



Taphonomy of small mammal bone accumulations generated by the Chaco owl (*Strix chacoensis*, Strigiformes) from the Monte Desert (Mendoza, Argentina): a contribution to South American archaeological and palaeontological studies

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BOREAS



López, J. M., Fernández, F. J., Castillo, L. & Pereyra-Lobos, R. 2018 (July): Taphonomy of small mammal bone accumulations generated by the Chaco owl (*Strix chacoensis*, Strigiformes) from the Monte Desert (Mendoza, Argentina): a contribution to South American archaeological and palaeontological studies. *Boreas*, Vol. 47, pp. 780–791. <https://doi.org/10.1111/bor.12313>. ISSN 0300-9483.

The present study analyses the taphonomic features of recent small mammal bone and teeth accumulations recovered from pellets generated by *Strix chacoensis* in a Natural Protected Area in the central Monte Desert of Mendoza, Argentina. In order to identify the taphonomic signature of this predator in the formation of zooarchaeological and palaeontological accumulations, taxonomic profiles, relative abundances, bone breakage patterns and digestive corrosion were evaluated. Taphonomic results locate *S. chacoensis* in modification category 2 (intermediate). Although the general taphonomic patterns detected in the present study were similar to a typical owl pattern, some differences from that pattern were detected. This sample showed lesser relative abundances of skeletal elements, greater loss of teeth and a larger number of incisors modified by digestion than those generated by other strigiforms. The comparison with reported archaeological accumulations suggested that the small mammal remains recovered in some sites from the Monte Desert may correspond to the predatory activity of *S. chacoensis*. The identification of the action of *S. chacoensis* in archaeological and palaeontological small mammal bone and teeth accumulations is a promising tool to evaluate the conservation status of native forests in the past.

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Taphonomy is essential to understanding the processes and agents involved in the formation of fossil/archaeological records (Andrews 1990). Small mammals (<1 kg) are frequent prey items of several avian raptors and carnivorous mammals (e.g. Andrews 1990; Thiollay 1994; White *et al.* 1994; Bruce 1999; Marks *et al.* 1999). These predators have contributed, through the deposition of their pellets and scats, respectively, to the formation of numerous zooarchaeological and palaeontological bone and teeth accumulations (e.g. Mayhew 1977; Andrews 1990; Pardiñas 1999; Fernández 2012a; Fernandez-Jalvo *et al.* 2016). Given that small mammals often have strict ecological requirements, knowledge of the agents responsible for small mammal bone accumulations recovered from archaeological and palaeontological sites is a valuable tool with which to make palaeobiological and palaeoecological inferences (e.g. Andrews 1990; Pardiñas 1999).

In South America, mainly in Argentina, many taphonomic studies have analysed the role of several avian raptors and carnivorous mammals as small mammal bone accumulators in archaeological and palaeontological sites

(e.g. Gómez 2005; Montalvo *et al.* 2012, 2014, 2016; Rudzik *et al.* 2015; Fernández & Montalvo 2017; Fernández *et al.* 2017a; Mondini 2017). At the same time, several zooarchaeological and palaeontological research projects have been carried out with taphonomic and palaeoenvironmental objectives (mainly in Pampa, Patagonia, Espinal and Puna biomes). Such studies have tried not only to ‘asses’ or ‘determine’ the taxonomic composition of small mammal prey assemblages, but also the predators responsible for such bone accumulations (e.g. Fernández *et al.* 2009, 2011a, 2015a, b; Fernández 2012a; López *et al.* 2016; Montalvo *et al.* 2017). From a palaeoenvironmental point of view, the consideration of both aspects strengthens the inferences about past environments and their variations over time (Fernández-Jalvo *et al.* 2014). Thus, assuming similar hunting and feeding behaviours between past and present predators, actualistic taphonomic studies on recent bone accumulations can help to establish taphonomic patterns to assess the accumulating agents of small mammal bone remains from archaeological and palaeontological sites (Andrews 1990; Fernández & Montalvo 2017; Fernández *et al.* 2017a).

Several zooarchaeological studies have been conducted in the Monte Desert, the most arid rangeland of Argentina. However, considering that the distinctive feature of the Monte is reflected in the varied composition of its small mammal fauna, including rodents and marsupials (Ojeda *et al.* 2002), numerous small mammal bone accumulations must still be studied from a taphonomic perspective.

In order to establish patterns to assess possible accumulating agents of small mammal remains from archaeological and palaeontological sites, a few regional actualistic taphonomic studies have been conducted in the Monte Desert, but these focused only on some species of small carnivorous mammals and accipitriform raptors (Montalvo *et al.* 2012; López *et al.* 2017a, b). Thus, zooarchaeological and palaeontological research on small mammal bone accumulations carried out in this area (e.g. Fernández *et al.* 2011a, 2012, 2016; Fernández 2012a; Fernández & De Santis 2013; López *et al.* 2016; Castillo *et al.* 2017) have been forced to use taphonomic models developed for other regions of the world (e.g. Andrews 1990; Fernández-Jalvo *et al.* 2014). This may have limited or skewed inferences on possible accumulating agents as well as palaeoenvironmental interpretations. However, a taphonomic model that considers the dentary morphology of rodents and marsupials from South America has been developed recently, also considering taxa from the Monte Desert (Fernández *et al.* 2017a). The results achieved to date have allowed both higher levels of detail and better interpretations of small mammal bone assemblages recovered from archaeological and palaeontological sites in South America to be obtained (Fernández & Montalvo 2017; López *et al.* 2017b; Montalvo *et al.* 2017).

