



## Actualistic taphonomic study of the rodents digested by the Achala culpeo fox (*Lycalopex culpaeus smithersi*) in the highlands of central Argentina

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We present the first actualistic study of the rodents consumed by the South American fox *Lycalopex culpaeus smithersi* (Achala culpeo fox), a subspecies of the culpeo fox that is endemic to the highlands of central Argentina. We provide a taphonomic characterization of this canid based on digested micromammal bones, and compare it to other carnivores. We studied over 1000 bones derived from 83 scats collected in Quebrada del Condorito National Park, Córdoba province, Argentina, corresponding to caviomorph and myomorph rodents. *Galea leucoblephara* was the main prey (59.8% MNI, 93.1% biomass). Average relative abundance for the total assemblage was 26.7. Cranial and, to a lesser extent, proximal limb bones were the most abundant elements. A high degree of breakage was observed in cranial elements and, to a lesser extent, in limb bones. A high proportion of heavy and extreme digestion was inferred, while some elements bear light or no digestion traces at all. Overall, the Achala culpeo fox fits best with other mammalian carnivores in the category of extreme modification, and shows types and proportions of taphonomic attributes similar to other South American mammalian predators. These results contribute to the understanding of regional taphonomic processes and of digestive modifications by *Lycalopex* foxes generally, and are thus relevant to interpreting the presence of micromammal remains in the archaeological and palaeontological records and the impact of these foxes upon their formation.

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The taphonomy of mammalian carnivores is relevant to the interpretation of the fossil record. Carnivores may accumulate, transport, modify and destroy faunal specimens, including those associated with anthropic remains (e.g. Binford 1981; Brain 1981; Andrews 1990; Lyman 1994a). Different groups of carnivores leave distinctive traces in the resulting fossil record. Thus, taphonomic evaluation of their signatures may provide relevant palaeoecological information.

The study of carnivore taphonomy has been developing in southern South America, particularly in Argentina, since the 1980s (Mondini 2017). South American foxes are among the most ubiquitous carnivores in the continent (Redford & Eisenberg 1992). They are known to take part in the formation of the palaeontological and archaeological record by accumulating, removing and modifying bones of their prey (e.g. Mondini 2004; Martín 2013). Several studies have been undertaken to assess their taphonomic patterns on prey ranging from large- to small-sized (see Mondini 2018; Montalvo & Fernández 2019, and references therein). Yet, informa-

tion on these canids is still scarce in several areas and environments, and it is especially limited as regards ingested bones (Mondini 2000, 2018; Gómez & Kaufmann 2007; Cruz *et al.* 2010; Rafuse *et al.* 2014; Montalvo & Fernández 2019).

Here we present the first actualistic study of the rodents consumed by the canid *Lycalopex culpaeus smithersi*, known as the Achala fox, a subspecies of the culpeo fox that is endemic to the Pampa de Achala area in Córdoba province, central Argentina. We provide a taphonomic characterization of this canid based on digested micromammal bones, and compare it to previous studies on related foxes and other carnivores. This taphonomic characterization, in turn, may serve as a set of criteria to help identify the potential role of the Achala fox in the formation of the zooarchaeological and palaeontological records. Secondly, we aim at finding out whether there is any variation in taphonomic patterns between collection years, as previous studies in the area found significant interannual differences in fox diet (Pia 2011, 2013).

## South American canids and the Achala fox

Canids invaded South America during the Late Pliocene as part of the Great American Biotic Interchange, but their record in the continent remains poor until the Pleistocene. The earliest canid record in South America comes from the Late Pliocene of the Pampean region in Argentina (Cione & Tonni 2001). *Lycalopex* is the most diverse Canidae genus in the continent (Berta 1987, 1988; Perini *et al.* 2010). The oldest record of the genus is that of *L. cultridens* from the Late Pliocene of Buenos Aires province in the Pampas, which disappeared in the Pleistocene, while *L. culpaeus* has been present since the Pleistocene throughout much of South America (Prevosti & Forasiepi 2018).

Extant autochthonous canids in South America include *Atelocynus microtis*, *Chrysocyon brachyurus*, *Cerdocyon thous*, *Speothos venaticus*, *Lycalopex sechura*, *L. fulvipes*, *L. vetulus*, *L. gymnocercus* (*L. griseus* is provisionally treated as a junior synonym of *L. gymnocercus*; Chemisquy *et al.* 2018, 2019) and *L. culpaeus* (Ginsberg & MacDonald 1990; Wilson & Reeder 2005; Patton *et al.* 2015; Prevosti & Forasiepi 2018; SAyDS & SAREM 2019).

The most common foxes in Argentina are the closely related *L. gymnocercus* and *L. culpaeus* (Manfredi *et al.* 2004; Lucherini & Luengos Vidal 2008; Luengos Vidal *et al.* 2019; Pia *et al.* 2019). *L. gymnocercus*, known as the Pampas fox and South American gray fox, is smaller than culpeos (2.0–6.5 kg), and is known to hunt larger rodents such as the Plains viscacha (*Lagostomus maximus*), leporids (*Lepus europaeus*), and armadillos, and to prey upon other small mammals, birds, amphibians, reptiles, eggs and arthropods. Their generalist diet includes a scavenger component as well.

Culpeos (*L. culpaeus*) range across the Andean-Patagonian Neotropical subregion from northern Ecuador to southern Chile and Argentina, along the foothills of the Andes, including Tierra del Fuego, central Argentina and the Patagonian steppe (Fig. 1A, B; Novaro 1997; Jiménez & Novaro 2004). Their wide distribution and the stability of their populations have warranted their inclusion in the conservation category of Least Concern (Lucherini 2016; Pia *et al.* 2019). With a weight of ~3.4–14.0 kg, they are the largest representative of the genus and the second largest canid in South America (Redford & Eisenberg 1992; Novaro 1997; Jiménez & Novaro 2004; Pia *et al.* 2019). They are mainly nocturnal, occasionally gregarious, opportunist and have a generalist diet, seasonally varied in some areas, preying and scavenging upon medium to small mammals, birds, lizards, and arthropods. They use small rockshelters or just rock cracks as lairs and build burrows at the bases of trees and bushes (Novaro 1997; Mondini 2012). *L. culpaeus* includes six subspecies, two of which have isolated populations, including the target subspecies *L. c. smithersi*, the

Achala fox (Thomas 1914; Novaro 1997; Martínez *et al.* 2018; Pia *et al.* 2019).

The Achala fox is endemic to the high mountains of central Argentina (Fig. 1C), and it is geographically isolated from other populations of *L. culpaeus* (Pia *et al.* 2019). It has a highly carnivorous diet, with no major seasonal variations, which includes primarily small native prey, namely caviomorph (Caviidae and Ctenomyidae) and myomorph (Cricetidae, Sigmodontinae) rodents (Pia *et al.* 2003; Pia 2011, 2013). Small livestock is less frequently consumed and contributes little biomass to the diet. Although the culpeo fox was listed as Least Concern, molecular studies have revealed that the conservation status of the Achala fox is worrying, due to its low genetic diversity, its geographical isolation, and the fact that its range is highly susceptible to climatic changes. These factors increase the vulnerability of the subspecies and place it in the Endangered category (Pia *et al.* 2019).

