Taphonomic analysis of small mammal bone remains preyed upon by wildcats (Carnivora: Felidae) from the central Monte Desert (Mendoza, Argentina)

JOSÉ MANUEL LÓPEZ, MARÍA I. ROSI, SOLANA TABENI, BENJAMÍN BENDER AND HORACIO CHIAVAZZA

The present study analysed the taphonomic characteristics of small mammal bone accumulations produced by small felids in an area from the central Monte Desert (Mendoza, Argentina). In order to provide criteria to identify the role that these predators had in the formation of zooarchaeological assemblages, the anatomical representation, bone breakage patterns and degrees of digestive corrosion were evaluated. The main taphonomic results are: low average values for the relative abundance of skeletal elements; greater representation of mandibles, maxillae, isolated incisors, humeri and femora than the remaining elements; preponderance of cranial elements with high proportion of isolated teeth; elevated frequencies of proximal limb bones compared with distal parts; high degree of breakage in all skeletal elements and digestive corrosion on almost all diagnostic bones (mainly moderate and heavy). The values of the studied taphonomic variables indicate that small felids in this area made severe alterations to the bones of their prey (mainly rodents), attributable to the category of extreme modifier, while preserving enough skeletal elements to allow their taphonomic characterization. Tooth marks or grooves on bone surfaces produced by scratching and chewing were not detected. The low relative abundance of skeletal elements, the high degree of breakage and the elevated frequency of elements with digestion traces represent general taphonomic patterns that fall within those reported for other South American small carnivores.

José Manuel López (mlopez@mendoza-conicet.gob.ar), Instituto de Arqueología y Etnología, Facultad de Filosofía y Letras (Universidad Nacional de Cuyo), CONICET – Centro de Investigaciones Ruinas de San Francisco , Centro Universitario s/n, Parque General San Martín, 5500 Mendoza, Argentina; María I. Rosi, Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA, UNCuyo, Gob. Mendoza) CONICET, Vertebrate Ecology and Management Group, CCT–Mendoza, Av. Ruiz Leal s/n, Parque General San Martín, CC. 507, 5500 Mendoza, Argentina; Solana Tabeni, Benjamín Bender, Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA, UNCuyo, Gob. Mendoza) CONICET, CCT–Mendoza, Av. Ruiz Leal s/n, Parque General San Martín, CC. 507, 5500 Mendoza, Argentina; Horacio Chiavazza, Museo del Área Fundacional, Instituto de Arqueología y Etnología, Facultad de Filosofía y Letras, Universidad Nacional de Cuyo, Centro Universitario s/n, Parque General San Martín, 5500 Mendoza, Argentina; received 24th May 2016, accepted 1st October 2016.

During the last three decades, the vertebrate bone remains found in archaeological contexts have attracted increasing interest and both zooarchaeological and taphonomic analyses have become valuable tools to understand the process and agents involved in the formation of the fossil/archaeological record (Behrensmeyer *et al.* 2000; Fernández-Jalvo *et al.* 2011; Mondini & Muñoz 2011). In South America, mainly in Argentina, several taphonomic studies have emphasized the role of vertebrate predators as potential accumulating agents of prey bone remains in archaeological contexts (e.g. Martín & Borrero 1997; Pardiñas 1999; Mondini 2000, 2002; Mondini & Muñoz 2008; Fernández 2012).

Small mammals, especially small rodents, are highly frequent items in the diet of several avian raptors and small carnivorous mammals (e.g. Pillado & Trejo 2000; Teta & Andrade 2002; Andrade *et al.* 2004, 2010; Trejo & Ojeda 2004; Bisceglia *et al.* 2008, 2011; Tabeni *et al.* 2012), which through their pellets and faeces, respectively, have contributed to the formation of important palaeontological and zooarchaeological accumulations (e.g. Mayhew 1977; Andrews 1990; Fernández-Jalvo

et al. 1998; Matthews *et al.* 2006; Demirel *et al.* 2011; Fernández 2012 and references therein). In this context, and assuming relatively similar hunting and feeding behaviours between past and present predators, taphonomic studies on recent bone accumulations can help to establish patterns of skeletal abundance, bone breakage and digestive corrosion for different predator species (Andrews 1990). However, some taphonomic differences have been detected amongst prey bones consumed by the same type of predator in environmentally different regions, associated with regional factors such as size and prey availability, amongst others (Matthews 2006; Montalvo *et al.* 2008; Andrade 2015). This emphasizes the need for regional taphonomic studies on predators and their prey, in order to develop patterns relevant to local conditions of archaeofaunal sets under study, a point already highlighted by other authors (e.g. Mondini & Muñoz 2011 and references therein).

Actualistic taphonomic research carried out in Argentina focused on prey of avian raptors and carnivorous mammals, including study areas mostly located within Pampean, Puna, Espinal and

Patagonian biomes (e.g. Mondini 2002, 2003; Montalvo *et al.* 2014, 2015; Rudzik *et al.* 2015; Ballejo *et al.* 2016). In the Monte Desert, the most arid rangeland of Argentina, less is known about the modifications that different predators make on the bones of their prey (Montalvo *et al.* 2012). Taking into account that the distinctive feature of the Monte is reflected by the different composition of its mammal fauna, particularly prey mammals (hystricognath and sigmodontine rodents) (Ojeda *et al.* 2002), several zooarchaeological sets of small mammals still need to be studied from a taphonomic perspective (e.g. Chiavazza 2007, 2010, 2012; García Llorca & Cahiza 2007; López *et al.* 2016).

