

Taphonomic Analysis of Micromammal Remains from Striped Owl (*Pseudoscops clamator*) Pellets in Northeastern Buenos Aires Province, Argentina: Implications for Archaeological Sites Formation

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ABSTRACT The main objective of this study was to determine the taxonomic and taphonomic characteristics of the micromammal remains recovered from pellets of *Pseudoscops clamator* (striped owl), collected at three localities in northeastern Buenos Aires Province, Argentina (Punta Lara Natural Reserve, 34°49'02,6"S, 58°03'03,9"W; Costanera Sur Ecological Reserve, 34°36'6,44"S, 58°21'33,22"W; Los Robles Park, 34°40'22,03"S, 58°52'18,88"W). The main taphonomic variables (e.g. evidence of digestive action, breakage patterns and relative abundance of skeletal elements) suggest that this owl mainly produces intermediate to moderate modification. On the other hand, *P. clamator* preyed mainly upon large-sized (>150 g) micromammals (e.g. *Lutreolina crassicaudata*, *Cavia aperea*, *Holochilus brasiliensis* and *Rattus* sp.), and to a lesser degree on medium- (50–150 g) and small-sized species (<50 g) (e.g. *Scapteromys aquaticus*, *Calomys* sp., *Oligoryzomys flavescens*, *Akodon azarae* and *Mus musculus*). Fossil assemblages with a dominance of large-sized micromammals are commonly associated with humans as agents of accumulation. However, this study demonstrates that this owl produces assemblages with abundant large-sized micromammals, which introduces an equifinality problem. In that sense, digestive corrosion marks, breakage patterns and the relative abundance of skeletal remains are the main attributes to differentiate *P. clamator* from humans, as agents of accumulation. Finally, our results might serve as an analytical model for the taphonomic interpretation of the fossil record of micromammals from paleontological and archaeological sites, which fall within the distributional range and habitat of *P. clamator*. Copyright © 2013 John Wiley & Sons, Ltd.

Key words: equifinality; micromammalian assemblages; pellets; predation; South America; Strigiformes; taphonomy
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Introduction

Actualistic taphonomic studies on micromammal remains produced by different predators constitute an appropriate analytical model for the interpretation of assemblages from archaeological and paleontological sites (e.g. Andrews, 1990; Fernández-Jalvo & Andrews, 1992; Stahl, 1996; Denys, 2002; Terry, 2007; Souttou *et al.*, 2012). In Argentina, this type of studies has been on the rise in recent years (Pardiñas, 1999; Gómez, 2005, 2007; Gómez & Kauffmann, 2007; Montalvo *et al.*, 2007, 2008, 2012; Iglesias, 2009; Montalvo &

Tallade, 2009, 2010; Montalvo & Tejerina, 2009; Carrera & Fernández, 2010; Álvarez *et al.*, 2012). However, even when a large part of micromammal assemblages from archaeological sites tend to be accumulated by Strigiformes, only a few of those studies have considered these raptor birds (Pardiñas, 1999; Gómez, 2005, 2007; Montalvo & Tejerina, 2009; Carrera & Fernández, 2010).

Carrera & Fernández (2010) carried out an experimental taphonomic study on remains of *Mus musculus* (house mouse) consumed by *Pseudoscops clamator* (striped owl). The authors concluded that this species might fall into category I or 'with light modifications' (*sensu* Andrews, 1990). This mid-sized (320–500 g) owl nests on the ground, frequently perches upon trees and has nocturnal and crepuscular habits (del Hoyo *et al.*, 1999; Pautasso &

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de la Peña, 2001). It is distributed from Mexico, through large parts of the tropical and subtropical zone of Central and South America, down to La Pampa and Buenos Aires provinces in Argentina (Martinez *et al.*, 1996; Marks *et al.*, 1999). It is found in diverse habitats from sea level to 1400 m asl, including xerophytic forests, jungles, grasslands and suburban areas (Marks *et al.*, 1999). Its diet is based mainly on rodents, and occasionally on birds, other vertebrates and insects (Massoia, 1988; Isacch *et al.*, 2000; Motta-Junior *et al.*, 2004; Delgado *et al.*, 2005; Pautasso, 2006; Aguiar & Naiff, 2009; Lo Coco *et al.*, 2012). Most of the diet studies agree on the relatively large size of its prey items, in comparison with other South American Strigiformes, counting *Holochilus* spp. (marsh rats), *Rattus* spp. (rats) and *Cavia aperea* (Brazilian guinea pig) among its rodent prey. The larger size of this owl and its robust beak and hindlimbs (mainly tarsometatarsus and claws) might enable this owl to hunt for larger animals (see Motta-Junior, 2006).

This study focuses on the taphonomic analysis of micromammal remains recovered from pellets of *P. clamator*, collected in northeastern Buenos Aires province, Argentina. Moreover, comparisons are made

with previous studies performed with other raptors, with special reference to the work of Carrera & Fernández (2010) on *P. clamator*. Comparisons are made with the purpose of categorizing this owl as a taphonomic agent and relate its micromammals deposits with archaeological assemblages, mainly those derived from human accumulations.

Materials and methods

Materials

Bone and teeth remains from rodents and marsupials [number of identified specimens per taxon (NISP) = 5952; minimum number of elements (MNE) = 5766; minimum number of individuals (MNI) = 103] were recovered from three samples of pellets of *P. clamator* from the northeastern Pampean Region (Figure 1):

- (1) Punta Lara Natural Reserve (PLNR; 34°49'02.6"S, 58°03'03.9"W). This reserve occupies an area of 6000 ha and has several habitat types including