## Study area

Pampa de Achala is a ~2000 m a.s.l. plateau located over the high mountains of Córdoba province in central Argentina (latitude 31°50'S, longitude 64°52'W; Fig. 2). The area represents a biogeographical island, with over 40 endemic plant and animal taxa, including the culpeo fox subspecies *L. c. smithersi* (Luti *et al.* 1979). The landscape is heterogeneous, dominated by granite outcrops (56% of the surface area) intermingled with mosaics of grasslands, shrublands and xeric forests: grasses, lawns at higher altitude, areas with exposed rock surfaces due to erosion, and *Polylepis* forests and shrublands restricted to steep slopes in mid- to low topographic positions (Cingolani *et al.* 2004). Mean monthly temperatures at 2100 m a.s.l. range from 5 °C in winter to 11.4 °C in summer (Cabido & Acosta 1985). Mean annual precipitation is 850 mm and is mainly concentrated between October and April (Cabrera 1976).

Livestock rearing (cattle, sheep, horses and goats) was introduced in the high mountains of Córdoba province in the 17th century, and it represents the main driver affecting vegetation composition at the local scale (Cabido *et al.* 1999). Quebrada del Condorito National Park (26 000 ha, Fig. 2) was created in this area in 1996, and livestock was removed from its range (Cingolani *et al.* 2008). This resulted in an increase in vegetation cover and height, which in turn contributed to an augmented presence of rodents (Pia *et al.* 2003).

The Pampa de Achala high plateau has been dominated by savannah and/or grassland vegetation since the Late Pleistocene – with trees and shrubs becoming more abundant along with wetter and colder conditions from the Middle Holocene to ~1500 BP – and by faunas adapted to the Andean-Patagonian subregion, including some elements of the Guianan-Brazilian subregion as

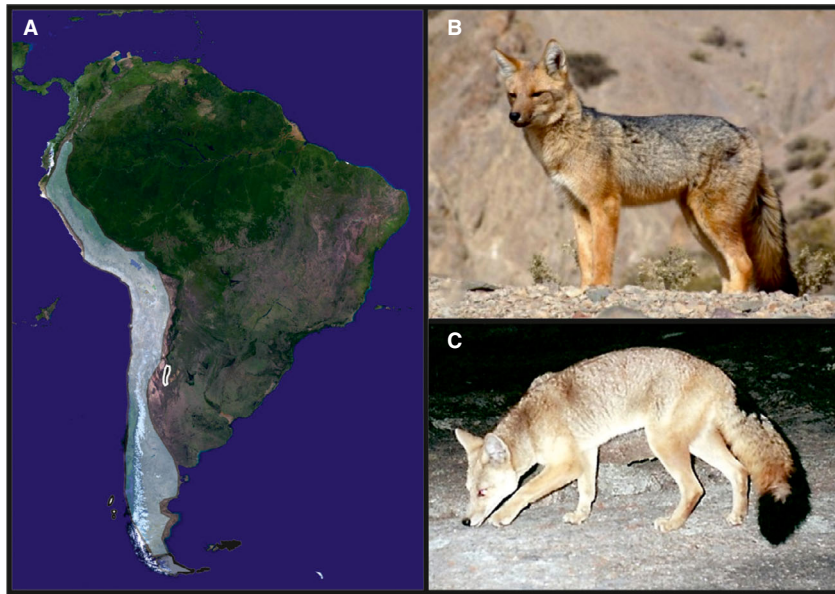


Fig. 1. A. Distribution of *Lycalopex culpaeus* (larger area) and *L. c. smithersi* (smaller area) in South America. B. *Lycalopex culpaeus*. C. *L. c. smithersi*.

well, as the area was comprised in an ecotonal fringe with it (Krapovickas & Tauber 2016; Krapovickas *et al.* 2017). The area has been occupied by human populations since the Late Pleistocene (Rivero 2012). Rodents were a significant part of their diet (Rivero *et al.* 2008–2009; Medina *et al.* 2011; Rivero & Medina 2016; Pastor *et al.* 2017), including a now extinct *Ctenomys* species (De Santi *et al.* 2020) and a *Holochilus* species currently restricted to lower areas (Teta *et al.* 2005).

## Material and methods

In this study we report the taphonomic patterns on the rodents consumed by the Achala fox based on 83 scats collected in 2004, 2007 and 2008 in Quebrada del Condorito National Park by one of us (MVP), currently deposited at the Laboratorio de Zooarqueología y Tafonomía de Zonas Áridas (LaZTA, IDACOR, CONICET-UNC). The sample was randomly selected from a larger assemblage originally surveyed for a study aimed at determining the occurrence of foxes and pumas (*Puma concolor*) in the area, as well as their diet, based on prey remains in scats (Pia 2011). The scats were collected through opportunistic searches on foot and horseback over rock outcrops and internal roads – where faeces are commonly found – covering the whole Park area (>300 km<sup>2</sup>) and its various environments, as well as along some 5 m by 1000 m transects set up on riverside sandbanks for counting carnivore traces like scats and footprints (Pia 2011). Surveys throughout the whole area were repeated annually for 6 years. It should be noted that there are few rocky shelters in the area where fox latrines are usually located elsewhere in the *Lycalopex*

genus range (e.g. Walker *et al.* 2007; Mondini 2012), and thus faeces are not found as concentrated in the landscape here. In all the sampling years of the study (2003–2008), no scat accumulations making up marking spots were found (Pia 2011).

Collected scats were preliminary identified in the field, stored in labelled paper bags, and then described, measured and washed in the laboratory (Pia 2011). Identification was then confirmed based on morphology and size, as well as contents (Chame 2003; Jouy-Avantin *et al.* 2003; Palacios 2007; Pia 2011). Unidentifiable faeces – over 20% of the total collection, in which the zoological origin could not be confirmed unambiguously after laboratory analyses – were not considered (Pia 2011). Faeces of Achala foxes were determined based on their sausage shape with separated constrictions and pointed end, their fairly small size ( $1.9 \pm 0.05$  cm diameter), and also a diet focused on small native prey as suggested by their contents (Pia 2011). While dogs (*Canis lupus familiaris*) are few and not allowed to range freely within Quebrada del Condorito National Park, an area of 200 m around a few inhabited households was excluded from sampling locations (Pia 2011). In any case, the shape, size and content criteria were applied to all canid scats so as to ensure that no dog faeces were collected by mistake, considering that faeces of this domestic canid differ from those of wild foxes in morphology, dimensions and composition due to differential diet (e.g. Mitchell & Banks 2005). The closest living wild canid, the Pampas fox (*Lycalopex gymnocercus*), occurs at lower elevations and does not reach the area covered in this study; hence, there was no chance of mistaking scats of the two foxes. On the other hand,

