consumption varies in space and time at different scales, and also according to the prey and predator taxa involved. As compared to other regions, greater similarity is observed in bone modifications and assemblage composition in digested assemblages, and greater variability in residual and transported assemblages.

One case is worth mentioning here by way of example. While the degree of carcass modification by pumas is generally described as low (Mondini & Muñoz, 2008; Kaufmann *et al.*, in press; Borrero *et al.*, in press; and bibliography therein), two case studies show dramatic departures from the norm: one in the Patagonian forest of the La Plata lake (Chubut, Argentina) and another in the high Andes at Diamante lake (Mendoza, Argentina). The former consists of at least eight huemul deer (*Hippocamelus bisulcus*) carcasses, where full utilization (*sensu* Haynes, 1981, 1982; also see Sala *et al.*, 2014) by pumas is inferred (Fernández & Forlano, 2009). The latter case consists of two guanaco (*Lama*

guanicoe) carcasses where full consumption by pumas is also inferred (one of which has been described in detail in Muñoz *et al.*, 2008). The intensive exploitation of several anatomical units in these carcasses denotes the consumption of not just flesh, other soft tissues and blood: the intra-bone and intra-skull-case nutrients were also consumed. The heavy consumption of the head is particularly remarkable. Yet, as Stiner (1991, 1994) noted, intra-skull fat is very stable even in under-nourished prey, although it requires intensive processing of the bone to access it. Under some conditions, such as carnivore food stress at the end of the winter in the high Andes, intensive processing may yield important life-sustaining nutrients. Also, it has been observed that when puma mothers hunt with their offspring, predation becomes more intensive, with more extensive disarticulation and gnawing (*e.g.*, Martin & Borrero, 1997; Borrero *et al.*, 2005). These and other conditions may introduce some more extreme variation than the usual range in puma predatory patterns and their taphonomic signals.

The heavy consumption of prey heads by pumas is not unique or based on an isolated observation, as several instances have been identified. Other signatures in these cases are similar to those identified in most other puma studies –such as the proportion and anatomical distribution of gnawed bones and puncture mark sizes–. While lighter carcass consumption by pumas is mostly found in open Patagonian and Pampean environments, the only studies out of these ecoregions have identified this more intensive pattern (Figure 6). Thus, variation in puma taphonomic patterns, especially as a function of ecological factors, should be further investigated.

Actualistic carnivore taphonomy in the southern neotropics

- general naturalistic studies including carnivores
- naturalistic studies focused on carnivores
- experimental studies focused on carnivores

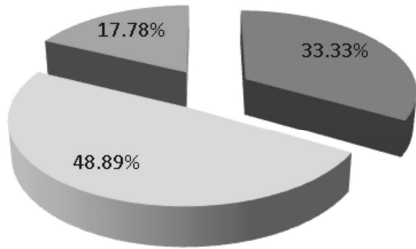


Figure 7. Naturalistic and experimental taphonomic studies (%) on southern Neotropical carnivores.

- residual assemblages
- transported assemblages
- digested assemblages

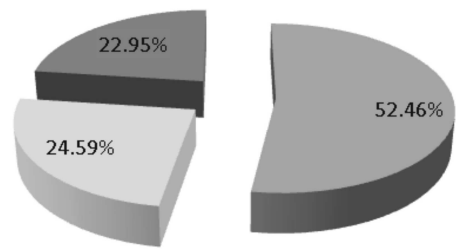


Figure 8. Types of assemblages dealt with by actualistic studies on southern Neotropical carnivores.

- pumas
- foxes
- mephitis
- small cats
- mustelids
- multiple families

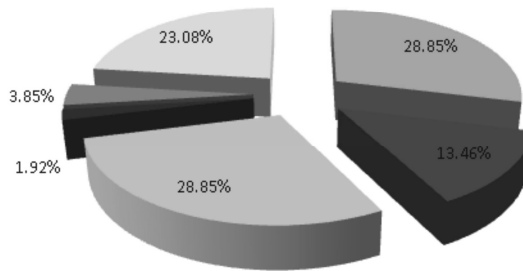


Figure 9. Proportion of studies on different Neotropical Carnivora taxa.