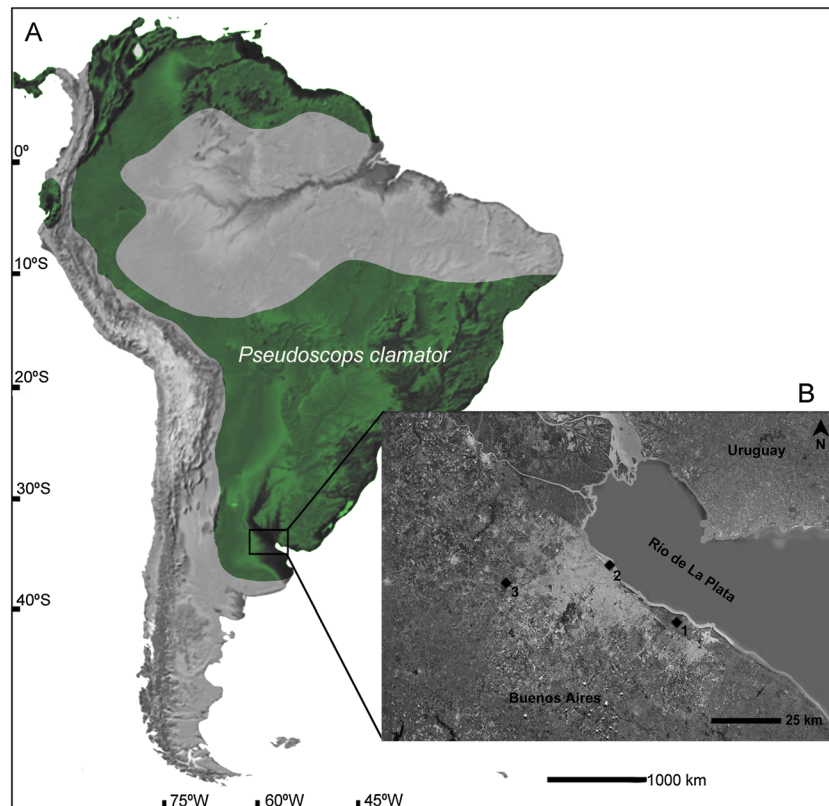


Figure 1. (A) Distribution of *Pseudoscops clamator* at South America. (B) Detail of the study area including the samples analyzed: 1. Punta Lara Natural Reserve (PLNR); 2. Costanera Sur Ecological Reserve (CSER); 3. Los Robles Park (LRP). This figure is available in colour online at wileyonlinelibrary.com/journal/oa.

native grasslands, marshes, riverine forests and groves of *Eucalyptus* spp. (eucalyptus) and *Celtis tala* (tala), together with shallow lakes, channels and brooks. An adult individual of *P. clamator* was observed between November 2008 and January 2009, perched upon *C. tala* trees, and 24 pellets were recovered from that site. These samples yielded a NISP = 1201; MNE = 1151 and MNI = 34.

- (2) Costanera Sur Ecological Reserve (CSER; 34°36'6.44"S, 58°21'33.22"W). This reserve occupies an area of 353 ha and presents shallow lakes surrounded by marshes, grasslands and groves of *Tipuana tipu* (tipu tree), *Phoenix canariensis* (Canary Island date palm) and *Melia azedarach* (chinaberry). In April 2009, a mating couple of *P. clamator* was found nesting in a dried grassland of *Schoenoplectus californicus* (totora), from where 21 pellets were recovered. These yielded a NISP = 1236; MNE = 1210 and MNI = 28.
- (3) Los Robles Park (LRP; 34°40'22.03"S, 58°52'18.88"W). This park comprises an area of 1000 ha, with native grasslands, marshes and exotic species plantations. Between July and August 2010, a mating couple of *P. clamator* was found in a *Salix humboldtiana* (pencil willow) grove stand surrounded by native grassland invaded by *Gleditsia triacanthos* (honey locust), from where 45 pellets were collected. These yielded a NISP = 3515; MNE = 3405 and MNI = 41.

The landscape of the region is composed of plains with some undulations, and the native vegetation is characterized by grasslands of *Stipa*, *Poa* and *Bromus* (Cabrera, 1976). The climate is dictated by the Atlantic anticyclone, with average annual precipitation = 1200 mm and average annual temperature = 18°C (Burgos, 1968).

Methods

Owl pellets were disaggregated while moist, after a quick dip in warm water. Bone and teeth were separated and studied under a dissecting scope. Remains were identified using reference materials from the mammal collection at Museo de La Plata and published references (e.g. Massoia & Fornes, 1965; Massoia, 1976). Average weights for each taxon were obtained from a previous work performed on the same study area (Leveau et al., 2006), and the percent biomass contributed by each prey species was estimated as $(B_i) = [(Sp_i N_i) / \sum (Sp_i N_i)] \times 100$, where Sp_i is the weight of species i , N_i is the number of consumed individuals of species i (Martí, 1987).

For the taphonomic analysis of micromammals, the classification proposed by Andrews (1990) and Fernández-Jalvo & Andrews (1992) was followed. This

classification makes the distinction between five categories of modification of skeletal and teeth remains (i.e. light, intermediate, moderate, heavy and extreme), including Strigiformes, Falconiformes and carnivore mammals. According to Andrews (1990), these categories are based both on degree of modification and frequencies of elements affected. Corrosion marks, produced by digestive acids, were observed on the surfaces of teeth (i.e. incisors and molars) and postcranial remains (i.e. proximal epiphysis of femur and distal epiphysis of humerus). Additionally, the degree of breakage of cranial and postcranial remains was analyzed by counting whole remains and the different portions (i.e. diaphysis, proximal epiphysis and distal epiphysis).

The relative abundance of skeletal elements was evaluated considering the representativity of each one in the sample (MNE_i) as a function of the expected number of that specific skeletal element in the individual (E_i) and MNI, after: $MNE_i / (E_i \times MNI) \times 100$. In order to analyze the relationships between cranial and postcranial elements, two indices were calculated: $I = [(femur + tibia + humerus + radius + ulna) \times 16 / (mandible + maxilla + molars) \times 10] \times 100$, and $II = [(humerus + femur) / (mandible + maxilla)] \times 100$. In order to study relationships between distal and proximal limb elements, the following index was calculated: $[(tibia + radius) / (femur + humerus)] \times 100$. Additionally, two indices that evaluate the proportion of isolated teeth were calculated $[(maxillary\ alveoli + mandibular\ alveoli) / (molars)] \times 100$, and $[(premaxillary\ alveoli + mandibular\ alveoli) / (incisors)] \times 100$.

Micromammals (mammals <1 kg), were divided into three size-categories: small (<50 g), medium (between 50 and 150 g) and large (>150 g) (modified from Pardiñas, 1996–1998).