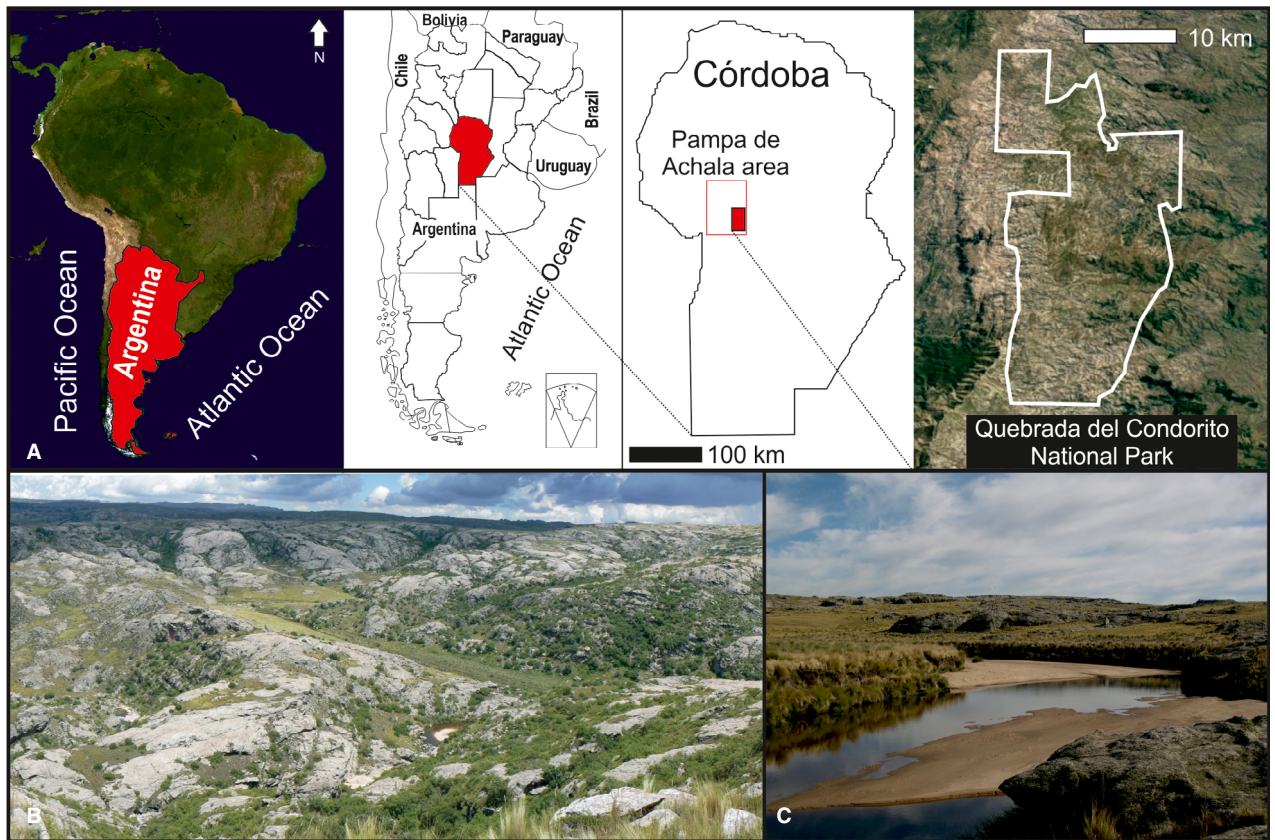


Fig. 2. A. Location of the study area, the Quebrada del Condorito National Park, in the Pampa de Achala, Córdoba province, Argentina. B and C. Landscapes in the study area.

another wild carnivore in the area addressed in the original study is the puma, and its faeces were distinguished from fox scats based on shape and content as well as size, which was found to be significantly different (puma =  $3.3 \pm 0.05$  cm diameter; Pia 2011).

In the original study (Pia 2011), scat contents were analysed to determine food items based on bones and other vertebrate remains like hair, following the methods of Reynolds & Aebischer (1991). Most food items were mammals, and only 2.4% were birds (Pia 2011). The most common mammalian item (50–70%) was Caviidae, followed by Cricetidae and Ctenomyidae. Rodents made up over 90% of the biomass consumed. A small carnivore was also found, possibly *Conepatus chinga* or *Galictis cuja*. Among exotic prey and carrion, *Lepus europaeus* and large (*Bos primigenius taurus* and/or *Equus ferus caballus*) and medium (*Ovis* and/or *Capra* sp.) livestock were identified in low frequencies, in agreement with their low densities within the National Park.

Taphonomic evaluation for this study was based on the rodent bones of the 83 Achala fox scat samples. One of the scats also contained a snake skull, and some others contained bird feathers and mammalian hair. Yet, most hair, unidentifiable bone splinters and other remains were discarded after the previous study on food habits

(Pia 2011). Thus, unidentified bone fragments are not included in this work.

Taxonomic identification of the rodent remains was based on mandibles, maxillary bones and teeth, and was done to the finest possible level (e.g. Fernández *et al.* 2011; Patton *et al.* 2015). The average body mass of the species represented was obtained from the Macroecological Database of Mammalian Body Mass (MOM), version 4.1 (Smith *et al.* 2003). The percentage of biomass contributed by each prey species was estimated as  $(B_i) = [(S_{pi} N_i) / \Sigma(S_{pi} N_i)] \times 100$ , where  $S_{pi}$  is the weight of species  $i$  and  $N_i$  is the number of consumed individuals of species  $i$  (Marti *et al.* 2007).

The taphonomic analysis included evaluation of some indices (Lyman 1994b): NISP (number of identified specimens per taxon); MNE (minimum number of elements that account for the NISP, taking into account laterality in paired bones), and MNI (minimum number of individuals that account for the MNE). MNI was evaluated using two criteria. On the one hand, we took an MNI for taxonomic abundance (MNI<sub>t</sub>) by taking into account the minimum number of individuals per taxon present in each scat and then summing them up. On the other hand, we took an MNI for anatomical abundance (MNI<sub>a</sub>), which was calculated based on

commonest skeletal element of each yearly bone assemblage regardless of the scat and the specific rodent taxon. The latter method emulates that applied to fossil assemblages, in which the contents of different scats are aggregated, and it has been used in previous studies on carnivore taphonomy, thus making it comparable. We also considered the totals and percentages (% NISP/MNE/MNI).

The analysis of bone and tooth specimens followed the methodology proposed by Andrews (1990) and Fernández-Jalvo & Andrews (1992), and considered the subsequent modifications made to account for the digestive corrosion of molars and incisors specifically of sigmodontine and caviomorph rodents of South America (Fernández *et al.* 2017; Montalvo & Fernández 2019; Montalvo *et al.* 2020). This methodology includes the following estimations:

- Calculation of the relative abundance of different skeletal elements, taking into account the representation of each element relative to the minimum number of individuals, as follows:  $MNE_i / (E_i \times MNI_a) \times 100$ , where  $MNE_i$  is the minimum number of a skeletal element in the sample, and  $E_i$  is the expected number of that skeletal element in an individual. Isolated incisors and molars are included in these calculations, by considering 16 molars per individual for caviomorphs and 12 for sigmodontines. In order to compare the Achala fox to other carnivores, we estimate the average relative abundance of all skeletal elements considered, as well as the average of breakage and digestion degrees, as considered by Gómez & Kaufmann (2007), Cruz *et al.* (2010) and Montalvo & Fernández (2019).
- Calculation of the ratio of cranial to postcranial elements by evaluating the  $[(f + h)/(md + mx)]$  index, where  $f$  is femora,  $h$  is humeri,  $md$  is mandibles and  $mx$  is maxillae, and the ratio of proximal to distal limb elements after the index  $[(t + u)/(f + h)]$ , where  $t$  is tibiae and  $u$  is ulnae.
- Evaluation of skeletal element breakage degree, which included estimating the proportion of complete and incomplete elements, and assessing breakage degrees for specific elements. Rodent skull breakage was evaluated by considering the nine categories proposed by Montalvo *et al.* (2020). To the five categories proposed by Montalvo *et al.* (2020) for mandible breakage, another one was added for even smaller fragments including just the ascending ramus and angular process. The number of broken molars and incisive teeth was also considered. Breakage degree of postcranial elements was evaluated in humeri, femora, ulnae and tibiae.
- Evaluation of the digestive corrosion degree, based on modifications produced by digestive acids on incisors, molars, proximal femora and distal humeri, after Andrews (1990) and Fernández *et al.* (2017).