It is well known that medium and small rodents are the basis of the diet of small cats such as *Leopardus colocolo* (pampas cat) and *Leopardus geoffroyi* (Geoffroy's cat) in different habitat types of Argentina (Manfredi *et al.* 2004; Bisceglia *et al.* 2008, 2011; García Esponda *et al.* 2009; Pereira *et al.* 2012; Tabeni *et al.* 2012); it follows that wildcats can generate significant accumulations of prey bones through the deposition of faeces in communal latrines (Rodgers *et al.* 2015 and references therein).

The modifications that *L. geoffroyi* produces on the bones of its prey have been analysed in the Monte Desert, showing high relative abundances and degree of breakage of skeletal elements, as well as high frequencies of bones with digestion traces. According to these features the species was assigned to the 'heavy modification' category with respect to small mammal remains (Montalvo *et al.* 2012).

The present study analysed the taphonomic features of small mammal bone accumulations produced by small felids – wildcats (Carnivora; Felidae) – in an area of the central Monte Desert (Mendoza, Argentina). In order to provide criteria to identify the role of these predators in the formation of zooarchaeological assemblages, the anatomical representation, bone breakage patterns and degrees of digestive corrosion were evaluated. By comparisons of these taphonomic variables with those reported for other mammalian carnivores, we hope to provide useful tools for the interpretation of small mammal bone accumulations recovered in archaeological and palaeontological sites from South America.

Study area

This study was carried out in the Man and Biosphere Reserve of Ñacuñán (latitude 34°02′S, longitude 67°58′W) and an adjoining unprotected area, in the central region of the Monte Desert (Morello 1958), Mendoza province, Argentina (Fig. 1). The climate is semiarid and markedly seasonal, with a mean annual rainfall of 326 mm, concentrated in summer months. Mean daily temperatures are below 10 °C in winter and above 20 °C in summer (Roig 1971; Ojeda *et al.*

1998). A heterogeneous vegetation mosaic characterizes this region. The major habitat types at this study site are open woodlands of *Prosopis flexuosa*, shrublands dominated by *Larrea divaricata*, and less extensive habitats such as sand dunes with sparse woody and herbaceous plants (Roig 1971).

Material and methods

Samplings of scats of small felids were performed throughout 2001 and 2002, within an area of 75 ha where 86 faeces were randomly recovered. Cranial and dental remains recovered from these samples were analysed in a previous study on small felids' predation upon small and medium prey mammals. Details about the collection, identification and processing of the faeces, as well as on the taxonomic identification of microvertebrate prey, have been described in Tabeni *et al.* (2012).

The small felid species that inhabit the Ñacuñán Reserve are *L. geoffroyi*, *Puma yagouaroundi* (eyra cat) and *L. colocolo*, the latter being the most common (Tognelli *et al.* 2001). The first one (2.5–8 kg) is distributed from Bolivia to southern Brazil and throughout southern Argentina and Chile (Nowell & Jackson 1996). These areas include mainly arid and semiarid environments, such as the Monte Desert, the Patagonian steppe and Chaco (Perovic & Pereira 2006; Bisceglia *et al.* 2008). Although *L. geoffroyi* prefers shrubland habitats with dense ground cover, it also occupies a wide variety of habitats such as tall grasslands, open forests, and wetlands (Nowell & Jackson 1996). *L. colocolo* (3–7 kg) has a wide distribution with disjunct areas from Ecuador to southern Argentina and Chile, and also through most of Paraguay, Uruguay, and central and southern Brazil (Nowell & Jackson 1996). With an altitudinal range from 100 up to over 5000 m a.s.l., this wildcat commonly inhabits open grasslands and shrublands, although it also occurs in several forest types such as the Gran Chaco and the Yungas (Nowell & Jackson 1996). The broad distribution of *P. yagouaroundi* (2.5–6 kg) comprises regions ranging up to 3200 m a.s.l., from coastal areas of México, Central America and South America up to ~39°S (Oliveira 1998; Caso *et al.* 2015). It is found in both open and closed habitats, from dry and humid forests, swampy savannas and grasslands, arid and semiarid thorn scrubs, to disturbed areas and human-induced grasslands (Nowell & Jackson 1996; Oliveira 1998).