Additionally, Pardiñas (1999) developed two indices to evaluate the action of raptor birds and humans in the origin of assemblages; namely (i) Size Index $[(MNI_{small} + MNI_{medium}) / (MNI_{large})] \times 100$ and (ii) Predictability Index $[(MNI_{colonial} + MNI_{gregarious} + MNI_{grouped}) / (MNI_{cryptic} + MNI_{solitary})] \times 100$. On the one hand, hystricognath (*C. aperea*) and murid (*Rattus* sp.) rodents are included in the grouped category, and on the other hand, cricetid rodents and marsupials correspond to the cryptic and solitary categories.

Finally, ordination (Principal Component Analysis, PCA) and grouping (Cluster Analysis) multivariate statistics were performed in order to test for relationships between micromammal samples produced by *P. clamator* and those generated by other Strigiformes from South America, North America, Europe, Asia and Africa, for which there exists taphonomic information. These tests were performed using the software PAleontological

STatistics version 2.07 (Hammer, 1999–2011), which is based on a data matrix composed of the main taphonomic attributes considered (i.e. S1). Moreover, the similitude coefficient used in the cluster analysis was based on Euclidean distances, and the phenograms produced were plotted according to the Unweighted Pair Group Method Average method.

Results

Predation

Nine micromammal taxa were identified from pellets of *P. clamator* from the three locations considered, including a marsupial and eight rodents (Table 1).

A total of 34 prey items were registered in the sample from PLNR (expressed in MNI). The main species were the hystricognath rodent *C. aperea* and the sigmodont rodent *Holochilus brasiliensis* (web-footed marsh rat), followed by the sigmodonts *Akodon azarae* (Azara's grass mouse), *Scapteromys aquaticus* (water rat), *Oligoryzomys flavescens* (yellow pygmy rice rat) and a juvenile of the didelphid marsupial *Lutreolina crassicaudata* (little water opossum). A total of 28 prey items were found in the sample from CSER, with *O. flavescens* being the most abundant species, and *C. aperea* and the introduced murid *M. musculus* found in smaller proportion. The sample from LRP yielded 41 prey items, with the

introduced murid *Rattus* sp. being the most consumed species, followed by *O. flavescens*, *C. aperea*, *Calomys* sp. (vesper mice) and *A. azarae*.

In terms of biomass, *C. aperea* was important to the owl diet in the three samples analyzed, while *H. brasiliensis* and *Rattus* sp. contributed significantly to the total biomass in samples from PLNR and LRP, respectively (Table 1).

Size index values indicated that *P. clamator* preyed mainly upon large-sized micromammals (e.g. *C. aperea*, *H. brasiliensis* and *Rattus* sp.) in samples from PLNR and LRP, while it preyed upon small-sized rodents (e.g. *O. flavescens* and *M. musculus*) in the sample from CSER (Table 2).

Finally, predictability index values indicated that *P. clamator* mainly consumed micromammals with solitary habits (i.e. *A. azarae*, *S. aquaticus*, *H. brasiliensis*, *O. flavescens*, *M. musculus* and *L. crassicaudata*) in samples from PLNR and CSER, and predictable micromammals (i.e. *C. aperea* and *Rattus* sp.) in the sample from LRP (Table 2).

Anatomical representation

Average relative abundance of skeletal parts indicates a high integrity in samples from CSER and LRP and a medium integrity in PLNR (Table 3). Despite variations in some elements, samples from the three locations showed a similar representativity pattern of skeletal

Table 1. Average weight (W), minimum number of individuals (MNI), percentage of minimum number of individuals (MNI%) and total percent biomass (%B) of the taxa consumed by *Pseudoscops clamator* in the samples studied. For abbreviations, see Figure 1 caption

	PLNR			CSER			LRP			
	W	MNI	MNI%	%B	MNI	MNI%	%B	MNI	MNI%	%B
Mammalia										
Didelphimorphia										
<i>Lutreolina crassicaudata</i>	445	0	0	0	1	3.6	15	0	0	0
Rodentia										
Caviidae										
<i>Cavia aperea</i>	525	13	38.2	59.7	4	14.3	70.6	6	14.6	43.7
Muroidea										
Cricetidae indet.										
<i>Calomys</i> sp.	19 ^a	0	0	0	3	10.7	1.9	0	0	0
<i>Akodon azarae</i>	14	0	0	0	0	0	0	1	2.4	0.2
<i>Scapteromys aquaticus</i>	28	4	11.8	1	0	0	0	1	2.4	0.4
<i>Holochilus brasiliensis</i>	112	2	5.9	2	0	0	0	0	0	0
<i>Oligoryzomys flavescens</i>	326	13	38.2	37	0	0	0	0	0	0
	19	2	5.9	0.3	18	64.3	11.5	9	21.9	2.4
Muridae										
<i>Rattus</i> sp.	160	0	0	0	0	0	0	24	58.6	53.3
<i>Mus musculus</i>	14	0	0	0	2	7.1	0.9	0	0	0
Total		34			28			41		

^aData from *O. flavescens*, the single cricetid in CSER sample.

Table 2. Values of the indices calculated for small mammals from *Pseudoscops clamator* samples studied: f=femur; t=tibia; h=humerus; r=radius; c=ulna; mx=maxilla; mb=mandible; m=molar; i: incisor. For abbreviations, see Figure 1 caption

	PLNR	CSER	LRP
Postcranial/Cranial			
I. f+t+h+r+c/mx+mb+m	401	379.5	384.4
II. h+f/mx+mb	132.9	136.4	115.2
Distal/Proximal elements			
t+r/f+h	74.2	74.4	97.9
% Isolated teeth			
Alveoli mx+alveoli mb/m	13.8	46.4	19.9
Alveoli mx+alveoli mb/i	5.6	4.9	3.8
Size index	30.8	460	36.7
Predictability index	61.9	16.7	272.7

parts, where the most abundant elements were the mandibles, humeri, femurs and tibias, while the least abundant were ribs and autopodia (Figure 2A). There were no important variations in the relative abundance of elements between the different size-classes of micromammals (Figure 2B).

On the other hand, the two indices evaluating the relationship between postcranial and cranial elements suggest a better preservation of the former in all samples (Table 2). The index quantifying the relationship between distal and proximal limbs indicates an abundance of proximal elements in the samples from PLNR and CSER, and an even representativity in LRP. Finally, the teeth loss indices showed that in all samples, most molars and incisors were retained in their alveoli (Table 2).