- Presence of tooth marks (e.g. scores, punctures) on bone surfaces.

## Results

More than 1000 rodent specimens (total NISP = 1195) were found in the 83 scats. Of these, 400 (33.5% NISP) are from the 2007 sample, 524 (43.8% NISP) from 2004 and 271 (22.7% NISP) from 2008.

### Taxonomic abundance

Over 100 rodent individuals (total MNI<sub>t</sub> = 107) were identified, 85.1% of which could be determined at least to the genus level, including the caviomorphs *Galea leucoblephara* and *Ctenomys* sp., and the myomorphs *Reithrodon auritus*, *Phyllotis xanthopygus*, *Akodon dolores*, *Akodon azarae* and *Calomys musculinus* (Table 1). The caviid *G. leucoblephara* was the taxon with the highest relative frequency (59.8% MNI<sub>t</sub>), followed by *R. auritus* and *P. xanthopygus* and the ctenomyid *Ctenomys* sp. with ~7.5–4.7%. The rest of the rodents yielded even lower values (<4.7% MNI<sub>t</sub>). *Ctenomys* sp., *G. leucoblephara* and *R. auritus* were identified in samples from all years. A few sigmodontine individuals (MNI<sub>t</sub> = 4) could only be identified to this level. Another 12 (MNI<sub>t</sub>) individuals that could only be determined as Rodentia were identified in 10 scats that generally only contained postcranial elements, and in one case contained *R. auritus* cranial elements along with some postcranial ones of a different taxon. On the other hand, the MNI<sub>a</sub> for the whole assemblage was based on mandibles and rendered over 30 individuals (total MNI<sub>a</sub> = 32; 13 in 2004, 10 in 2007 and 9 in 2008).

Some temporal variation in sigmodontine richness was found, with *C. musculinus*, *P. xanthopygus*, *A. dolores* and *A. azarae* being represented in only one or two years (Table 1). In terms of biomass, among the small mammals, the caviid *G. leucoblephara* played the most important role in the diet of the Achala culpeo fox in the three years, reaching 93.1% of the total sample, while the rest of the rodents hardly contributed to its diet, ranging between 0.1–3.4% of the total biomass (Table 1).

### Relative abundance

A total of 892 rodent elements (MNE) were identified in the whole sample (Table 2). Relative abundance was assessed by considering rodent MNI<sub>a</sub> (Table 2). Average relative abundance for the total assemblage was 26.7 (total MNI<sub>a</sub> = 32), and it was 20.5 in the 2004 assemblage (MNI<sub>a</sub> = 13), 32.5 in 2007 (MNI<sub>a</sub> = 10) and 29.0 in 2008 (MNI<sub>a</sub> = 9). The relative abundance of most skeletal elements was low in the total sample and throughout all years. Cranial and, to a lesser extent, proximal limb bones

**Table 1.** Average body mass, taxonomic minimum number of individuals (MNI) and biomass percentage (% B) of the rodents consumed by the Achala fox per year and in the total sample.

Taxon	Body mass (g)	2004		2007		2008		Total	
		MNI	% B	MNI	% B	MNI	% B	MNI	% B
Rodentia indet.	–	4	–	4	–	4	–	12	–
<i>Ctenomys</i> sp.	223	1	1.2	2	5.3	2	7.9	5	3.4
<i>Galea leucoblephara</i>	480	38	96	16	91.8	10	85.2	64	93.1
Sigmodontinae indet.	–	1	–	0	–	3	–	4	–
<i>Akodon dolores</i>	50.5	0	0	0	0	3	2.7	3	0.5
<i>Akodon azarae</i>	25	0	0	3	0.9	1	0.4	4	0.3
<i>Akodon</i> sp.	38	0	0	1	0.4	0	0	1	0.1
<i>Calomys musculus</i>	20.1	1	0.1	0	0	0	0	1	0.1
<i>Reithrodon auritus</i>	70.9	4	1.5	1	0.9	3	3.8	8	1.7
<i>Phyllotis xanthopygus</i>	56.3	4	1.2	1	0.7	0	0	5	0.8
Total		53		28		26		107	

were the most abundant elements, and mandibles, maxillae and isolated teeth prevailed in all years (Fig. 3). It should be noted that many incisors and molars ( $n = 143$ ) were broken to less than a half, and so they are not included in the MNE counts. In the 2004 assemblage, many elements are missing, including scapulae, humeri, radii, ulnae, tibiae, calcanea, astragali and ribs, and in 2008 no astragali were preserved.

Anatomical indices show that cranial elements are generally dominant, although as in 2004 the cranial to postcranial index was particularly low, the total sample shows a slight predominance of postcranial elements (Table 3). Among limb elements, proximal ones prevailed (Table 3). In 2004 only femora were found, and there were no distal elements to allow application of the proximal to distal limb elements index.

### Breakage degree

No complete skulls were found in the analysed samples, and skull breakage categories 1, 2, 3 and 7 (*sensu* Montalvo *et al.* 2020) are not represented at all. The most frequent skull breakage categories throughout all years are 8 and 9, especially the latter, and there is only one specimen in category 4 (Table 4, Fig. 4A, B). Categories 8 and 9 represent the highest degree of breakage and include small maxilla fragments (with or without teeth).

Mandibles also display different degrees of breakage (Fig. 4C, D). Only a few mandibles were complete (4.8% MNE) and the most commonly represented category was 4 (ascending ramus and diastema missing, *sensu* Montalvo *et al.* 2020; Table 4). A few specimens were so broken, just represented by fragments of the ascending