Field identification of small felid scats was based on typical morphological features such as constricted cylindrical, beaded appearance, with one end sharpened and hairy (Chame 2003; Palacios 2007). All collected scats were gathered in a single group given that interspecific differentiation through their physical characteristics was not possible. These faeces were
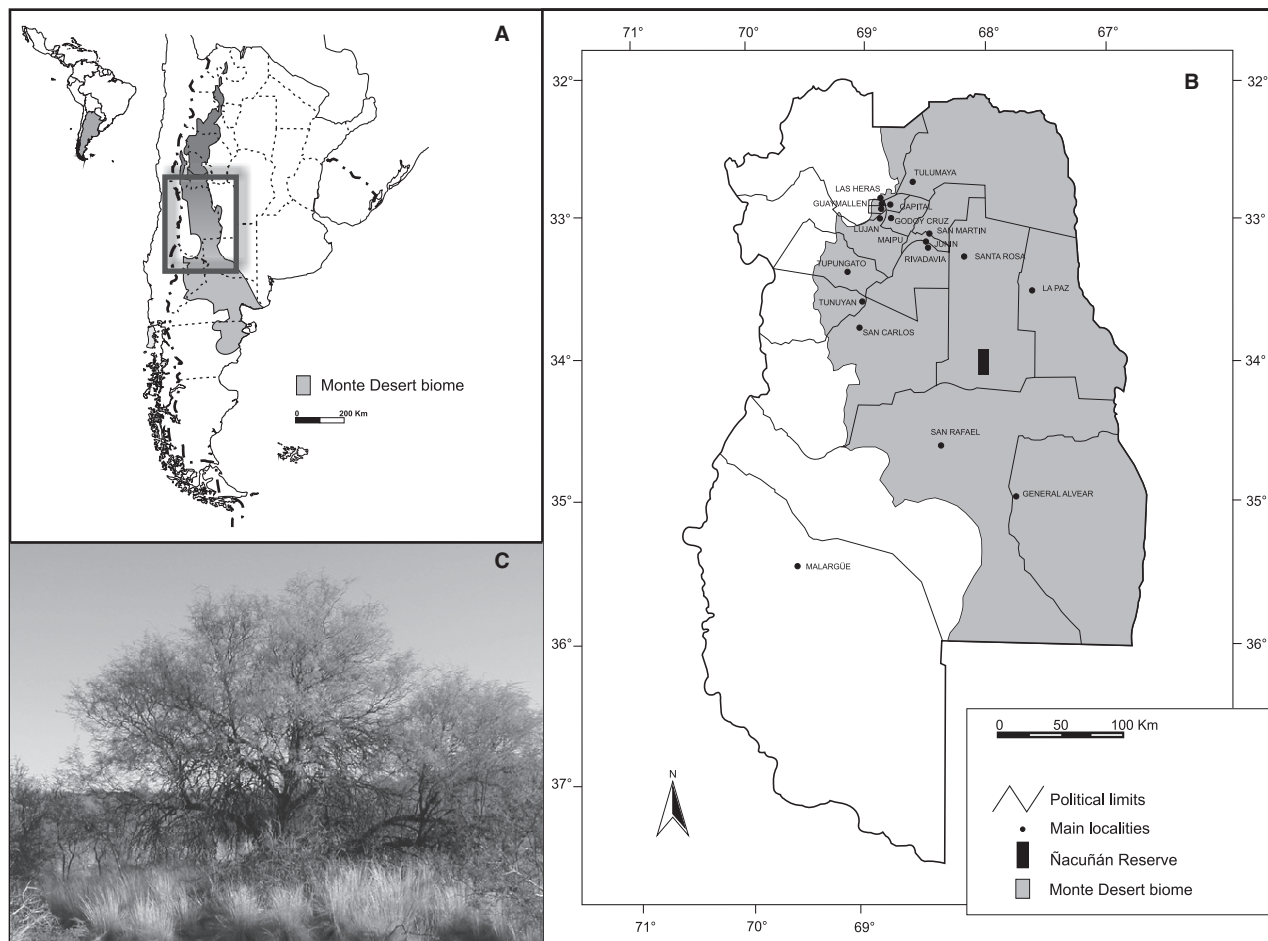
Fig. 1. A. Location map of the Monte Desert biome in Argentina. B. Location of the study area (Ñacuñán Reserve) in the central Monte Desert (Mendoza Province, Argentina). C. Picture of study site showing a typical landscape of the Monte.

easily differentiated from those of other carnivores present in the study area, such as *Puma concolor* (puma), whose faeces are distinctly different in shape, size, weight and bulk, or *Lycalopex griseus* (grey fox), clearly distinguishable by physical features as well as presence of insect, fruit and/or seed remains (Tognelli *et al.* 2001).

In order to have an adequate number of identifiable bone elements to obtain reliable taphonomic variables, the samples were analysed without differentiation between years. Although the small felids from Ñacuñán preyed on reptiles and birds in low frequencies (Tabeni *et al.* 2012), only small mammal prey (under 350 g) were analysed in the present study. Bone material was observed through a binocular loupe and some of them were photographed using a scanning electron microscope (JEOL JSM-6490LV -10 kV-, CONICET, Mendoza).

The taphonomic analysis was carried out following the methodology of Andrews (1990), Fernández-Jalvo & Andrews (1992) and Fernández-Jalvo *et al.* (2016). The degree of digestive corrosion was observed in dental elements as well as in proximal ends of the femora and distal portions of the humeri. Each element was classified as one of four digestive categories based on the proportion and intensity of corrosion (light, moderate, heavy and extreme). The breakage patterns were evaluated on cranial and postcranial remains considering separately complete elements and fractured ones. The breakage percentages were calculated for cranial elements and long bones. Each bone remain was observed to identify presence or absence of tooth marks.

The minimum number of individuals (MNI) and minimum number of skeletal elements (MNE) were calculated. The value of MNI was obtained in two different ways, using the best-represented homologous element. The first was calculated as the addition of MNI obtained for each scat. This is an adequate estimation taking into account that the samples were obtained during a period of 2 years within a wide area, which suggests that the scats came from different individuals. The second was calculated for the whole sample, as this method is typically used in zooarchaeological research.

Table 1. Relative frequencies (RF) of the small mammals identified in the sample. Taxonomic composition, minimum number of individuals (MNI), and body mass range and average. Body masses calculated on the basis of individuals deposited in the Vertebrate Collection of IADIZA.