Table 3. Minimum number of elements (MNE) and relative abundances of elements for small mammals from *Pseudoscops clamator* samples studied. For abbreviations, see Figure 1 caption

	PLNR		CSER		LRP	
	MNE	Relative abundance	MNE	Relative abundance	MNE	Relative abundance
Maxilla	22	32.4	29	51.8	60	73.2
Mandible	48	70.6	37	66.1	65	79.3
Isolated incisors	7	5.2	44	39.3	52	31.7
Isolated molars	9	1.7	12	3.6	24	3.7
Vertebra	372	36.5	326	38.8	960	78
Ribs	107	13.1	190	28.3	575	58.4
Scapula	17	25	28	50	46	56.1
Humerus	51	75	35	62.5	75	91.5
Ulna	36	52.9	28	50	73	89
Radius	29	42.6	33	58.9	67	81.7
Pelvis	31	45.6	33	58.9	81	98.8
Femur	42	61.8	55	98.2	69	84.1
Tibia	40	58.8	34	60.7	74	90.2
Calcaneus	19	27.9	11	19.6	44	53.7
Astragalus	4	5.9	5	8.9	38	46.3
Metapodia	116	17.1	149	26.6	252	30.7
Phalange	201	10.6	161	10.3	850	37
Total	1151		1210		3405	
Average		32.3		48.2		63.2

Digestion

82% of skeletal and teeth remains suffered some degree of alteration, due to digestive action. The light and moderate modification categories were the most frequent ones (45.7% and 27.9%, respectively), followed by the heavy (8.3%) and extreme (0.1%) categories (Table 4).

In samples from PLNR and LRP, >80% of remains showed corrosion marks, mainly in the light (PLNR = 42.8% and LRP = 46.6%) and moderate categories (PLNR = 25.9% and LRP = 32.9%). On the other hand, the sample from CSER presented a light reduction, with percentages <70%, especially in the light (41.2%) and moderate categories (16.9%). In that sense, a part of postcranial remains showed small pits on the epiphysis surfaces, and some appeared to be polished (Figure 3A–F). Some molars showed cups with a rounded contour, while some others showed small cracking and scaling in the enamel (Figure 3G). Corrosion was more intense on some incisors tips, while on others, it extended to a larger surface, leaving them with an undulated appearance (Figure 3H–I).

Breakage

29.8% of all specimens recovered from samples showed some degree of breakage. Moreover, the proportion of breakage elements across the different samples was similar (PLNR = 22.6%; CSER = 29.2% and LRP = 32.5%).

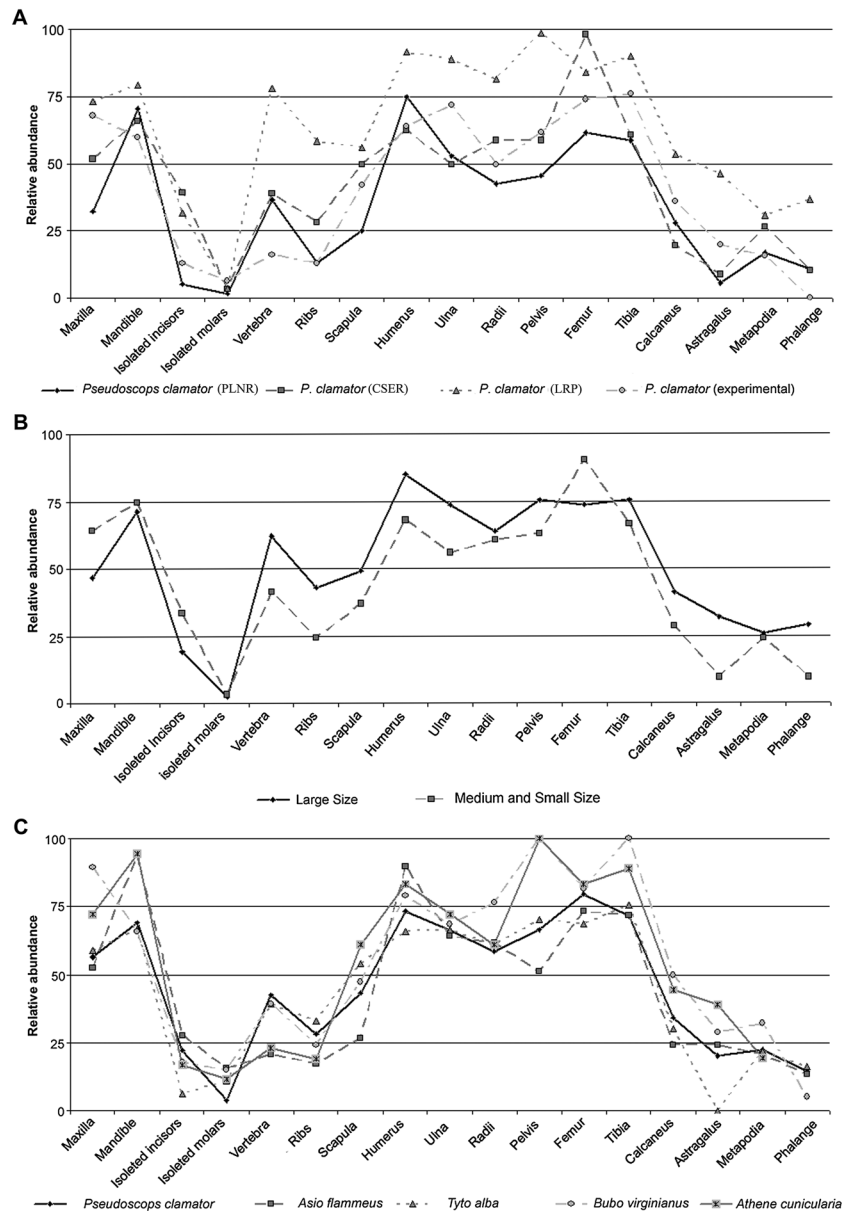


Figure 2. Values of relative abundance of different anatomical elements, comparing samples produced by *Pseudoscops clamator* (A), groups of sizes of micromammals produced by *P. clamator* (B), and average of the values of *P. clamator* (this work, and Carrera & Fernández, 2010), *Asio flammeus* (Andrews, 1990), *Tyto alba* (Andrews, 1990), *Bubo virginianus* (Gómez, 2005) and *Athene cucularia* (Montalvo & Tejerina, 2009) (C). For abbreviations, see Figure 1 caption.