**Table 2.** Rodent skeletal element frequencies (MNE, % MNE and relative abundance) per year and in the total sample.

Skeletal element	2004			2007			2008			Total		
	MNE	% MNE	Rel. ab.	MNE	% MNE	Rel. ab.	MNE	% MNE	Rel. ab.	MNE	% MNE	Rel. ab.
Mandibles	25	9.1	96.2	20	5	100	18	8.4	100	63	7.1	98.4
Maxillae	17	6.2	65.4	11	2.7	55	13	6	72.22	41	4.6	64.1
Scapulae	0	0	0	7	1.7	35	7	3.3	38.89	14	1.6	21.9
Humeri	0	0	0	7	1.7	35	8	3.7	44.44	15	1.7	23.4
Radii	0	0	0	6	1.5	30	1	0.5	5.56	7	0.8	10.9
Ulnae	0	0	0	9	2.2	45	7	3.2	38.89	16	1.8	25
Pelvis	1	0.4	3.8	6	1.5	30	8	3.7	44.44	15	1.7	23.4
Femora	8	2.9	30.8	10	2.5	50	10	4.7	55.56	28	3.1	43.8
Tibiae	0	0	0	5	1.2	25	3	1.4	16.67	8	0.9	12.5
Vertebrae	11	4	2.4	42	10.5	11.7	34	15.8	10.49	87	9.8	7.6
Incisors	51	18.5	98.1	32	8	80	20	9.3	55.56	103	11.5	80.5
Molars (Caviomorpha)	129	46.9	62.0	37	9.2	23.1	25	11.6	17.36	191	21.4	37.3
Molars (Sigmodontinae)	8	2.9	5.1	6	1.5	5	6	2.8	5.56	20	2.2	5.2
Metapodials	11	4	4.2	52	12.9	26	2	0.9	1.11	65	7.3	10.2
Phalanges	14	5.1	1.9	144	35.8	25.7	51	23.7	10.12	209	23.4	11.7
Calcanea	0	0	0	0	0	0	1	0.5	5.56	1	0.1	1.6
Astragali	0	0	0	1	0.3	5	0	0	0.00	1	0.1	1.6
Ribs	0	0	0	7	1.8	2.9	1	0.5	0.46	8	0.9	1
Total	275			402			215			892		
Average			20.5			32.5			29.0			26.7

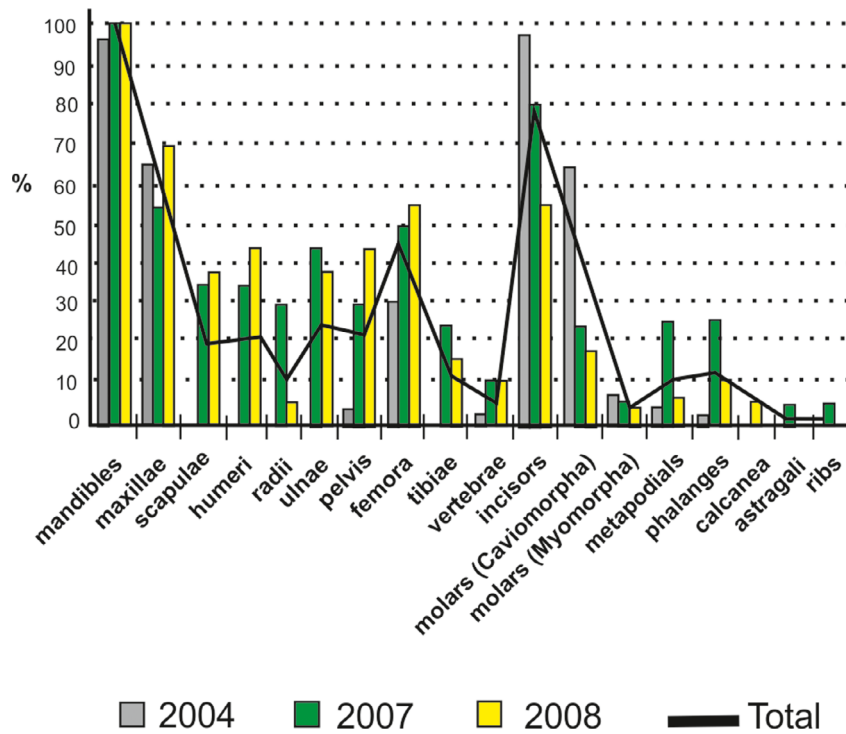


Fig. 3. Relative abundance of rodent skeletal elements per year and in the total sample.

Table 3. Rodent anatomical indices per year and in the total sample.

Indices	2004	2007	2008	Total
$[(f + h)/(md + mx)]$	19.05	54.8	58.1	41.3
$[(t + u)/(f + h)]$	–	82.4	55.6	55.8

ramus and angular process, that we defined a new category, number 6, to encompass them.

As regards the postcranial elements assessed, a high proportion of broken limb elements (82.8%) was observed for all years (Table 5). In 2004 scats, only incomplete femora were found. In other years, more diverse limb bone fragments were preserved, even some complete ones, although no complete tibiae were found. The only isolated shafts corresponded precisely to the tibia.

Other skeletal elements like scapulae, ribs and pelvis also displayed a high degree of breakage, and only 10.8% of these elements were complete. It should be noted that even after scat disassembling and cleaning, some elements remained articulated, among them 10 sets of 2–10 vertebrae and 20 segments of autopodials with articulated metapodials and phalanges (Fig. 4F).

#### Bone modifications

All degrees of digestion modifications (after Andrews 1990; Fernández *et al.* 2017) are represented, and both

bones and teeth are affected (Table 6, Fig. 5). In 2004, remains with moderate digestion prevailed, in 2007 bones with light digestion did, and in 2008 heavy digestion was dominant.

Among incisor teeth, both *in situ* and isolated, light and moderate digestion prevail in all collection years (Fig. 5B, C), while in molars, moderate and strong digestion modifications were more common (Fig. 5D, E). Teeth with extreme modifications were recorded in all years. In 10.9% of the caviomorph isolated and *in situ* molars, saliences of cementum over the enamel were corroded by digestion, resulting in depressions (Fernández *et al.* 2017; Montalvo & Fernández 2019). Caviomorph isolated molars were more affected than *in situ* molars, with 22% displaying extreme corrosion (Table 6). A similar pattern was observed in cricetid isolated vs. *in situ* molars. Corrosion was not as intense in *in situ* cricetid molars as compared to caviomorph *in situ* molars, though, which is consistent with their morphology (Fernández *et al.* 2017; Montalvo & Fernández 2019).

While moderate and heavy digestion was observed in postcranial elements (humeri and femora) (Fig. 5F, G), light digestion prevailed throughout all sampling years (Table 6). Evidence of digestion is observed in several long bones as the rounding of broken edges (Fig. 5G). It is worth noting that no tooth marks were observed on any of the bones or teeth.

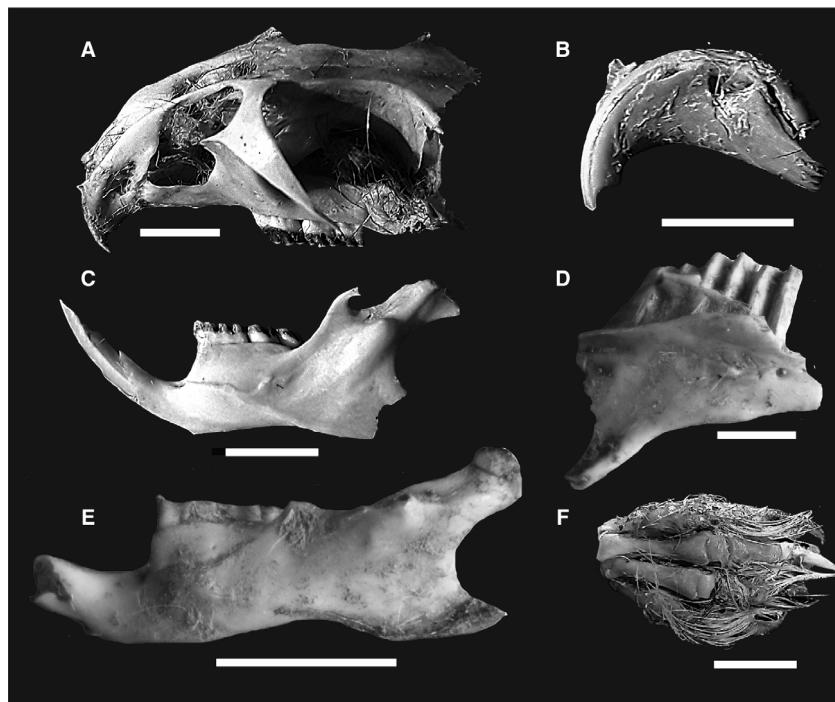
*Table 4.* Skull and mandible breakage categories represented per year and in the total sample.