Small mammals are the most dominant prey in the diet of owls that inhabit different regions of Argentina, such as *Tyto alba*, *Athene cucularia* and *Strix chacoensis* (e.g. Belloq 2000; Andrade *et al.* 2010; Santander *et al.* 2012). These predators can generate significant accumulations of prey bones and teeth (Andrews 1990; Fernández & Montalvo 2017). The action of these raptors has been inferred from different archaeological accumulations from various biomes within South America, including those from Monte Desert environments (Fernández 2012a; López *et al.* 2016; Castillo *et al.* 2017). However, little is known about the modifications that different owls that inhabit this area generate on their prey bones.

Strix chacoensis is a little-known endemic nocturnal, opportunistic and generalist raptor distributed from the south of Bolivia, Paraguay and Brazil to central Argentina. This species feeds mostly on small mammals (mainly sigmodontine rodents), although insects and birds are also important components of its diet (Santander *et al.* 2012). This species preferentially inhabits dense and semi-open old or primary dry forests with arboreal and shrubby vegetation. In the Monte Desert, this predator builds its nests mainly in trees of *Prosopis*

chilensis and *Prosopis flexuosa* (Pereyra-Lobos & Jara 2012, 2013a,b; Santander *et al.* 2012). These habitat preferences are coincident with other species of the same genus distributed in America (*Strix rufipes*; e.g. Figueroa *et al.* 2006; Alvarado *et al.* 2007 and *Strix nebulosa*; e.g. Duncan 1997) and Europe (*Strix aluco* and *S. nebulosa*; Andrews 1990).

This paper performs a taphonomic analysis of small mammal bone and teeth accumulations recovered from modern pellets generated by the Chaco owl (*S. chacoensis*) in the southernmost limit of its geographical distribution (Mendoza Province). In addition, to assess the potential of this owl as an accumulating agent, the present work involves comparisons with small mammal assemblages from two open-air archaeological sites and one archaeological cave site from the Mendoza Province.

Material and methods

The study was carried out in the Natural Protected Area called 'Reserva Natural Bosques Telteca' (Telteca, hereafter, latitude 32°23'27"S; longitude 68°01'30"W, altitude 500–580 m a.s.l., 20 400 ha, northeastern Mendoza Province, Argentina; Fig. 1). Telteca belongs to the Monte Phytogeographic Province, an arid and semiarid area dominated by shrubby steppes of *Larrea* and *Bulnesia retama* species, an edaphic steppe of halophytes and a dense arboreum stratum dominated by *Prosopis flexuosa* and *Geoffroea decorticans* (González-Loyarte *et al.* 1990; Flores *et al.* 2004).

Samplings of pellets generated by *S. chacoensis* were made in 2008 through 2009, with 147 pellets collected at the foot of trees. First, pellets were weighed and measured, followed by dry disaggregation with surgical instruments, after which bone remains were recovered. Although bird and insect remains were also detected, in the present work only small mammal bones and teeth were analysed. Cranial and dental bone remains were examined using a stereomicroscope. Taxonomic identifications of small mammals were made to species level, when possible, by comparison both with current specimens from the Vertebrate Collection of IADIZA (CCT-Mendoza) and the literature (Fernández *et al.* 2011b; Patton *et al.* 2015). The number of identified specimens, minimum number of individuals (MNI) and minimum number of elements (MNE) were calculated (Lyman 2008).

Taphonomic analysis followed the methodology proposed by Andrews (1990), Fernández-Jalvo & Andrews (1992) and Fernández *et al.* (2017a). This methodology proposes the identification of five modification categories (light, intermediate, moderate, heavy and extreme) considering all the possible predators of small mammals, including avian raptors and carnivorous mammals. These modification categories consider degrees of alterations and frequencies of affected elements based on three main variables (relative abundances, breakage and digestion). Relative abundances of skeletal elements were evaluated