Table 5 shows the different types of breakage in the cranial and postcranial elements.

Few complete crania were found, and most of them were highly broken with loss of parietal and frontal elements (PLNR = 95.3%; CSER = 100% and LRP = 98.9%). Most corresponded to maxillary and zygomatic arches, and other minor isolated remains (e.g. tympanic bullae and premaxillars). Moreover, the loss of molars from maxillars was light in all samples, and the loss of incisors

from premaxillars was minimal in samples from PLNR, and even absent in CSER and LRP (Table 5).

Those samples from PLNR and CSER registered a moderate proportion of complete mandibles, while the sample from LRP yielded few complete mandibles (Table 5). A part of broken mandibles preserved the ascending branches in good condition, and very few mandibles presented a broken lower border of the mandibular branch (Table 5). The loss of incisors from

Table 4. Representation of the various categories of digestive corrosion for small mammals from *Pseudoscops clamator* samples studied. For abbreviations, see Figure 1 caption

	Digestion classes <i>sensu</i> Andrews (1990)									
	Absent		Light		Moderate		Heavy		Extreme	
	(N)	%	(N)	%	(N)	%	(N)	%	(N)	%
PLNR										
Digestion of teeth										
Incisors <i>in situ</i>	9	12.7	31	43.7	19	26.8	12	16.9	0	0
Isolated incisors	0	0	5	71.4	2	28.6	0	0	0	0
Incisors Total	9	11.5	36	46.2	21	26.9	12	15.4	0	0
Molars <i>in situ</i>	31	14.3	91	41.9	63	29	32	14.7	0	0
Isolated molars	5	55.6	4	44.4	0	0	0	0	0	0
Molars Total	36	15.9	95	42	63	27.9	32	14.2	0	0
Digestion in postcranial										
Proximal femur	8	19	17	40.5	11	26.2	6	14.3	0	0
Distal humerus	20	39.2	22	43.1	8	15.7	1	2	0	0
CSER										
Digestion of teeth										
Incisors <i>in situ</i>	21	51.2	11	26.8	5	12.2	4	9.8	0	0
Isolated incisors	15	34.1	11	25	13	29.5	5	11.4	0	0
Incisors Total	36	42.3	22	25.9	18	21.2	9	10.6	0	0
Molars <i>in situ</i>	46	33.3	71	51.4	15	10.9	6	4.3	0	0
Isolated molars	3	25	7	58.3	2	16.7	0	0	0	0
Molars Total	49	32.7	78	52	17	11.3	6	4	0	0
Digestion in postcranial										
Proximal femur	12	21.8	17	30.9	18	32.7	8	14.5	0	0
Distal humerus	9	25.7	17	48.6	2	5.7	6	17.1	1	2.9
LRP										
Digestion of teeth										
Incisors <i>in situ</i>	15	19.2	31	39.7	30	38.5	2	2.6	0	0
Isolated incisors	6	11.5	22	42.3	20	38.5	4	7.7	0	0
Incisors Total	21	16.2	53	40.8	50	38.5	6	4.6	0	0
Molars <i>in situ</i>	37	11.7	162	51.3	108	34.2	9	2.8	0	0
Isolated molars	13	54.2	11	45.8	0	0	0	0	0	0
Molars Total	50	14.7	173	50.9	108	31.8	9	2.6	0	0
Digestion in postcranial										
Proximal femur	8	11.6	31	44.9	24	34.8	6	8.7	0	0
Distal humerus	20	26.7	29	38.7	20	26.7	6	8	0	0

the mandibles was light in all samples, and the loss of molars was scarce in the sample from PLNR, and moderate in CSER and LRP (Table 5).

In all samples, the proportion of broken teeth was small (PLNR = 1.3%; CSER = 2.1% and LRP = 0.6%), and particularly for incisors, those that were found in isolation were more broken up than those found *in situ* (Table 5).

Breakage values for postcranial elements were moderate in all samples (PLNR = 21%; CSER = 39.8% and LRP = 18.5%). Moreover, the proximal epiphysis prevailed in the femur and ulna, while in the humerus and tibia, it was the distal epiphysis that predominated (Table 5). It is noteworthy, that all samples had a larger proportion of broken postcranial elements, with breakage surfaces at obtuse angles and smooth edges (PLNR = 76.3%; CSER = 72.9% and LRP = 94.7%).

Finally, in all samples, the majority of autopodia elements (i.e. calcanea, astragalus, metapodia and phalanges) were complete (PLNR = 0.3%; CSER = 8.6% and LRP = 0.1%). However, the most fragile elements such as ribs, scapulae and pelvis presented a high degree of breakage in all samples (Table 5).

Discussion

Multivariate analyses (Figure 4) yielded coherent values separating samples of *P. clamator* with respect to the other owl species compared. Specifically, axis 1 of the PCA (39.4% of variance; Figure 4A), *P. clamator* showed a marked separation from *Tyto alba* (barn owl), *Bubo lacteus* (Verreaux's eagle owl), *Strix nebulosa* (great grey owl) and *Asio otus* (long eared owl); moderate separation from