	RF MNI = 194	RF MNI = 94	Body mass in g (n)	Body mass range (min.–max.)
Didelphimorphia				
Thylamys pallidior	1.5	1.1	21.4 (20)	14.3–33.0
Caviidae				
Galea leucoblephara	19.1	21.3	190 (4)	105.0–287.0
Microcavia australis	4.1	5.3	223.2 (15)	84.0–322.0
Ctenomyidae				
Ctenomys sp.	13.9	11.7	127.9 (39)	90.0–190.0
Cricetidae				
Sigmodontinae indet	4.1	4.2		
Akodon dolores	20.6	22.3	34.7 (26)	18.0–54.0
Calomys musculinus	8.2	9.6	20.5 (22)	10.5–32.0
Eligmodontia sp.	9.8	6.4	21.1 (14)	16.4–27.0
Graomys griseoflavus	18	18.1	66.7 (37)	46.0–92.0

The relative abundance of the skeletal elements was evaluated considering the representation of each element in the sample, taking into account the two calculated MNI values, by using the following formula: $MNEi/(Ei \times MNI) \times 100$, where $MNEi$ is the minimum number of a given skeletal element in the sample, and Ei is the expected number of that skeletal element in an individual. In order to evaluate the relationship between cranial and postcranial elements, two indexes were calculated: pc/c [(femur + tibia + humerus + radius + ulna) × 16/(mandible + maxilla + molars) × 10], and [(humerus + femur)/(mandible + maxilla)]. The relationship between distal and proximal elements was calculated using the following index: [(tibia + ulna)/(femur + humerus)] × 100. Finally, two indexes were calculated to evaluate the proportions of isolated teeth in relation to the empty alveoli in mandibles and maxillae: [(premaxillary alveoli + mandibular alveoli)/(incisors)], and [(maxillary alveoli + mandibular alveoli)/(molars)].

Results

Anatomical representation

Out of a total of 86 analysed faeces, 2157 skeletal elements were identified. Thereof, 785 corresponded to cranial elements whereas the rest were identified as postcranials. In addition, 2554 bone splinters unidentifiable anatomically were recovered. There were no bone remains with tooth marks or grooves. The number of bones identifiable anatomically ranged from two to 110 by scat, with a mean value of 25.1 (SD = 22.5). The MNE calculated for the whole sample was 1997 skeletal elements.

The MNI by scat ranged between one and eight (mean = 2.3; SD = 1.26) and a high percentage of faeces (90.7%) contained one to three individuals. The MNI value calculated as the addition of MNI for each scat was markedly higher than that obtained from the whole sample (194 and 94, respectively; Table 1).

All the skeletal elements were represented in the sample, although mandibles, maxillae, isolated incisors, humeri and femora were the most frequent elements, most of them showing values higher than 40%. Ribs, metapodials and phalanges reached percentages lower than 5% (Fig. 2; Table 2). The average of relative abundance based upon the MNI of 194 was 11.9%, whereas the value obtained from the MNI of 94 was 24.5%.

The indexes that evaluate the relationships between cranial and postcranial elements showed a better representation of the former. The (t+u/f+h) index showed a higher representation of proximal elements compared with distal bones. The indexes used for evaluating proportions of isolated teeth showed values lower than 100, indicating a considerable loss of mandibles and maxillae (Table 3). More than 90% of isolated teeth belonged to larger-sized rodents (Caviidae and Ctenomyidae).

Breakage patterns

A high degree of breakage was detected amongst the long bones (81.0%), especially in tibiae, femora and humeri (97.9, 93.0 and 73.9%, respectively), whereas the proportion of broken ulnae was moderate (57.1%; Table 4). All long bones recovered belonging to the largest rodents (hystricognaths) were broken, whereas the complete ones (19.0%) only corresponded to smaller rodents (Cricetidae). The higher proportions of proximal segments corresponded to femora and ulnae whereas the distal segments were higher in tibiae and humeri. Recovered shafts were very scarce. Most small

Fig. 2. Relative abundance of skeletal elements (on the basis of the MNI for the whole sample *sensu* Andrews (1990)) in the small mammal sample generated by small felids in Ñacuñán and comparison with known taphonomic data of small mammal assemblages generated by other carnivorous mammals. *C. chinga* (Montalvo *et al.* 2008), *L. griseus* (Gómez & Kaufmann 2007), *L. geoffroyi* (Montalvo *et al.* 2012), average carnivorous mammals (Andrews 1990). [Colour figure can be viewed at wileyonlinelibrary.com]
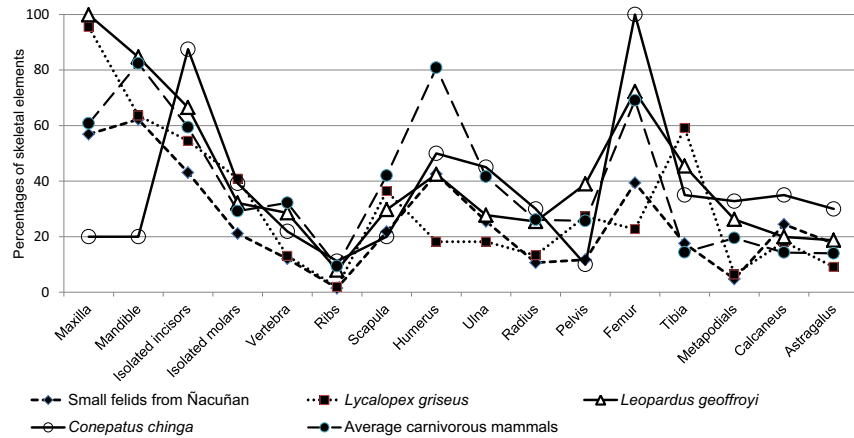
Table 2. Minimum number of skeletal elements (MNE) and MNE% according to minimal number of individuals (MNI) calculated by scat (MNI = 194) and for the whole sample (MNI = 94).