Categories	2004		2007		2008		Total	
	MNE	%	MNE	%	MNE	%	MNE	%
Skull	4	0	0	0	1	8.3	1	2
	5	3	11.1	0	0	0	3	6
	6	1	3.7	0	0	0	1	2
	8	8	29.6	5	45.5	6	19	38
	9	15	55.6	6	54.5	5	26	52
Total	27		11		12		50	
Mandible	1	1	4	0	2	11.1	3	4.8
	2	0	0	0	3	16.7	3	4.8
	3	6	24	4	5	27.8	15	23.8
	4	15	60	5	3	16.7	23	36.5
	5	3	12	9	45	4	16	25.3
	6	0	0	2	10	1	3	4.8
	Total	25		20		18		63

## Discussion

The main prey of the Achala fox in the studied sample were autochthonous micromammals, namely rodents. Caviomorph rodents were the most important items in their diet considering both the number of individuals (% MNI) and their biomass (% B). We identified the rodent taxa found in the scats to the finest possible level. The identified rodent species currently inhabit the Pampa de Achala throughout the environmental mosaic of shrublands, xeric forests (*Galea leucoblephara* and *Akodon*

*dolores*), grasslands (*Reithrodon auritus* and *Akodon azarae*) and rocky outcrops (*Phyllotis xanthopygus*) therein (Polop 1989; Patton *et al.* 2015). The only exception is *Calomys musculus*, which has not been recorded in the Pampa de Achala before, but it has in lower, nearby areas such as Yacanto (900 m a.s.l., ~40 km SW of our study area), the type locality of one of its synonyms, *Hesperomys murillus cordovensis* (Thomas 1916). This generalist and opportunistic species occupies a wide variety of habitats, including natural grasslands, shrub steppes, crop borders, and disturbed



*Fig. 4.* Breakage and articulation in several cranial elements. A. Broken *Reithrodon auritus* (category 4). B. Rodent rostrum (category 8). C. Complete *R. auritus* mandible (category 2). D. Incomplete *Galea leucoblephara* mandible (category 4). E. Complete *Akodon* sp. mandible (category 1). F. Articulated elements from autopodial. Scale bars = 5 mm.



Table 5. Proportion of limb bone portions represented per year and in the total sample.

		% MNE				
		Femur	Tibia	Humerus	Ulna	Radius
2004	Complete	0	0	0	0	0
	Proximal	50	0	0	0	0
	Distal	50	0	0	0	0
	Shaft	0	0	0	0	0
2007	Complete	0	0	9.1	18.2	20
	Proximal	41.2	0	36.4	63.6	40
	Distal	58.8	60	54.5	18.2	40
	Shaft	0	40	0	0	0
2008	Complete	11.8	0	75	37.5	100
	Proximal	47.1	0	0	50	0
	Distal	41.2	33.3	25	12.5	0
	Shaft	0	66.7	0	0	0
Total	Complete	4.8	0	36.8	26.3	27.2
	Proximal	45.2	0	21.1	57.9	36.4
	Distal	50	50	42.1	15.8	36.4
	Shaft	0	50	0	0	0

environments (e.g. Salazar-Bravo 2015). Fossil, genetic and ecological evidence indicates that its recent geographical expansion is associated with the advancement of the agricultural frontier (Teta *et al.* 2014, and references therein).

The taphonomic patterns inferred for the Achala fox are generally similar to those previously described for South American foxes, although some specific charac-

teristics can be inferred, partly related to the highly carnivorous diet of the Achala fox, preferentially focused on rodents (Pia *et al.* 2003; Pia 2011, 2013). In previous taphonomic studies on *Lycalopex foxes*, high levels of fragmentation and breakage were observed, with few or no complete bones found in scats (Martin 1998; Mondini 2000, 2012; Gómez 2007; Gómez & Kaufmann 2007; Cruz *et al.* 2010; Rafuse *et al.* 2014). This is partly related to the presence of larger prey, including leporids and even ungulates. While breakage patterns in *L. c. smithersi* samples generally resemble those of other South American foxes, a relatively higher integrity of some elements was observed in our study. In spite of the high degree of digestion damage, several prey remains are complete enough as to be identifiable, both anatomically and taxonomically. This is probably related to the dominance of small prey in the diet of *L. c. smithersi*. This fact may also help explain the absence of tooth marks in the Achala fox samples, unlike scatological bones digested by other South American carnivores (Montalvo & Fernández 2019). The sets of articulated bones that pass through the digestive tract covered by skin and hair are protected by these tissues, which prevents breakage and damage by digestive acids (Mondini 2000). Overall, breakage patterns by the Achala fox are consistent with the intense fragmentation of cranial elements of South American carnivores generally, while some limb bones may be preserved complete (Montalvo & Fernández 2019).

Table 6. Proportion of digestion degrees in teeth (incisors and molars) and in postcranial elements (proximal femur and distal humerus) per year and in the total sample. N/A = not available.

	Isolated incisor	<i>In situ</i> incisor	Caviomorpha		Sigmodontinae		Femur	Humerus
			Isolated molar	<i>In situ</i> molar	Isolated molar	<i>In situ</i> molar		
2004 Total MNE	47	16	129	53	8	17	8	0
% non-digested	8.5	0	0	0	0	0	50	N/A
% light	46.8	50	12.4	22.6	37.5	29.4	25	N/A
% moderate	31.9	30	28.7	34	25	58.8	0	N/A
% heavy	4.3	20	31.8	43.4	25	11.8	25	N/A
% extreme	8.5	0	27.1	0	12.5	0	0	N/A
2007 Total MNE	30	16	37	24	6	19	10	7
% non-digested	0	9.1	5.5	0	0	0	14.3	71.4
% light	66.7	81.8	35.1	41.6	16.7	15.8	42.9	14.3
% moderate	26.7	9.1	18.9	16.7	49.9	26.3	28.5	14.3
% heavy	3.3	0	27	29.2	16.7	57.9	14.3	0
% extreme	3.3	0	13.5	12.5	16.7	0	0	0
2008 Total MNE	20	16	25	16	6	34	10	8
% non-digested	5	0	0	0	0	0	11.1	12.5
% light	60	68.7	12	0	0	0	77.8	50
% moderate	10	18.8	28	69	0	0	11.1	25
% heavy	5	12.5	52	6	50	91.2	0	12.5
% extreme	20	0	8	25	50	8.8	0	0
Total sample MNE	97	48	191	93	20	70	28	15
% non-digested	5.1	2.1	1	0	10	0	20	40
% light	55.7	62.5	16.8	23.7	16	11.4	55	33.3
% moderate	25.8	20.8	26.7	35.5	30	21.4	15	20
% heavy	4.1	14.6	33.5	33.3	24	62.9	10	6.7
% extreme	9.3	0	22	7.5	20	4.3	0	0



Fig. 5. Digestion traces in several cranial and postcranial elements. A. *Galea leucoblephara* mandible with heavy modification. B and C. Incisors with heavy and extreme modifications. D and E. *Galea leucoblephara* molars with heavy and moderate modifications. F. Distal humerus with moderate modification. G. Proximal femur with extreme modification and rounded broken edges. Scale bars = 1 mm.