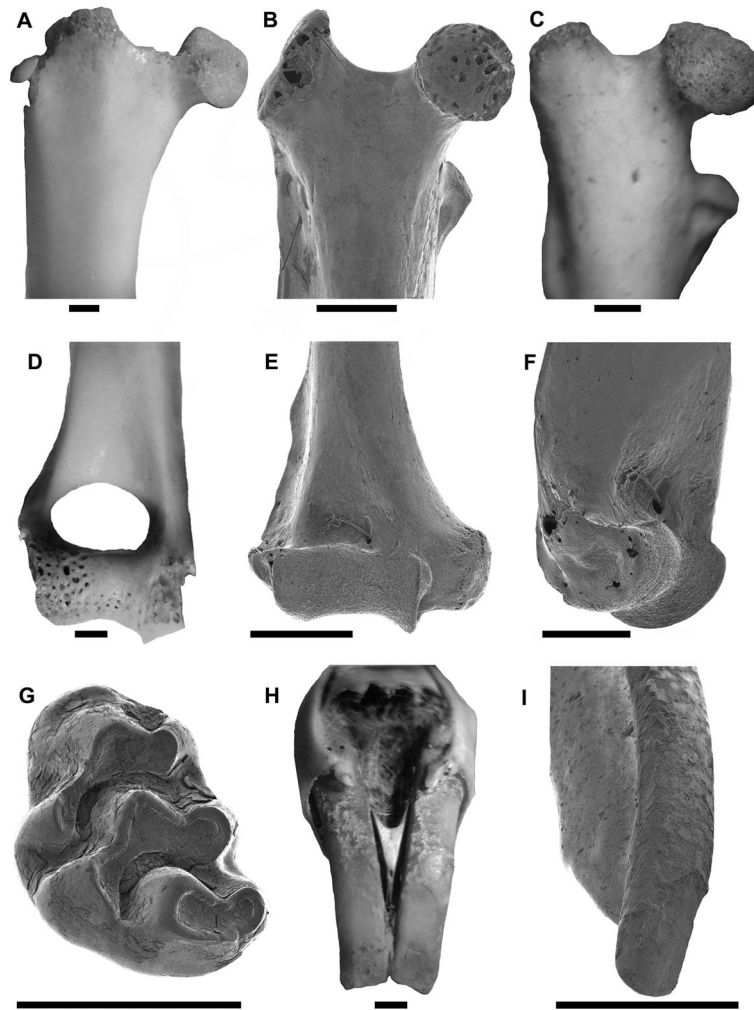


Figure 3. Different types of digestive alteration in remains recovered from *Pseudoscops clamator* samples analyzed. (A) Femur of *Cavia aperea* with light alteration (CSER). (B) Femur of Muroidea with moderate alteration (CSER). (C) Femur de *Rattus* sp. with light alteration (LRP). (D) Humerus of *C. aperea* with moderate alteration (CSER). (E) Humerus of Muroidea with light alteration (CSER). (F) Humerus of *C. aperea* with light alteration (CSER). (G) Isolated molar of *Mus musculus* with light alteration (CSER). (H) Upper incisors of *Holochilus brasiliensis* with moderate alteration (PLNR). (I) Upper incisor of Muroidea with moderate alteration (CSER). Scales: 1 mm. For abbreviations, see Figure 1 caption.

Asio flammeus (short-eared owl), *Bubo bubo* (european eagle owl), *Strix aluco* (tawny owl), *Bubo virginianus* (great horned owl), *Bubo africanus* (spotted eagle owl), and close to *Athene cunicularia* (burrowing owl). While axis 2 (24.4% of variance) showed a marked separation from *B. africanus* and *S. aluco*, moderate separation from *A. flammeus*, *B. bubo*, *B. virginianus*, *B. lacteus* and *S. nebulosa*, and close to *A. cunicularia*, *T. alba* and *A. otus*. Moreover, the phenogram generated from cluster analysis shows more clearly the separation between the *P. clamator* samples, and the others owl species (Figure 4B).

Previous studies on the taphonomy of different Strigiform species have shown that the digestive activity of these birds characteristically affects bone

and teeth remains in light to moderate categories (e.g. S1; Andrews, 1990; Gómez, 2005, 2007, Carrera & Fernández, 2010; Montalvo & Tejerina, 2010). In that sense, *P. clamator* mainly caused light and moderate digestive corrosion alterations in high percentages (Table 4, S1), to the wild micromammal assemblages analyzed in this study, as well as in an experimental sample studied by Carrera & Fernández (2010). Also, high and moderate frequencies of digestive corrosion were registered in micromammal assemblages generated by *A. cunicularia*, *Bubo* spp., *Strix* spp. and *A. otus*. (S1; Andrews, 1990; Gómez, 2007; Montalvo & Tejerina, 2010). While in those assemblages generated by *T. alba*, *A. flammeus* presented lower levels of corrosion (S1; Andrews, 1990).

Table 5. Breakage in cranial, dental and post-cranial elements for small mammals from *Pseudoscops clamator* samples studied. For abbreviations, see Figure 1 caption

	PLNR		CSER		LRP	
	N	%	N	%	N	%
Breakage of skulls						
Complete skull	2	4.7	0	0	1	1.1
Maxillary with zygomatic	12	27.9	3	10.3	4	4.3
Maxillary without zygomatic	8	18.6	26	89.7	55	59.8
Minor fragments	21	48.8	0	0	32	34.8
Molars missing from maxillary	13	12.3	27	28.7	23	12.2
Incisors missing from premaxillary	1	3.6	0	0	0	0
Breakage of mandible						
Complete mandible	15	31.2	14	37.8	11	16.9
Ascendant ramus broken	17	35.4	8	21.6	28	43.1
Without ascendant ramus	12	25	12	32.4	20	30.8
Without ascendant ramus and inferior edge broken	4	8.3	3	8.1	6	9.2
Molars missing from mandible	17	12.1	37	34.3	40	21.1
Incisors missing from mandible	3	6.4	2	5.4	3	4.7
Breakage of teeth						
Broken molars <i>in situ</i>	2	0.9	1	0.7	1	0.3
Broken isolated molars	0	0	0	0	0	0
Total broken molars	2	0.9	1	0.7	1	0.3
Broken incisors <i>in situ</i>	1	1.4	1	2.4	1	1.3
Broken isolated incisors	1	14.3	3	42.9	1	5.8
Total broken incisors	2	2.6	4	8.3	2	1.5
Breakage of postcranial elements						
Femur						
Complete	34	73.9	35	60.3	55	73.3
Proximal	8	17.4	20	34.5	14	18.7
Shaft	0	0	2	3.4	0	0
Distal	4	8.7	1	1.7	6	8
Humerus						
Complete	48	94.1	25	69.4	71	93.4
Proximal	0	0	0	0	1	1.3
Shaft	0	0	1	2.8	0	0
Distal	3	5.9	10	27.8	4	5.3
Tibia						
Complete	30	62.5	22	44.9	66	79.5
Proximal	7	14.6	12	24.5	7	8.4
Shaft	1	2.1	3	6.1	2	2.4
Distal	10	20.8	12	24.5	8	9.6
Ulna						
Complete	31	86.1	21	75	59	79.7
Proximal	5	13.9	7	25	14	18.9
Shaft	0	0	0	0	0	0
Distal	0	0	0	0	1	1.4
Breakage of others postcranial elements						
Vertebra	24	6.5	46	14.1	288	30
Rib	75	70.1	97	51	477	83
Scapula	18	85.7	27	96.4	44	81.5
Radius	0	0	8	24.2	4	5.9
Pelvis	37	84.1	30	75	122	91.7
Calcaneus	0	0	0	0	1	2.3
Astragalus	0	0	0	0	0	0
Metapodia	1	0.9	28	18.8	0	0
Phalange	0	0	0	0	0	0