	MNE	MNI = 194 MNE%	MNI = 94 MNE%
Maxilla	107	56.9	27.6
Mandible	117	62.2	30.1
Isolated incisors	162	43.1	20.9
Isolated molars	278	21.1	10.2
Vertebra	567	12.1	5.8
Ribs	33	1.5	0.7
Scapula	41	21.8	10.6
Humerus	80	42.5	20.6
Ulna	48	25.5	12.4
Radius	20	10.6	5.1
Pelvis	22	11.7	5.7
Femur	74	39.4	19.1
Tibia	33	17.5	8.0
Metapodials	90	4.8	2.3
Calcaneus	46	24.5	11.8
Astragalus	33	17.5	8.5
Phalanges	246	4.7	2.3
Average		24.5	11.9

bones were preserved unbroken, such as vertebrae, phalanges, calcaneus, metapodials and astragali. Although articulated elements were also found (e.g. metapodials–phalanges, vertebrae), they were scarce.

The cranial elements were represented only by small bone fragments and maxillae, both in similar proportions, as no complete skulls were found

Table 3. Values of the taphonomic indexes calculated for the small mammal sample generated by small felids from Ñacuñán. pc/c = postcranial/cranial; f = femur; t = tibia; h = humerus; r = radius; u = ulna; mx = maxilla; md = mandible; alv = alveoli; m = molars; i = incisors.

pc/c f+t+h+r+u/md+mx+mo	0.81
f+h/md+mx	0.68
t+u/f+h	0.52
alv mx+alv md/m	0.67
alv mx+alv md/i	0.25

(Table 5). More than half of maxillae maintained their full zygomatic arches and a high frequency of molars and incisors remained in maxillae and pre-maxillae. A high amount of the mandibles (96.4%) was broken, primarily consisting of those without ascendant ramus and with the inferior edge broken. In contrast, considering all dental elements analysed (n = 1036), a low proportion (13.2%) was fractured. Amongst them, isolated teeth were more abundant than those *in situ*.

Digestion

Almost all the diagnostic elements analysed, including molars, incisors, humeri and femora (98.7%), showed signs of modification by digestion to some extent (Table 6), predominantly in the moderate and heavy categories, although light and extreme degrees also were observed. This type of modification to the bone surface was also observed in most of the non-diagnostic bones, except for a few skeletal remains partially protected by skin and hair. Most remains had part of their surfaces polished and had rounded edges, and some fragments showed holes and thinned walls (Figs 3, 4).

Regarding long bones, 99.3% of proximal parts of the femora and distal portions of the humeri were modified by digestive corrosion, mainly identified as being in the heavy (42.9%) and moderate (35.3%) categories. The great majority of these elements showed traces of digestion expanded to the whole surface, as well as broken edges with rounded surfaces, and digested and damaged articular ends.

Most of the isolated and *in situ* teeth were altered by digestion (99.6 and 98.0%, respectively), mainly showing moderate and heavy levels of corrosion. The enamel of molars and incisors was found to be partially or wholly removed, leaving the dentine exposed and rounded edges. In many cases, the exposed dentine also showed evidence of digestive corrosion.

Table 4. Breakage of postcranial elements in the small mammal assemblage generated by wildcats from the Ñacuñán region (n and % by element).

		n	%
Femur	Complete	6	7.0
	Proximal	68	79.1
	Shaft	2	2.3
	Distal	10	11.6
Humerus	Complete	24	26.1
	Proximal	21	22.8
	Shaft	4	4.3
	Distal	43	46.7
Tibia	Complete	1	2.1
	Proximal	20	42.5
	Shaft	1	2.1
	Distal	25	53.2
Ulna	Complete	21	42.8
	Proximal	27	55.1
	Shaft	0	0.0
	Distal	1	2.0

Discussion

Small rodents were found to be the most abundant dietary resources for wildcats inhabiting the Ñacuñán region (central Monte Desert; Tabeni *et al.* 2012), in concordance with the dietary preferences documented for small felids in different regions of Argentina, such as *L. colocolo* and *L. geoffroyi* (Novaro *et al.* 2000; Manfredi *et al.* 2004; Bisceglia *et al.* 2008, 2011; García Esponda *et al.* 2009; Pereira *et al.* 2012).

The analyses of the wildcat scats from Ñacuñán allowed the recovery of a large number of bone

Table 5. Breakage in cranial and dental elements of the small mammal assemblage generated by wildcats from Ñacuñán.

	n	%
Breakage of skulls		
Complete skull	0	0.0
Maxilla with zygomatic process	61	29.0
Maxilla without zygomatic process	46	21.9
Minor fragments	103	49.0
Molars missing from maxilla	87	25.1
Incisors missing from premaxilla	11	15.3
Breakage of mandible		
Complete mandible	4	3.6
Ascendant ramus broken	14	12.6
Without ascendant ramus	33	29.7
Without ascendant ramus and inferior edge broken	60	54.1
Molars missing from mandible	102	26.3
Incisors missing from mandible	30	24.6
Breakage of teeth		
Broken molars *in situ*	22	5.5
Broken isolated molars	58	20.7
Total broken molars	80	11.8
Broken incisors *in situ*	10	8.1
Broken isolated incisors	45	26.3
Total broken incisors	55	18.7

remains, although slightly less than half were anatomically identifiable elements. These features, together with the high frequency of scats containing very few individuals (one to three), are similar to those reported for *L. geoffroyi* by Montalvo *et al.* (2012).