Mammalian carnivores produce a high proportion of digested bones in scatological assemblages, both generally and in South America in particular (Andrews 1990; Montalvo & Fernández 2019). Our study on the Achala fox showed all degrees of digestive corrosion, including bones with no digestion traces, although a high proportion of heavy and extreme digestion was observed. This compares well to other South American foxes. Evidence of digestive corrosion by these canids has been characterized as heavy to extreme in previous studies (Gómez & Kaufmann 2007; Cruz *et al.* 2010).

In order to be able to compare our results to the digestion patterns by other South American foxes, we have selected the few available studies applying a similar methodological approach. Among these, there is the study by Cruz *et al.* (2010) of scat-derived bones from a *L. culpaeus* lair in Chubut province, Argentina, in Patagonia. In this sample, leporids, which live in high densities in the area, were dominant, while rodents were less frequent. Average relative abundance was 28.7 (unpublished data), and cranial and proximal limb bones prevailed in similar proportions. A high degree of breakage was observed, and bones of the smaller-sized rodents were best preserved. Strong and even extreme digestion was noted, and *L. culpaeus* was categorized as

a strong to extreme bone modifier predator (Cruz *et al.* 2010).

Another study applying a similar methodology to that used in this work is that by Gómez & Kaufmann (2007) on a sample of *L. gymnocercus* (cited as *Pseudalopex griseus*) scats from Río Negro province, also in Argentinean Patagonia. Small rodents were reported (with no finer taxonomic specification). Average relative abundance was 28.2, with cranial and proximal limb elements prevailing. Bone breakage degree was high, and no complete skulls or mandibles were found. The proportion of elements with digestion damage was also high. While light digestion prevailed, strong and extreme digestion degrees were abundant. According to this evidence, Gómez & Kaufmann (2007) considered *L. gymnocercus* to be in the highest category of bone modification (category 5, *sensu* Andrews 1990).

Gómez (2007) also undertook an experimental study with a similar methodological approach. He fed captive *L. gymnocercus* (cited as *Canis [Pseudalopex] gymnocercus*) individuals with *Mus musculus* rodents and analysed the digested bones. Very little bone material was recovered out of the 32 mice provided, and thus relative abundance was very low, with few cranial parts and no femora or humeri surviving. Given the scarce resulting

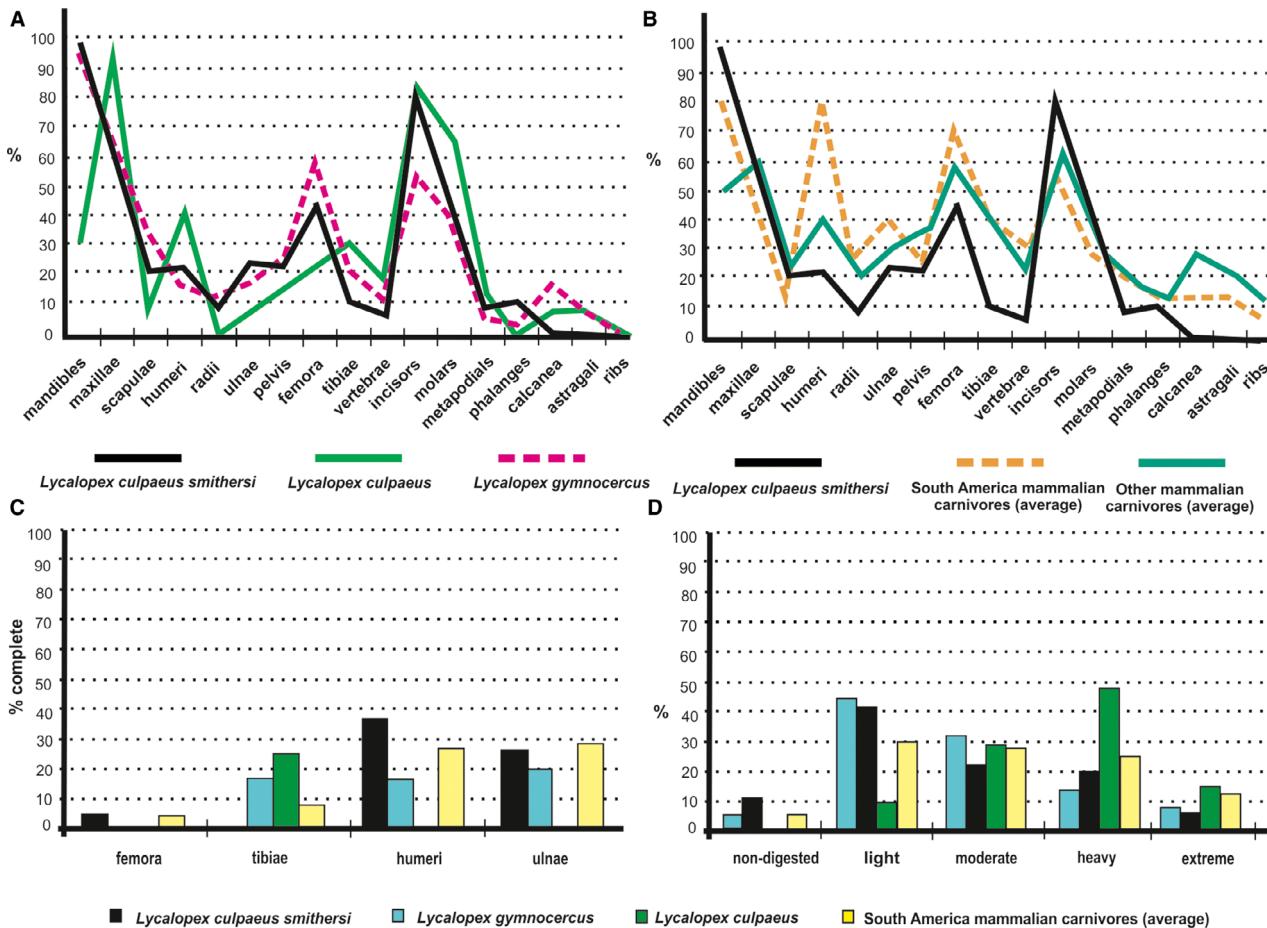


Fig. 6. A. Relative abundance of rodent prey ingested by *Lycalopex culpeus smithersi* (this study) compared to data of *L. culpeus* (Cruz *et al.* 2010, unpublished data) and *L. gymnocercus* (Gómez & Kaufmann 2007). B. Relative abundance of rodent prey ingested by *L. c. smithersi* (this study) compared to averaged data of South American mammalian carnivores (Montalvo & Fernández 2019) and of mammalian carnivores generally (Andrews 1990). C. Proportion of complete limb bones in *L. c. smithersi* scat assemblages (this study) compared to *L. culpeus* (Cruz *et al.* 2010, unpublished data), *L. gymnocercus* (Gómez & Kaufmann 2007) and averaged data of South American mammalian carnivores (Montalvo & Fernández 2019). D. Proportion of digestion modification degrees (average) in *L. c. smithersi* (this study) compared to *L. culpeus* (Cruz *et al.* 2010, unpublished data), *L. gymnocercus* (Gómez & Kaufmann 2007) and averaged data of South American mammalian carnivores (Montalvo & Fernández 2019).

sample, other taphonomic characteristics could not be estimated in detail (Gómez 2007).