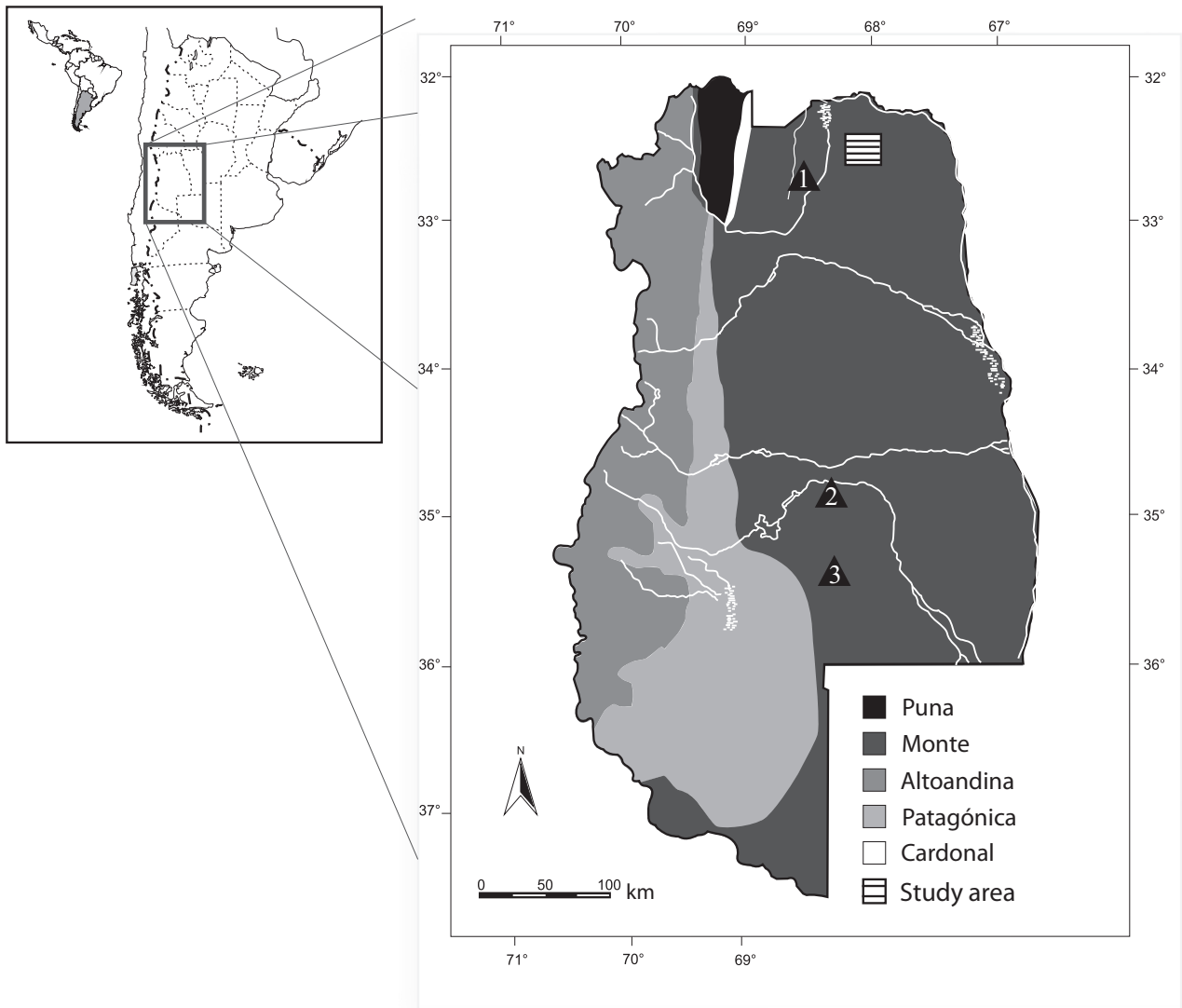


Fig. 1. Phytogeographical map of the study area in the 'Reserva Natural Bosques Telteca' (striped area) and archaeological sites compared (triangles): 1 = PA 70; 2 = Rincón del Atuel-1; 3 = Agua de los Caballos.

taking into account the representation of each element in the whole sample (MNE_i) on the basis of the expected number of each element in one individual (E_i) and on the basis of MNI by using the following formula: $MNE_i / (E_i \times MNI) \times 100$. To evaluate the relationships between cranial and postcranial elements, two indexes were calculated:

$$\begin{aligned} & \text{postcrania/crania (pc/c)} \\ & = [(femora+tibiae+humeri+radii+ulnae) \times (8)] \quad (1) \\ & \quad /[(mandibles+maxillae+molars) \times (5) \times 100] \end{aligned}$$

$$f+h/md+mx = [(femora+humeri/mandibles + maxillae) \times (100)]. \quad (2)$$

To evaluate the relationship between the representation of distal and proximal elements, one index was used:

$$t+u/f+h = [(tibiae+ulnae/femora+humeri) \times (100)], \quad (3)$$

whereas two formulas were used for measuring tooth loss:

$$alv/m = [(mandibular alveoli + maxillary alveoli/molars) \times (100)] \quad (4)$$

$$alv/i = [(mandibular alveoli + premaxillary alveoli/incisors) \times (100)]. \quad (5)$$

Didelphid mammals were not included in the last two calculations as their dental formula was considerably different from that of rodents.

Breakage patterns on cranial (skull, mandible, teeth) and postcranial bones (femora, humeri, tibiae, ulnae) were analysed taking into account the degree of completeness of each element, on which the percentage of breakage was also calculated.

Modifications by digestion were observed on diagnostic elements (molars, incisors, femora and humeri), distinguishing four degrees of digestive corrosion (light, moderate, heavy and extreme), except when digestion was absent. Digestion is the most reliable taphonomic variable to identify the possible accumulating agent of small mammal bone remains from archaeological and palaeontological sites, owing to its clear taphonomic signals, which can be differentiated from other taphonomic alterations, and whose traces are not modified by postdepositional processes (Andrews 1990; Fernández-Jalvo *et al.* 2014; Fernández *et al.* 2017a).

In order to explore archaeological applications, taphonomic results were compared with those reported for previously analysed archaeological samples from the Monte Desert, where strigiform raptors were the accumulating agents (Supporting Information Table S1).

Principal component analysis (PCA) was conducted against previously reported archaeological and modern samples in order to explore the samples ordination in a multivariate space.

The PCAs were conducted on a data matrix composed of values for percentage of digestion on incisors, molars and postcranial elements; percentage of breakage on cranial and postcranial elements; calculated indexes; and averages of relative abundance of skeletal elements. PCAs were performed using the software PAST – Paleontological Statistics – version 3.12 (Hammer *et al.* 2001).

Results

*Small mammal assemblage from recent pellets generated by *Strix chacoensis**

The average weight of pellets was 2.56 g, whereas the average length and width were 39.1 and 18.9 mm, respectively. In total, 141 prey mammal items including caviomorph and cricetid rodents and marsupials were identified (Table 1) from which five taxa were identified. Small-sized rodents were the most frequent prey items (96.45%). The most abundant prey was the cricetid *Graomys griseoflavus*, with a relative frequency slightly lower than 35%, followed by *Eligmodontia* sp. and *Thylamys pallidior*, with relative frequencies close to 30% each. The remaining species were represented by percentages lower than 4%. These were the cricetid *Akodon dolores* and the caviid *Microcavia australis*.

Anatomical representation

A total of 2413 small mammal bone specimens were recovered from the pellet sample. Thereof, 500 corre-

Table 1. Relative frequencies (RF) of the small mammals identified in the modern sample generated by *Strix chacoensis* in Telteca. Taxonomic composition, minimum number of individuals (MNI) and body mass range and average. Weights after López *et al.* (2017a).