The mean values of the different taphonomic variables obtained in the present study (Table 7) were compared with those reported for other carnivorous mammals from Argentina that also inhabit the study area (*L. geoffroyi*, *L. griseus*, *P. concolor* and *C. chinga*) and for South African small carnivores (*Felis serval* (serval) and *Genetta genetta* (genet)). The relative abundance average of skeletal elements was low, similar to the values reported for *L. griseus* (Gómez & Kaufmann 2007) and *P. concolor* (Montalvo *et al.* 2007), although lower than those for *C. chinga* (Montalvo *et al.* 2008), *L. geoffroyi* (Montalvo *et al.* 2012) and South African small carnivores (Matthews 2006). This low average value, added to the better representation of mandibles, maxillae, isolated incisors, humeri and femora, compared with the remaining elements, evidenced a great loss of bones in assemblages generated by Ñacuñán wildcats. Several taphonomic research studies have mentioned bone loss and high breakage due to the prey handling and chewing mechanisms of carnivorous mammals (Mondini 2000; Gómez & Kaufmann 2007; Montalvo *et al.* 2008).

The relative abundances of cranial portions calculated in this study showed lower values than those found for *L. geoffroyi* (Montalvo *et al.* 2012) and for *L. griseus* (Gómez & Kaufmann 2007), whereas postcranial elements were similarly represented (Fig. 2). A taphonomic analysis of *C. chinga*, a carnivore of smaller size, showed lower preservation of maxillae and mandibles and higher conservation of isolated teeth (Montalvo *et al.* 2008) compared with the small carnivores mentioned above, which is attributed to the fact that this predator does not swallow whole heads of its prey.

The higher representation of cranial elements in relation to postcranial ones was also supported by the values of the relative abundance indexes (pc/c and h+f/md+mx), which were in most cases slightly lower than those documented for other carnivores such as *L. griseus* and *L. geoffroyi* (Gómez & Kaufmann 2007; Montalvo *et al.* 2012), and even for larger carnivores such as *P. concolor* (Montalvo *et al.* 2007). In contrast, a higher relative proportion of postcranial elements was documented for small mammal assemblages generated by European and African carnivores (Andrews 1990; Matthews 2006). Amongst limb components, the remarkable loss of distal elements compared with the proximal ones was not different from that reported for the above-mentioned carnivorous predators.

Table 6. Percentages of digestive corrosion degrees for the small mammal bones accumulated by wildcats from the Ñacuñán region.

	Absent	%	Light	%	Moderate	%	Heavy	%	Extreme	%
Digestion of teeth										
Incisors *in situ*	7	6.0	44	37.6	52	44.4	14	12.0	0	0.0
Isolated incisors	1	0.6	38	23.0	66	40.0	50	30.3	10	6.1
Incisors total	8	2.8	82	29.1	118	41.8	64	22.7	10	3.5
Molars *in situ*	5	1.1	58	12.3	228	48.4	176	37.4	4	0.8
Isolated molars	1	0.3	12	4.3	44	15.8	181	65.1	40	14.4
Molars total	6	0.8	70	9.3	272	36.3	357	47.7	44	5.9
Digestion of postcranials										
Proximal femur	0	0.0	6	8.4	22	31.0	35	49.3	8	11.3
Distal humerus	1	1.6	9	14.5	25	40.3	22	35.5	5	8.1

The higher relative proportions of isolated teeth in relation to empty alveoli suggest considerable destruction of maxillae and mandibles during prey chewing. Besides, in agreement with what has been reported for other small carnivores (Gómez & Kaufmann 2007; Montalvo *et al.* 2012), the chewing effects were also noticeable in the high number of bone fragments and splinters unidentifiable anatomically, and in the high degree of breakage detected in all skeletal bones, affecting especially mandibles and maxillae amongst the cranial bones, and femora, tibiae and humeri amongst the postcranial bones.

The chewing effects by small felids from Ñacuñán had a stronger impact on bones of the largest rodents (Caviidae and Ctenomyidae), whose sizes possibly preclude swallowing of these prey whole. Mondini (2000) pointed out that recognition of bone remains decreases as prey size increases. However, despite the high degree of breakage of such bones, good anatomical and taxonomic recognition levels were achieved in the present study, in contrast to what was reported for assemblages generated by other carnivores (e.g. Andrews & Evans 1983; Andrews 1990).

In taphonomic studies, the analysis of tooth marks on prey bones is used as a useful tool to infer predation by carnivorous mammals (e.g. Álvarez *et al.* 2012; Andrés *et al.* 2012). In relation to small mammal bones, these modifications are common in remains recovered from canid scats (Andrews & Evans 1983). However, the absence of such marks in the small mammal set from Ñacuñán agrees with findings reported for other felids such as *P. concolor* (Montalvo *et al.* 2007) and *L. geoffroyi* (Montalvo *et al.* 2012). The last two felids produce, but in very low frequencies, tooth marks on ingested bones of prey mammals with a body mass over 1 kg (Montalvo *et al.* 2007; Álvarez *et al.* 2012).

In relation to digestive corrosion, the high amount of diagnostic bones with evidence of this action on their surface (more than 98%) is remarkable. Probably, the breakage of elements contributed to the intensification of this action on the bones.