Average relative abundance of skeletal elements in the Achala fox assemblages (26.7%) was slightly lower than that found in *L. culpeus* (Cruz *et al.* 2010) and in *L. gymnocercus* (Gómez & Kaufmann 2007). On comparing the relative abundance of the different skeletal elements (Fig. 6A), the Achala fox curve is similar to that of other *Lycalopex* foxes, both *L. gymnocercus* (after Gómez & Kaufmann 2007) and *L. culpeus* (unpublished data from Cruz *et al.* 2010 study). In all fox samples there is a high representation of mandibles – especially in *L. gymnocercus* and *L. c. smithersi*, maxillae, isolated teeth – mainly incisors – and, to a lesser extent, upper limb bones, femora in *L. gymnocercus* and *L. c. smithersi*, and humeri in *L. culpeus*. By contrast, in radii, tibiae – in the case of *L. gymnocercus* and

especially of *L. c. smithersi*, scapulae, vertebrae, ribs and autopodium bones, low relative abundance is observed.

The relative abundance of skeletal elements in *L. c. smithersi* scats is somewhat lower than the average for South American carnivore mammals (33.1%, Montalvo & Fernández 2019). Yet, this relative abundance pattern (Fig. 6B) is similar to that inferred for mammalian carnivores globally, considering samples from both South America and other regions (Andrews 1990; Montalvo & Fernández 2019). Cranial bones and teeth display high values in all cases, while the relative abundance of some limb elements and autopodials is somewhat lower in foxes, including *L. c. smithersi*. When compared to other mammalian carnivores (Andrews 1990), the Achala fox also displays similar peaks of abundance for the maxillae, mandibles and incisors, and a similar but lower pattern of relative

	Categories				
	1	2	3	4	5
Relative abundance					■
Postcrania/crania				■	■
Distal element loss					■
Digestion of incisors				■	■
Digestion of molars				■	■
Digestion of postcrania				■	■
Breakage of skulls					■
Breakage of mandibles					■
Breakage of postcrania					■

Fig. 7. *Lycalopex culpaeus smithersi* categorization according to the different attributes considered.

abundance of limb bones, particularly lower in humeri (Fig. 6).

The scatological bone samples produced by the Achala fox display a high breakage degree of both cranial and postcranial elements. No complete skulls were identified, and while some mandibles were preserved complete, those strongly affected by breakage were more common. Incomplete postcranial elements were dominant, although a few complete ones were observed, mainly humeri and ulnae (Fig. 6C). Breakage degree was thus similar to that found in other *Lycalopex* foxes and other South American mammalian carnivores generally (Fig. 6C; Gómez & Kaufmann 2007; Cruz *et al.* 2010; Montalvo & Fernández 2019).

The intensity of bone modification produced by digestion found in the Achala fox samples is similar to that of other carnivores, characterized by an abundance of skeletal elements with strong and extreme digestion (Montalvo & Fernández 2019). However, as compared to other *Lycalopex* foxes and to averaged South American carnivores (Gómez & Kaufmann 2007; Cruz *et al.* 2010; Montalvo & Fernández 2019), *L. c. smithersi* samples display a higher proportion of remains with light and no digestion (Fig. 6D).

Overall, these results support the conclusion that the Achala culpeo fox fits best with other mammalian carnivores in the extreme category of modification (category 5) as defined by Andrews (1990), and shows types and proportions of taphonomic attributes similar to other South American mammalian predators (Fig. 7).

As regards interannual variations in Achala fox samples, while sample size differs, it is worth noting that some indices change substantially. Remarkably, in 2004 (NISP = 524) moderate digestion prevailed, in 2007 (NISP = 400) light digestion did, and in 2008 (NISP = 271) heavy digestion was dominant. This has implications for the fossil record. Importantly, while the characterization of any predator should be based on the largest possible sample – by averaging individual scats or smaller assemblages –, these the inferred patterns should not be expected as such in any given context, as factors

like temporally varying prey abundance condition them in specific situations. Thus taphonomic studies are more useful when they aim at characterizing not just average predator taphonomic patterns, but also the range of variation they may have under different conditions (Montalvo *et al.* 2012, 2020; Mondini 2017). We intend to increase sample size in future rounds of the research so as to assess variation in greater detail.

## Conclusions

We studied the skeletal contents of 83 Achala fox scats from a taphonomic perspective. They yielded over 1000 caviomorph and myomorph rodent bones and teeth (total NISP = 1195; total MNE = 892; total MNI<sub>t</sub> = 107; total MNI<sub>a</sub> = 32). Average relative abundance for the total assemblage was 26.7, and that of most skeletal elements was low, with cranial and, to a lesser extent, proximal limb bones prevailing. No complete skulls were found, and intensive breakage also affected mandibles and limb bones. A high proportion of heavy and extreme digestion was inferred, although light and even null digestion corrosion was also observed. Corrosion was not as intense in *in situ* cricetid molars as compared to caviomorph *in situ* molars, though, which is consistent with the presence of a thick enamel layer in the former that hampers corrosion. Most of these patterns displayed some interannual variation. Overall, the Achala culpeo fox fits best with other mammalian carnivores in the category of extreme modification (category 5 as defined by Andrews 1990), and displays types and proportions of taphonomic attributes that are similar to other South American mammalian predators.

This is the first actualistic taphonomic study on Achala fox prey remains, and one of the few available taphonomic studies on the digestion of bones by South American foxes. The results obtained are relevant to understanding regional taphonomic processes in the highlands of central Argentina, and help characterize digestive modifications by *Lycalopex* foxes generally in the Neotropics, the oldest record of which dates back to the Late Pliocene in Buenos Aires province, Argentina (Prevosti & Forasiepi 2018 and references therein). Given the similarity of the samples produced by *Lycalopex culpaeus smithersi* to those by other representatives of the genus, the implications of these results are thus relevant to understanding the presence of micromammal remains in the archaeological and palaeontological records and may help shed light on the impact of *Lycalopex* foxes upon their formation.

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*Author contributions.* – DGC and MM designed the taphonomic project. MVP did the fieldwork and provided the regional background information and all the details on the field survey. MM provided background archaeological information and CIM provided palaeontological background. DGC, CIM and FJF carried out the taxonomic and taphonomic analyses of the bones. DGC, MM, CIM and FJF had the idea for the paper. MVP provided the photographs – except for the fox picture in Fig. 1B, provided by J. Monguillot – and CIM and FJF prepared the figures. CIM and DGC prepared the tables. CIM, FJF, DGC, MM and MVP contributed to the interpretation of the results.

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