	MNI	RF	MNE	Average body mass (g)	Body mass range (g; min–max)
Mammalia					
Didelphimorphia					
<i>Thylamys pallidior</i>	38	26.95	151	21.4	14.3–33.0
Caviidae					
<i>Microcavia australis</i>	5	3.55	10	223.2	84.0–322.0
Cricetidae					
Sigmodontinae indet.	8	5.67	63		
<i>Akodon dolores</i>	3	2.12	3	34.7	18.0–54.0
<i>Eligmodontia</i> sp.	40	28.36	137	21.1	16.4–27.0
<i>Graomys griseoflavus</i>	47	33.33	178	66.7	46.0–92.0
Total	141				

sponded to cranial remains, whereas the rest (1913) were postcranial ones. The MNE calculated for the whole sample was 2317 (Table S2).

All skeletal elements were represented in the recent pellet sample. However, on the one hand, the most abundant element was the mandible, with a relative abundance slightly higher than 80%, followed by the femur, maxilla, tibia, ulna and radius, with values ranging between 50–62% each. On the other hand, phalanges, calcaneus, astragalus, ribs, isolated molars, isolated incisors and vertebrae, were the least represented elements with percentages lower than 7% each (Fig. 2). The average of relative abundance for all the elements was approximately 30%.

Regarding the indexes calculated to evaluate the relationships between cranial and postcranial elements, *pc/c* (299.79), indicated a considerably better representation of the latter whereas *f+h/md+mx* (78.77) showed a slightly better representation of the former. The *t+u/f+h* (96.96) index showed an equitable representation between proximal and distal elements. The indexes calculated to evaluate proportions of isolated teeth (1245.45 for molars and 526.92 for incisors) resulted in values considerably higher than 100, indicating a great loss of dental elements.

Breakage patterns

A large proportion of complete mandibles and postcranial bones was detected (Table 2). Broken bone remains reached percentages slightly higher than 20% (513). Only two complete skulls were recovered, whereas the rest were broken, and about 60% of mandibles were complete.

In relation to postcranial elements, about 92% of long bones were complete, although the tibia was the most fractured (13%) and the ulna was the long bone with the highest percentage of completeness ($\geq 99\%$).

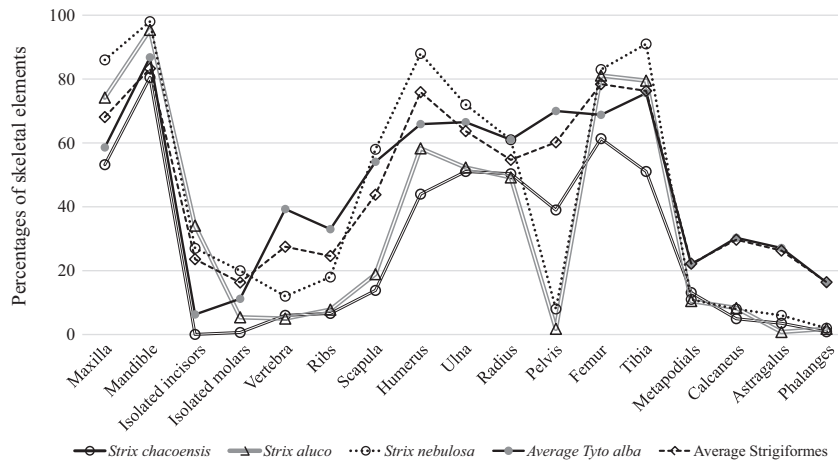


Fig. 2. Relative abundance of skeletal elements (based on the MNI) in the small mammal bone sample generated by *Strix chacoensis* in Telteca compared with small mammal assemblages generated by *Strix aluco*, *Strix nebulosa*, average of *Tyto alba* and average of Strigiformes (after Andrews 1990).

Around 25% of scapulae and 77% of the pelvis were complete. Recovered shafts of humeri and tibiae were very scarce, while neither shafts of ulnae nor femora were detected. Broken dental elements were also very scarce. Most of the smaller elements were complete, such as vertebrae, phalanges, astragali, calcaneus and metapodials. Dental elements were preserved *in situ* in a large proportion.

Digestion

Alterations by digestive corrosion were observed in 16.85% (192 out of 1139) of the whole sample, taking into account the different diagnostic elements observed (Fig. 3; Table 3). Almost all modifications by digestion corresponded to the light category ($\geq 91\%$).

Isolated incisors and molars were more affected than those recovered *in situ*. Incisors were the elements most modified by digestion. Around 50% ($n = 117$) of them were altered. Comparing isolated and *in situ* incisors, around 89% of isolated incisors and 45% of *in situ* incisors were altered by digestive corrosion. In these elements, in general, digestion just caused alteration by pitting and/or partial removal of the enamel. In relation to molars, 7.71% ($n = 48$) were modified by digestion, although isolated elements were also more modified than *in situ* molars (9.09 and 7.70%, respectively). Thus, 11.27% of cricetid molars showed matte enamel in labial view and/or smoothed rounded cusps in occlusal view; 3.7% of caviid molars were modified in the angles formed between the occlusal surface and the lateral walls of the crowns, which were rounded and flattened, whereas only two didelphid molars showed a matte surface.

Regarding long bones, 18.65% ($n = 22$) of distal humeri and 23.81% ($n = 40$) of proximal femora were modified by digestion. Postcranial bones were affected only on the articular surfaces.