Conversely, digestive action values produced by micromammal assemblages from human origins show an elevated degree of corrosion (S1; Crandall & Stahl, 1995; Dewar & Jerardino, 2007), comparable to those produced by carnivore mammals (e.g. Andrews & Evans,

1983; Andrews, 1990; Gómez & Kaufmann, 2007; Montalvo *et al.*, 2007, 2008, 2012).

Figure 2C shows that the relative abundance patterns of skeletal parts from *P. clamator* samples and those from other species of Strigiformes from the area, such

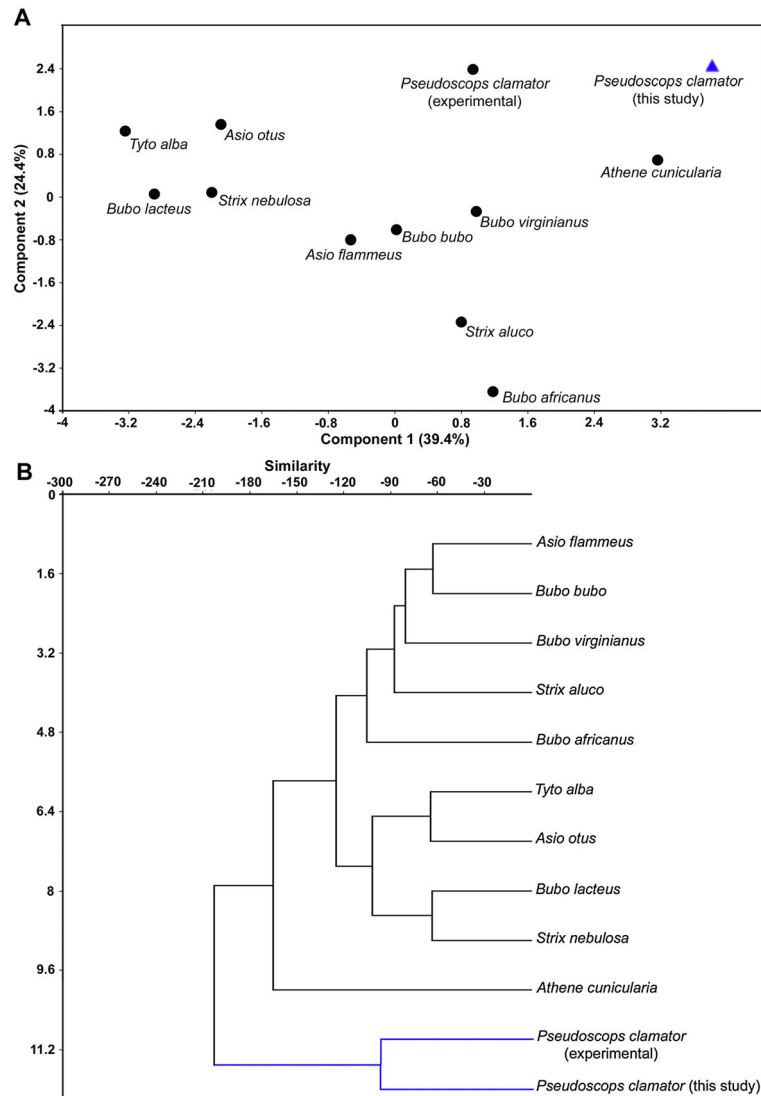


Figure 4. Multivariate analyses of small mammal samples of *Pseudoscops clamator* (this work, and Carrera & Fernández, 2010), averages of *Asio flammeus* (Andrews, 1990), *Tyto alba* (Andrews, 1990), *Bubo virginianus* (Gómez, 2005), and *Athene cucularia* (Montalvo & Tejerina, 2009), *Bubo bubo* (Andrews, 1990), *Bubo lacteus* (Andrews, 1990), *Bubo africanus* (Andrews, 1990), *Asio otus* (Andrews, 1990), *Strix aluco* (Andrews, 1990), and *Strix nebulosa* (Andrews, 1990). (A) Principal component analysis. (B) Cluster analysis (ccc = 0.8573). For abbreviations, see Figure 1 caption. This figure is available in colour online at wileyonlinelibrary.com/journal/oa.

as *A. flammeus*, *T. alba*, *B. virginianus* and *A. cucularia*, are fairly similar, with the most abundant elements being mandibles, humeri, femurs and tibias, while ribs and autopodia elements were the least frequent ones. However, in terms of average relative abundance, the samples generated by *P. clamator* exhibited a wide range of values (Table 3), above and below the values for the others of species of Strigiformes (S1). Moreover, the average relative abundance of skeletal parts from micromammal assemblages generated by humans is low (13–33%), and the patterns clearly show a dominance of maxillars, humeri elements (Crandall & Stahl, 1995; Dewar & Jerardino, 2007).

Contrary to Falconiformes, carnivore mammals and humans (cf. Andrews, 1990; Andrews & Evans, 1983; Dewar & Jerardino, 2007), Strigiform birds usually ingest their prey whole, producing light-to-moderate breakage levels in skeletal elements (S1). The analyzed *P. clamator* samples showed light to moderate values (Table 5, S1).