This high proportion is coincident with those observed on small mammal bones eaten by other small carnivores (e.g. Andrews & Evans 1983; Andrews 1990; Montalvo *et al.* 2008, 2012), although the dominant corrosion categories varied amongst different species. For example, for incisors, moderate and heavy categories prevailed in *L. geoffroyi* samples from central Argentina (71.0%; Montalvo *et al.* 2012), whereas light and moderate corrosion were the most frequent categories in samples from South African small carnivores (83.3%; Matthews 2006), as well as in the present study (70.9%). A different pattern was documented for *C. chinga* (Montalvo *et al.* 2008), with 37.1% of incisors showing moderate digestion, whereas the remaining incisors were categorized in the other three digestion categories, each one with values close to 20%. The low proportions of incisors with extreme digestion in our sample (3.5%) were similar to those identified for small carnivores from South Africa (3 to 6%; Matthews 2006), but lower than those reported for assemblages generated by *C. chinga* and *L. geoffroyi* (22.9 and 19.7%, respectively; Montalvo *et al.* 2008, 2012). Regarding molar elements, the predominant degrees of digestion varied between light and extreme in the Andean hognosed skunk (66%; Montalvo *et al.* 2008) and between light and moderate in *L. geoffroyi* (66.3%; Montalvo *et al.* 2012), whereas in the molars from the Ñacuñán scats, moderate and heavy categories were the most frequent (84.0%). Considering postcranial bones, moderate and heavy degrees were dominant in this sample (78.2%), with slight differences to those documented for the small carnivores mentioned above.

In summary, the main taphonomic features observed in the present study were: low average relative abundance of skeletal elements; better representation of mandibles, maxillae, isolated incisors, humeri and femora in relation to the remaining elements; preponderance of cranial elements with a high proportion of isolated teeth; elevated frequency
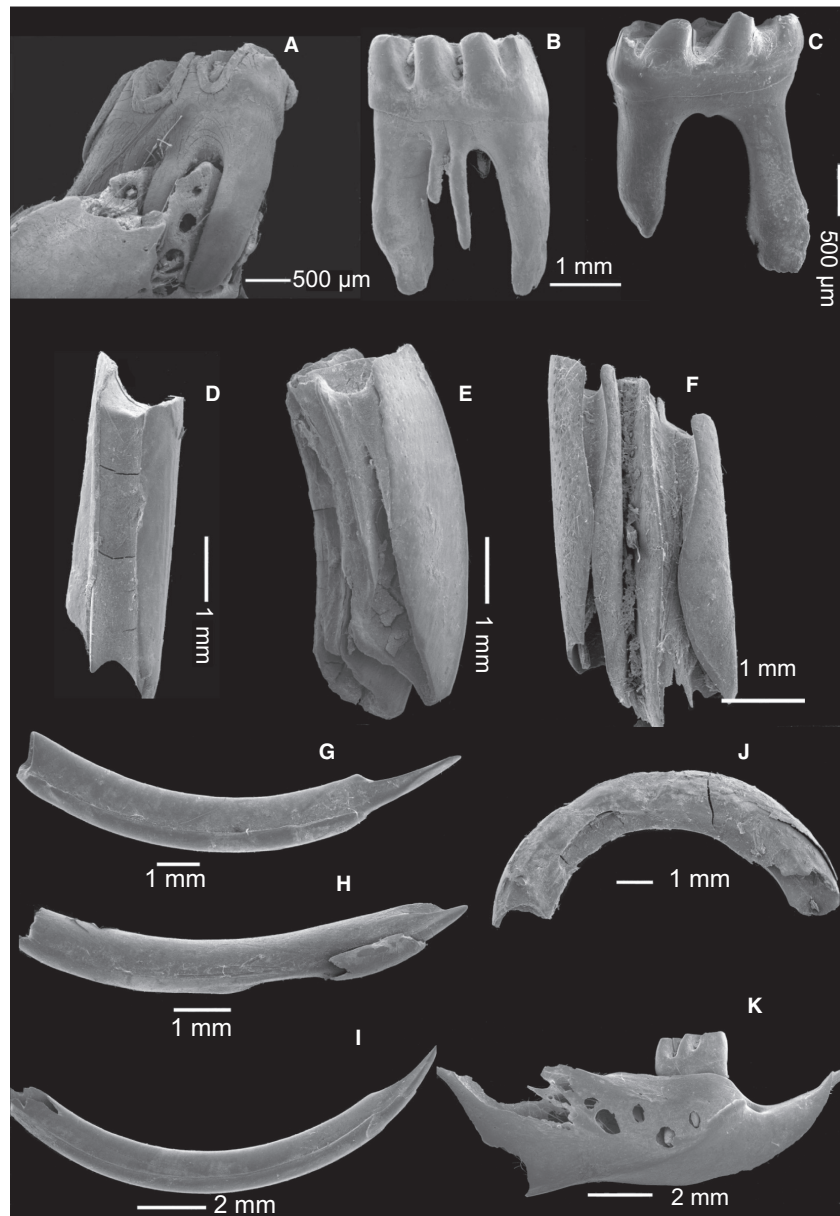
Fig. 3. Digestive corrosion on cranial bones (*sensu* Fernández-Jalvo *et al.* 2016) of the small mammal assemblage generated by small felids from Ñacuñán (Mendoza). A. Heavy digestion on cricetid molar. B and C. Light digestion on cricetid molar. D. Heavy digestion on ctenomyid molar. E. Heavy digestion on caviid molar. F. Extreme digestion on caviid molar. G. Light digestion on cricetid incisor. H. Heavy digestion on cricetid incisor. I. Light digestion on cricetid incisor. J. Extreme digestion on caviid incisor. K. Cricetid mandible affected by digestion with holes in labial view.

of proximal limb bones with respect to distal parts; high degree of breakage in all skeletal bones; absence of tooth marks and digestive corrosion on almost all diagnostic bones (mainly moderate and heavy). Several of these taphonomic characteristics have served as diagnostic features to identify carnivorous mammals, particularly felids, as the possible accumulating agents of small mammal bone sets recovered in archaeological contexts. Such is the case of research conducted in two sites in northern