Discussion

Taphonomic features of small mammal bone accumulations generated by Strix chacoensis

In general terms, the results obtained from the taphonomic analysis of small mammal bone remains accumulated by *S. chacoensis* correspond to a typical owl pattern. Generally, owls swallow their prey whole, generating low bone breakage; relatively equal representation amongst skeletal parts, with loss of elements from the autopodium; and, mainly, low levels of digestive corrosion on bones and teeth, both in intensity (degree) and frequency (proportion) (Andrews 1990; Fernández-Jalvo *et al.* 2014). However, the present study revealed some differences from the common owl pattern that are interesting from a taphonomic perspective. In fact, the sample of *S. chacoensis* showed more bone loss than that generated by other strigiforms. Thus, both average relative abundance (about 30%) and representation of several specific elements – even those better represented (e.g. mandible, maxilla, femur, tibia) – were lower than small mammal bone accumulations generated by the other owls that inhabit the study region, such as *T. alba*, *A. cucularia* and *B. v. nacurutu* (Andrews 1990; Gómez 2005; Montalvo & Tejerina 2009). The relative abundance of each element was also smaller than *Strix aluco* and *S. nebulosa* from Europe (Andrews 1990). The low average value of relative abundance and the better representation of some elements (e.g. mandible, femur, tibia, radio, ulna) compared with the remaining ones, also indicated a considerable bone loss in the small mammal bone assemblages generated by *S. chacoensis*. The values obtained from the calculated indexes to evaluate tooth loss, comparing empty alveoli with isolated teeth, indicated a great loss of molars and incisors evidenced in the small mammal bone accumu-

Table 2. Breakage of cranial, dental and postcranial elements in the small mammal bone assemblage generated by *Strix chacoensis* in Telteca (n and % by element).

Breakage of skulls	n	%
Complete skull	2	0.96
Maxillary with zygomatic	167	80.67
Maxillary without zygomatic	11	5.31
Minor fragments	27	13.04
Molars missing from maxillary	27	7.43
Incisors missing from premaxillary	5	6.02
Breakage of mandible		
Complete mandible	135	59.47
Ascendant ramus broken	56	24.66
Without ascendant ramus	32	14.09
Without ascendant ramus and inferior edge broken	4	1.76
Molars missing from mandible	102	27.27
Incisors missing from mandible	2	1.62
Breakage of teeth		
Broken molars <i>in situ</i>	3	0.49
Broken isolated molars	0	0.00
Broken incisors <i>in situ</i>	6	3.01
Broken isolated incisors	1	3.84
Breakage of femur		
Complete	170	96.6
Proximal	3	1.7
Shaft	0	0.0
Distal	3	1.7
Breakage of humerus		
Complete	120	93.0
Proximal	3	2.3
Shaft	2	1.5
Distal	4	3.1
Breakage of tibia		
Complete	132	87.4
Proximal	12	7.9
Shaft	3	2
Distal	4	2.6
Breakage of ulna		
Complete	143	99.3
Proximal	1	0.7
Shaft	0	0.0
Distal	0	0.0

lation produced by *S. chacoensis*. In contrast, the bone accumulations generated by strigiforms that inhabit the study area and by *S. nebulosa* from Europe, show neither tooth loss nor a considerable loss of mandibles and maxillae (e.g. Andrews 1990; Pardiñas 1999; Gómez 2005; Montalvo *et al.* 2016). However, a case of *S. aluco* from Poland reported similar proportions of losses of maxillae, mandibles and pelvis (Raczynski & Ruprecht 1974) to those detected in the present study.

Although the proportions and intensity of molars and postcranial elements affected by digestion were similar in the small mammal bone accumulation generated by *S. chacoensis* and in those reported for *S. aluco*, *S. nebulosa* and for the strigiforms that inhabit the study area, the frequency of incisors modified by this process was

different. In this respect, around 45% of *in situ* and 90% of isolated incisors were affected by digestion (mainly light), distinguishing *S. chacoensis* from the other predators that inhabit the study area and from *S. nebulosa*. *S. aluco* (predator not present in America) produces high proportions of incisors affected by digestion, although in smaller frequencies than *S. chacoensis*. *A. cucicularia* is a diurnal owl that also inhabits the area and generates similar or even greater proportions of incisors altered by digestion (Montalvo & Tejerina 2009; Montalvo *et al.* 2017). However, this raptor also produces considerably high levels of digestion on molars and postcranial elements (100%), while *S. chacoensis* does not present a large number of elements affected by this type of alteration (7.71 and 21.67%, respectively).

On the one hand, one PCA yielded values grouping the modern sample of *S. chacoensis* with *S. aluco* and separating them from samples of other avian raptors of the Strigiformes and Accipitriformes orders (Fig. 4). Components 1 and 2 accounted for 84.54% of the variation. On the other hand, another PCA was performed that considered both archaeological samples from the Monte Desert and modern ones of several strigiforms, where components 1 and 2 accounted for 75.25% of the variation. This PCA grouped modern samples of *S. chacoensis*, *S. aluco* and an archaeological sample from Rincón del Atuel 1 (Fig. 5). For this reason, some archaeological samples from this area attributed to the action of other strigiforms (cf. *B. v. magellanicus*; Fernández 2012a) could be the result of the action of *S. chacoensis*.

In summary, the main taphonomic features observed in the present study were: low average relative abundance of skeletal elements; better representation of mandible, femur, maxilla, tibia, ulna, radius and humerus compared with the remaining elements; equal representation amongst skeletal parts (cranial/postcranial–distal/proximal); great loss of teeth as indicated by empty alveoli from mandibles and maxillae; high breakage of skull and low breakage of mandible, teeth and postcranial elements altered by digestion; and high frequencies of incisors with evidence of digestive corrosion (mainly light). Several of these taphonomic trends have served as diagnostic evidence to identify strigiforms, *T. alba* in particular, as possible accumulating agents of small mammal bone accumulations recovered in archaeological and palaeontological contexts. Such is the case for several taphonomic studies conducted in various regions of Argentina (Fernández & Montalvo 2017 and references therein), which highlight the role of this type of raptor in the formation and accumulation of small mammal bone assemblages.