In the three samples analyzed in this study and the experimental sample analyzed by Carrera & Fernández (2010), postcranial elements were better preserved (Table 2, S1). Likely, Andrews (1990), Gómez (2007) and Montalvo & Tejerina (2010) found that most of the assemblages derived from Strigiformes presented

higher proportions of these elements (S1). It is noteworthy that in three archaeological sites from central Chile, Saavedra (1994) observed that the micromammal assemblages presented more cranial elements in large-sized rodents and an equilibrium of these elements in small-sized rodents (Saavedra, 1994: Figure 2: 14). This differential pattern was attributed to the fact that the cranium of large rodents might have been separated before consumption of postcranial elements by humans. Moreover, Dewar & Jerardino (2007) registered a complementary pattern in the micromammal assemblage recovered from a Late Stone Age occupation site in Namaqualand, South Africa (KVS02) and an assemblage recovered from the abdominal cavity of a human skeleton nearby (GRM5). In the first case (KVS02), cranial remains almost without digestive modifications (0.6%) dominated, while in the second case (GRM5), only postcranial remains with high levels of digestive corrosion (52.5%, mainly in heavy category) and breakage (100%) were found (S1).

In general, both wild animals and humans generate micromammal assemblages in which proximal elements dominate, which is attributed to the fact that distal elements are more fragile (S1; Andrews, 1990; Dewar & Jerardino, 2007). Accordingly, it was observed that *P. clamator* tends to produce micromammal assemblages with loss of distal limb elements (Table 2, S1). Moreover, in coincidence to several species of Strigiform, the assemblages generated by *P. clamator* presented their teeth in the alveoli of maxillars and mandibles (Table 2, S1).

Following the classification proposed by Andrews (1990), the results allow us to place *P. clamator* mostly in the category of moderate modification. However, our analysis indicates that the taphonomic alterations produced by this owl also include the light, intermediate and heavy categories (Figure 5, S1). In that sense, tooth loss, breakage of teeth and average of relative abundance

showed the smaller modification values in all samples. The values of postcranial element breakage, the proportion of cranial elements with respect to postcranial elements (Index II) and the distal elements loss fall in the intermediate category. The remains affected by digestive corrosion, the proportion of breakage of mandibles and the proportion of cranial elements with respect to postcranial elements (Index I) fell in moderate category. Finally, cranial breakage was included within the heavy modification category, while it should be mentioned that this variable could be affected by the processing of pellet samples in the lab (see Methods). These categories differ markedly from humans, who fall within the highest modification category (extreme) of micromammal assemblages (Crandall & Stahl, 1995; Dewar & Jerardino, 2007).

Simonetti & Cornejo (1991) and Pardiñas (1999) proposed that archaeofaunistic assemblages from South America with a dominance of large-sized and predictable micromammals might be associated with human consumption. In that sense, numerous micromammal assemblages from archaeological sites in southern South America have been attributed to human consumption due to this feature and other taphonomic variables, such as cut marks, thermal alteration and skeletal part patterns (e.g. El Manzano 1, La Batea 1 [Simonetti & Cornejo, 1991], Arroyo El Gaucho 1 [Rivero *et al.*, 2008], Quebrada del Real 1 [Medina *et al.*, 2011], La Bellaca 2, Las Vizcacheras [Acosta & Pafundi, 2005], Laguna Grande [Lezcano, 1991], Cueva Tixi [Quintana, 2005], Angostura 1, [Fernández *et al.*, 2011], Cueva and Paredón Loncomán, Cueva Sarita IV [Pardiñas, 1999; Teta *et al.*, 2005], Cueva Grande del Arroyo Feo, Cueva de las Manos, Cerro de los Indios [Mengoni, 1983], Orejas de Burro, El Condor 1 [Pardiñas *et al.*, 2011]).

Nevertheless, at locations within PLNR and LRP, *P. clamator* preyed mainly upon large-sized micromammals

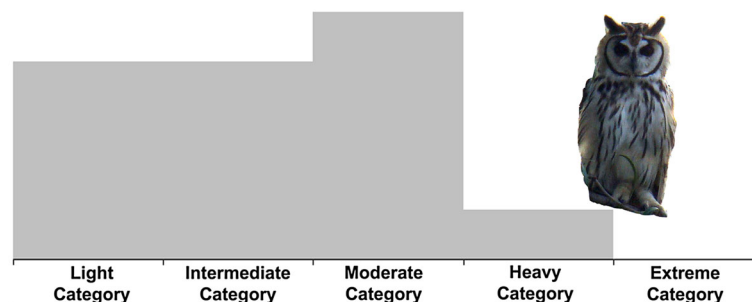


Figure 5. Bar diagram of *Pseudoscops clamator* categorization according to variables considered (cf. Andrews, 1990). This figure is available in colour online at wileyonlinelibrary.com/journal/oa.

(Tables 1 and 2). Coincidentally, the dominance of large-sized prey such as *L. crassicaudata*, *C. aperea*, *H. brasiliensis* and *Rattus* spp. in the diet of *P. clamator* has already been mentioned in the literature (e.g. Massoia, 1988; Isaach *et al.*, 2000; Pautasso, 2006; Baladrón, 2008). This tendency in predatory patterns was probably facilitated by the large size and robustness of the beak and hindlimbs (see Motta-Junior, 2006), a feature uncommon among other South American Strigiformes of comparable body mass (e.g. *A. flammeus*, *T. alba*). In that sense, it is suggested that the digestive corrosion marks, patterns of breakage and relative abundance of skeletal parts might be the main attributes to be used in the differentiation of this taphonomic agent, from humans.

Conclusions

From the taphonomic variables analyzed, it can be suggested that *P. clamator* is borderline between intermediate and moderate modification categories, coincident with the upper limit of the 'Strigiformes model', such as *A. cunicularia* and *Bubo* spp. (Andrews, 1990; Montalvo & Tejerina, 2009).

Fossil assemblages rich in postcranial remains from large-sized micromammals may be associated with humans acting as agents of accumulation. However, the evidence presented in this study demonstrated that *P. clamator* is able to produce assemblages of large-sized micromammal postcranial remains, which introduces an equifinality problem. In that sense, digestive corrosion marks, breakage patterns and the relative abundance of skeletal remains are the main attributes to differentiate this owl from humans, as agents of accumulation.

Finally, our results might serve as an analytical model for the taphonomic interpretation of the fossil record of micromammals from paleontological and archaeological sites, which fall within the distributional range and habitat of *P. clamator*.

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