Patagonia, Angostura 1 (Fernández *et al.* 2011) and Cueva Arroyo Colorado (Fernández *et al.* 2009; Fernández 2012), which highlighted the role of felid predators in the formation of zooarchaeological sets (Table 7) and allowed more accurate palaeoenvironmental inferences to be made. By contrast, in the central Monte Desert, many small mammal bone sets have been recovered from archaeological sites (e.g. Chiavazza 2007, 2010, 2012; García Llorca & Cahiza 2007; López *et al.* 2016) that have still not

Fig. 4. Digestive corrosion on postcranial bones of the small mammal assemblage generated by small felids from Ñacuñán (Mendoza). A. Heavy digestion on cricetid humerus. B. Moderate digestion on cricetid humerus. C. Heavy digestion on hystricognath femur. D. Extreme digestion on cricetid femur. E. Moderate digestion on hystricognath femoral head. F. Articulated foot. G. Digestion on vertebrae.

been studied from a taphonomic perspective, emphasizing the need for regional actualistic research, such as the present study.

Conclusions

The results of the different taphonomic variables used to analyse anatomical representation, fragmentation and digestive corrosion on small mammal bone remains eaten by wildcats from Ñacuñán are consistent with the 'extreme modification' category 5 proposed by Andrews (1990), although some variables were included in category 3, and less frequently in categories 2 and 4 (Table 8). This categorization distinguishes Ñacuñán wildcats as predators that cause very strong

modifications to prey bones, even greater than those reported for *L. geoffroyi* (Montalvo *et al.* 2012) in the Monte Desert.

Although *L. colocolo* is the most common wildcat in the Ñacuñán region, the small mammal assemblage analysed here may have been generated by the predation activities of all three small feline species inhabiting this study area (Tognelli *et al.* 2001). In this sense, the differences detected compared with the taphonomic modifications produced by *L. geoffroyi* could be related to the mixed nature of the small felid scats recovered in this study. This situation may emulate what happens in some archaeological or palaeontological sites, where often various predators have been responsible for the small mammal bone accumulations

Table 7. Summary and comparison of taphonomic features of small mammal bone assemblages from actualistic studies and archaeological sets accumulated by carnivores. ARA = average relative abundance of skeletal elements; pc = postcranial; c = cranial; md = mandible; mx = maxillae; f = femur; h = humerus; t = tibiae; u = ulnae; A = absent; L = light; M = moderate; H = heavy; E = extreme.

Taphonomic trace	Ñacuñán wildcats Present study	Current bone assemblages						Archaeological bone assemblages	
		Felidae			Canidae	Viverridae	Mephitidae		
		L. geoffroyi[1]	*P. concolor*[2]	*F. serval*[3]	*L. griseus*[4]	*G. genetta*[3]	*C. chinga*[5]	Cueva A. Colorado[6]	Angostura1[7]
ARA (%)	24.5	41.7	22.1	47.3	25.8	70.7	36.7	7.3	9.8
pc/c index	0.81	0.90	0.50	–	0.82	–	0.13	1.07	0.94
f+h/md+mx index	0.58	0.62	0.70	1.72	0.48	1.76	0.37	0.47	0.34
t+u/f+h index	0.52	0.61	0.24	0.45	0.47	0.89	0.43	0.68	0.57
Postcranial digestion (%)	99.2	100.0	100.0	–	64.7	–	100.0	75.5	52.9
Incisor digestion (%)	97.2	100.0	100.0	100.0	100.0	100.0	100.0	57.1	29.8
Molar digestion (%)	99.2	100.0	100.0	–	100.0	–	100.0	20.6	14.3
Main total digestion degrees	M–H	M–H	E–L	–	L–M	–	L–M	A–L	A–L–M
Main digestion degrees on teeth	M–H	M–H	H–E	L–M	L–M	L–M	L–M–E	A–H	A–L–M
Main digestion degrees on postcranial	M–H	L–M	L–M	–	L–M	–	L–M	A–L	A–L–M
Breakage maxillae and mandible (%)	98.7	100.0	100.0	–	100.0	–	100.0	95.6	98.2
Breakage postcranial (%)	81.0	77.7	86.5	–	87.5	–	100	78.1	94.0

[1]Montalvo *et al.* (2012).
[2]Montalvo *et al.* (2007).
[3]Matthews *et al.* (2006).
[4]Gómez & Kaufmann (2007).
[5]Montalvo *et al.* (2008).
[6]Fernández (2012).
[7]Fernández *et al.* (2011).

(e.g. Matthews 2006; Fernández *et al.* 2011). In this sense, actualistic research on bone assemblages generated by a mixture of predators would provide relevant taphonomic information to identify more than one accumulating agent at archaeological and palaeontological sites. However, diverse factors such as environmental heterogeneity, predator relative age, and prey size and availability, amongst others, also could account for differential effects on prey bones amongst predator species (Andrews 1990).

Despite the particular features found in the study set, the low relative abundance of skeletal elements, the high degree of breakage in all bones and the digestion traces identified in almost all diagnostic bones (moderate and heavy mainly) represent general taphonomic patterns that fall within those reported for other South American small carnivores.

Small mammal bone assemblages recovered from archaeological and palaeontological sites can be used as proxy data for palaeoenvironmental inferences. In this sense, this work contributes to the study of the processes and agents involved in such accumulations

Table 8. Categorization of small felid effects on prey remains according to the different taphonomic variables analysed (*sensu* Andrews 1990). The black bar indicates the modification category in which each variable fell.

with the intention of systematizing an actualistic perspective at regional scale that will strengthen our knowledge about past environments.

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