Therefore, the taphonomic results reported in the present work indicate a clear pattern with which to determine the action of *S. chacoensis* in the small mammal bone accumulations recovered from archaeological and palaeontological sites in South America.

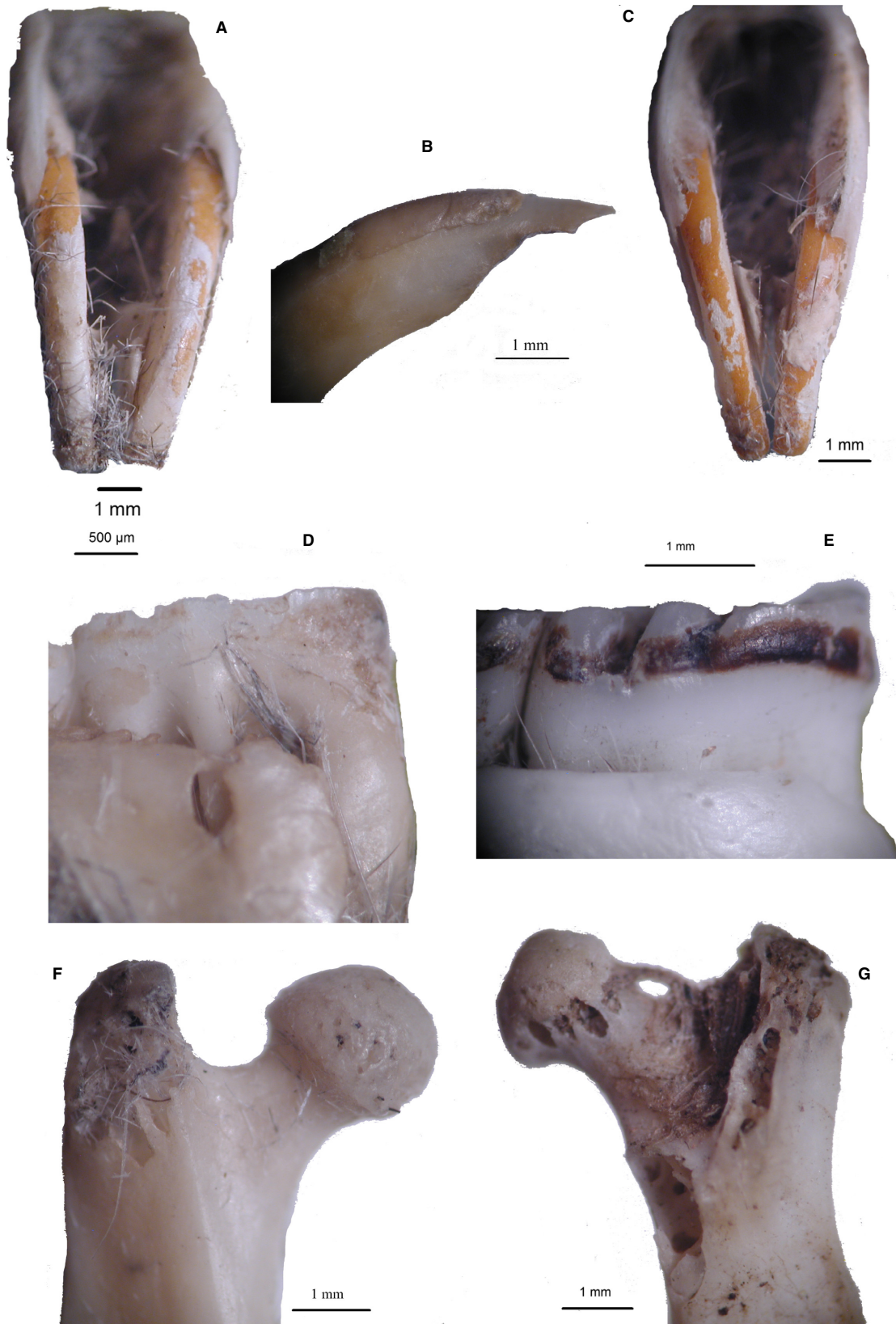


Fig. 3. Cranial and postcranial bones digested by *Strix chacoensis* in Telteca. A, C. Moderate digestion on cricetid upper incisors in frontal view. B. Light digestion on cricetid upper incisor in lateral view. D, E. Moderate digestion on cricetid first lower molars in lateral view. F. Light digestion on proximal portion of cricetid femur. G. Moderate digestion on proximal portion of cricetid femur. [Colour figure can be viewed at www.boreas.dk]

Table 3. Percentages of digestive corrosion degrees from the small mammal bones accumulated by *Strix chacoensis* in the Telteca Protected Area.

Digestion on teeth	Absent	%	Light	%	Moderate	%	Heavy	%	Extreme	%
Incisors <i>in situ</i>	111	54.14	86	41.95	8	3.90	0	0.00	0	0.00
Isolated incisors	3	11.53	16	61.53	7	26.92	0	0.00	0	0.00
Incisors total	114		102		15		0		0	
Molars <i>in situ</i>	564	92.30	47	7.70	0	0.00	0	0.00	0	0.00
Isolated molars	10	90.90	1	9.09	0	0.00	0	0.00	0	0.00
Molars total	574		48		0		0		0	
Digestion on postcranials										
Proximal femur	128	76.19	35	20.83	4	2.38	1	0.59	0	0.00
Distal humerus	96	81.35	22	18.64	0	0.00	0	0.00	0	0.00