- *Lycalopex culpeus*
- *Lycalopex griseus*
- *Lycalopex gymnocercus*
- indet./multiple species

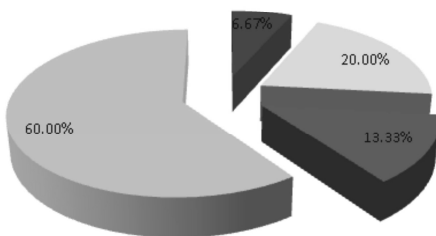


Figure 10. Proportion of studies on different Neotropical canids.

- *Leopardus geoffroyi*
- *Lynchailurus pajeros*
- *Herpailurus yaguarondi*

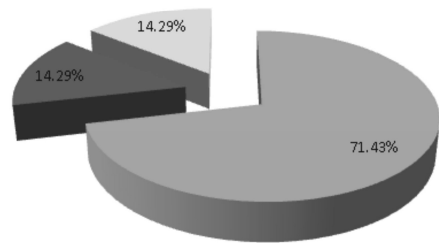


Figure 11. Proportion of studies on different Neotropical small felids.

Implications for a future agenda

Actualistic carnivore taphonomy looks like a healthy field in the southern Neotropics, especially within Argentinean archaeology, and appears to be growing, diversifying and evolving. The application of the models derived from them to archaeological research is also growing, although at a slower pace (Mondini & Muñoz, 2011, 2014). Taphonomic information cited in archaeological analyses is often just a formal step towards arguing that the zooarchaeological sample in question is not strongly biased, and thus allow for anthropic inferences. The positive contributions of taphonomy (*sensu* Behrensmeyer & Kidwell, 1985) are seldom elicited or used in these analyses. This is one direction where future developments are needed.

After four decades of research characterizing the action of different carnivores, mainly pumas and foxes, further rounds of research on some unexplored issues would certainly help fill current information gaps. More generally, research focused on variability in carnivore taphonomic action is crucial. This implies, as has been increasingly the case in taphonomic research, going beyond typical cases and patterns, applying wider spatial and temporal scales, and orienting research to the lesser known contexts, such as those out of the Patagonian and Pampean open lands. Another healthy way to intensify future research is the use of more integral diagnoses, taking into account the taphonomic “monitoring perspective” (*sensu* Thomas & Mayer, 1983; *cf.* Mondini, 2017) in the non-ingested bone assemblages and, in the case of ingested ones, considering both identifiable and non-identifiable bones, as well as other animal and non-animal scat-derived remains.

In the interpretive domain, the use of typological approaches and global analogies has been decreasing, and future rounds of research would benefit from further distinguishing the immanent *versus* configurational properties of the uniformitarian assumptions (*sensu* Simpson, 1970). By way of example, similarly sized carnivore teeth often leave differential traces if used with changing intensity and in variable behavioural contexts, including “boredom chewing”. One strength from the growth of taphonomic data is the awareness that models are specific to the target carnivores, environments and behavioral contexts, and that this mediates their relevance to the interpretation of the fossil record. As mentioned, more robust models would benefit from addressing variability in carnivore taphonomic action and the conditions under which it occurs. Naturalist studies (*sensu* Marean, 1995) are, in this regard, of great importance. A combined strategy, oriented simultaneously to recognize the relation between agents and traces and their variation and to explore the conditions under which such variation is produced, promises to be a very productive approach at this stage (Mondini & Muñoz, 2011; *cf.* Gifford-Gonzalez, 1991).

The fact that the production of taphonomic principles regarding Neotropical carnivores is represented by an ascending curve is encouraging. New generations are becoming involved in these issues. This would greatly benefit in future by strengthening some of the existing trends, such as increasing academic appraisalment of actualistic projects themselves and a progressively balanced concern with the negative –namely biasing– and positive –namely palaeoecological– contributions of these taphonomic processes

(*sensu* Behrensmeyer & Kidwell, 1985). One goal for the future might be the more active integration of taphonomic principles into archaeological research and analyses as a way to provide meaning to archaeological evidence and move beyond the goal of assuring the lack of important biases. This would also help move from pattern recognition and proximate explanations to more general ones and higher levels of causation. Importantly, as mentioned above, future actualistic studies should increasingly focus on recognizing and explaining variation in carnivore taphonomy.

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Appendix 1: Bibliographic Database of actualistic carnivore taphonomy in the Southern Neotropics

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