Potential contributions to palaeoenvironmental studies

Small-sized mammals are the most frequent items preyed upon by *S. chacoensis* in our study area in the central Monte Desert. The consumed species evidence that *S. chacoensis* hunts in different habitats present in the area. Thus, *G. griseoflavus* (the most abundant prey in the sample) prefers closed and complex habitats with trees and high shrub cover; *A. dolores* is associated preferentially with shrubby steppes with high coverage, thick grasslands and disperse shrubs; *Eligmodontia* sp. frequents open areas with stripped sandy soils and disperse shrubs, while *M. australis* and *T. pallidior* prefer bushy and forested environments (Gonnet & Ojeda 1998; Tabeni & Ojeda 2003; Corbalán 2004, 2006; Corbalán & Debandi 2005; Albanese 2010). In this sense, taking into account the representation of various species from

different habitat types and vegetation patches, small mammal bone assemblages accumulated by *S. chacoensis* can be a good tool for drawing palaeoenvironmental inferences based on the bone remains recovered from open-air archaeological and palaeontological sites. In addition, considering that in the Monte Desert *S. chacoensis* has only been detected in natural protected areas (Pereyra-Lobos & Jara 2012, 2013a, b; Santander *et al.* 2012), identifying the action of this raptor from the accumulation of small mammal bones in open-air archaeological or palaeontological sites may be another valuable tool from a palaeoenvironmental perspective. Thus, the close association between current forests of *Prosopis* and the presence of *S. chacoensis* is an interesting variable that may contribute to the knowledge of the development of landscapes related with these plant communities over time. In this sense, it has been pointed out that *S. chacoensis* could act as a bio-indicator of well-preserved Monte Desert environments from South America, mainly related to forests of *Prosopis* (Pereyra-Lobos & Jara 2012, 2013a, b; Santander *et al.* 2012). Some palaeoenvironmental studies have highlighted the deep impact of human activities (mainly land clearing, overgrazing, intensive agriculture and trading) on the native forest—mainly on forests of *P. flexuosa*—in the last 500 years with the arrival of European conquerors in the study region. This tree constitutes a structural species of the Monte Desert ecological system (Álvarez & Villagra 2010). The economic activities mentioned above resulted in its drastic reduction, disappearance and/or de-structuring (e.g. Roig 1993; Prieto *et al.* 2003; Villagra *et al.* 2009; Perosa *et al.* 2014; Mafferra 2015, 2017; Castillo *et al.* 2017). Such strong alterations in the landscape also affected negatively the existence and distribution of native mammals in the arid lands of South America and the Monte Desert in particular (Roig 1991; Tabeni & Ojeda 2003, 2005; Fernández 2014; Teta *et al.* 2014; López *et al.* 2016; Fernández *et al.* 2017b). In several cases, those impacts even influenced biological invasions of exotic species (Contreras & Rosi 1980; Castillo *et al.* 2017).

Several studies have mentioned that *Strix* species from diverse regions of the world inhabit areas associated mainly with primary or old growth forests (e.g. Andrews

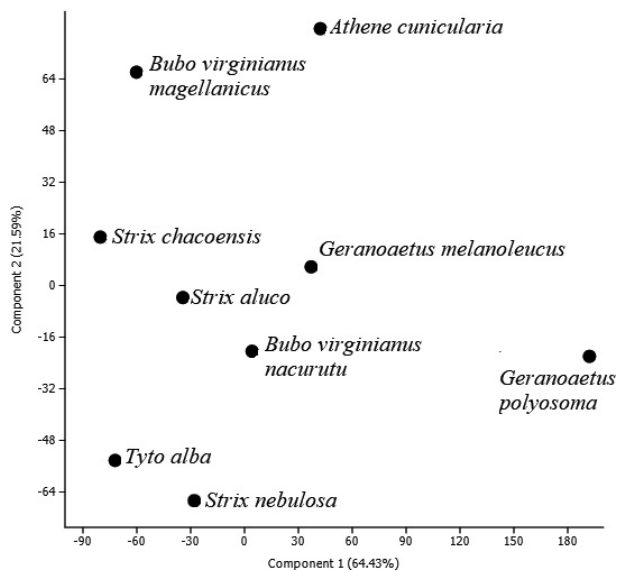


Fig. 4. Principal component analysis (based on taphonomic variables) of small mammal bone accumulation recovered from pellets of *Strix chacoensis* and comparison with other modern small mammal bone samples generated by other raptors. *Athene cucularia* (Montalvo & Tejerina 2009); *Strix aluco*, *Strix nebulosa* and *Tyto alba* (Andrews 1990); *Bubo virginianus nacurutu* (Gómez 2005); *Bubo virginianus magellanicus* (Montalvo *et al.* 2016); *Geranoaetus melanoleucus* and *Geranoaetus polyosoma* (López *et al.* 2017b).

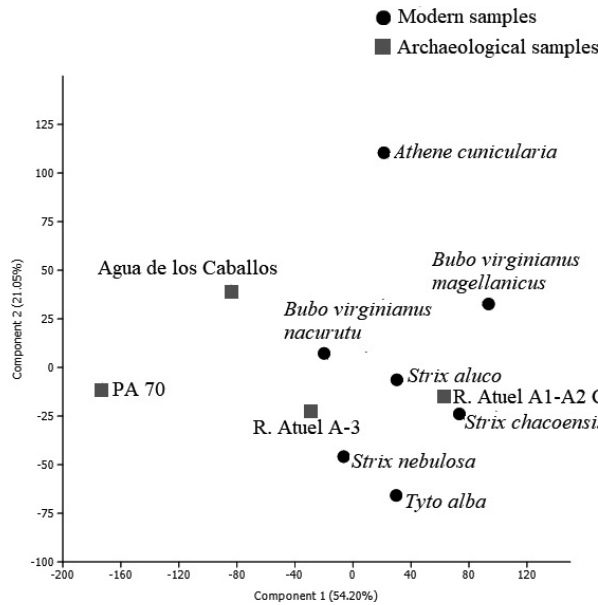


Fig. 5. Principal component analysis (based on taphonomic variables) of small mammal bone accumulation recovered from pellets of *Strix chacoensis* and comparison with archaeological and modern small mammal bone samples generated by other raptors. Archaeological samples from the Monte Desert: PA 70 (Castillo et al. 2017); Agua de los Caballos (Fernández 2012a, b); Rincón del Atuel-1 (R. Atuel A-3 and R. Atuel A1-A2 CS; Fernández 2012a). Modern samples: *Athene cunicularia* (Montalvo & Tejerina 2009); *Strix aluco*, *Strix nebulosa* and *Tyto alba* (Andrews 1990); *Bubo virginianus nacurutu* (Gómez 2005); *Bubo virginianus magellanicus* (Montalvo et al. 2016); *Geranoaetus melanoleucus* and *Geranoaetus polyosoma* (López et al. 2017b).

1990; Duncan 1997; Figueroa et al. 2006; Alvarado et al. 2007; Pereyra-Lobos & Jara 2012, 2013a, b; Santander et al. 2012), which is an interesting feature from a palaeoenvironmental and conservationist point of view. Therefore, the identification of the action of *Strix* in the accumulation of small mammal bone assemblages from open-air archaeological or palaeontological sites from South America may also be a valuable tool with which to infer well-preserved native forests in the past.

Conclusions

The results of the analysed variables of anatomical representation, breakage and digestion on small mammal bone and teeth remains recovered from pellets of *S. chacoensis* allowed this species to be placed in modification category 2 (intermediate modifier) sensu Andrews (1990), although some variables were included in categories 1, 3 and 4 (Table 4).

Both eaten prey and general taphonomic patterns detected in the sample were similar to those generated by other strigiforms—more specifically *T. alba*—that inhabit the study area in particular and South America in general. From a taphonomic and palaeoenvironmental perspective, considering that these predators, unlike *S. chacoensis*, may also inhabit human disturbed environments, it is essential to distinguish amongst them in small mammal bone accumulations recovered from archaeological and palaeontological sites. In this sense, some taphonomic features differentiate *S. chacoensis* from those predators. Such features are: lower representation of particular elements as well as average relative abundance – evidencing more element loss, high loss of dental elements compared with empty alveoli, and high levels of digestion on incisors (mainly light). In general, the taphonomic patterns obtained in the present study were similar to those reported for pellets of *S. aluco* from Europe.

In order to explore possible applications of the present study, the results presented here were used as an analytical model to interpret the micromammal fossil record from three open-air archaeological sites located in the Monte Desert (central western Argentina). However, strong postdepositional processes, such as weathering and trampling, generally affect open-air archaeological sites in the Monte Desert. Hence, archaeological and palaeontological studies should consider these aspects in addition to the taphonomic variables from actualistic research of several predators.

Table 4. Categorization of *Strix chacoensis* effects on prey remains according to the different taphonomic variables analysed (sensu Andrews 1990). The black bar indicates the modification category into which each variable fell.

Taphonomic trace	Category 1	Category 2	Category 3	Category 4	Category 5
Relative abundance pc/c			■		
Distal element loss	■				
Breakage of postcrania		■			
Breakage of skulls			■		
Loss of zygomatic processes		■			
Maxillary tooth loss		■			
Breakage of mandibles		■			
Mandibular tooth loss		■			
Proportions isolated teeth				■	
Breakage of teeth	■				
Digestion of molars		■			
Digestion of incisors				■	
Digestion of postcrania			■		

Small mammals from archaeological and palaeontological sites can be used as proxy data to make palaeoenvironmental inferences. *S. chacoensis* preys on taxa from different patches of vegetation. Therefore, small mammal assemblages generated by this predator may contribute to making more accurate inferences on regional past environments. Considering that knowledge of processes and agents involved in small mammal bone accumulations from archaeological and palaeontological sites is essential from a taphonomic and palaeoenvironmental perspective, the present work hopes to contribute to systematizing an actualistic taphonomic perspective at a regional scale to strengthen the inferences and knowledge about past environments. From an applied and conservationist perspective, this work also aims to evaluate native forest variations over time as well as to highlight the informative and ecological potential of natural protected areas.

Acknowledgements. – This work is dedicated to the memory of Santiago Maldonado, Facundo Ferreira and Rafael Nahuel. We wish to thank María I. Rosi for her continued support, help and critical reading of the manuscript. Two reviewers (Ulyses Pardiñas and Christiane Denys) and the Editor-in-Chief Jan A. Piotrowski provided valuable comments, corrections and suggestions that greatly improved the manuscript. This research was carried out in the framework of the following projects: Project ‘Ocupación Humana en el Monte Árido III (OHMA III)’ (06/G724. SECTyP, Universidad Nacional de Cuyo, Mendoza, Argentina); Project 11/N769 (Facultad de Ciencias Naturales y Museo, UNLP, Argentina); and Project 05-G (Facultad de Ciencias Exactas y Naturales, UNLPam, Argentina). J. M. López and L. Castillo are beneficiaries of a Ph.D. scholarships granted by CONICET (2014–2019).

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Table S1. Archaeological sites from the Monte Desert and small mammal assemblages detected in previous studies, where strigiforms were the possible accumulating agents of such bone sets.

Table S2. Minimum number of skeletal elements (MNE) and MNE% according to MNI in the modern sample generated by *Strix chacoensis* in Telteca.

Supporting Information

Additional Supporting Information may be found in the online version of this article at <http://www.boreas.dk>.