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# Taphonomy of modern communal burrow systems of the Plains vizcacha (*Lagostomus maximus*, Chinchillidae) in the Pampas region of Argentina: implications for the fossil record

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## ABSTRACT

The Plains vizcacha (*Lagostomus maximus*) is one of the largest rodents in South America. They live in communal burrow systems (vizcacheras) shaped by complex subterranean galleries which produce a strong impact on the local landscape. This paper presents the results of an actualistic study conducted with abandoned vizcacheras from the Pampas region of Argentina. The main objective is to evaluate the role of this rodent in the formation of the fossil record. Results indicate that the Plains vizcacha is responsible for the mixing, accumulation, and transport of materials; such as sticks, caliche, dung, feces, and abundant bone remains. Their burrowing activity and the accumulating habits, modifies the landscape, creating environments conducive to the buildup of objects and the reuse by different animals. These characteristics result in very complex associations of materials of different origins; making this rodent an important taphonomic agent with the potential to significantly impact the fossil record.

## ARTICLE HISTORY

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*Lagostomus maximus*;  
vizcacheras; burrow;  
bioturbation

## Introduction

Burrowing mammals are well known to produce significant modifications to the paleontological and archaeological record, including the vertical and horizontal movement of material across stratigraphic layers, and the accumulation of variable objects (Wood and Johnson 1978; Stein 1983; Erlandson 1984; Bocek 1986, 1992; Johnson 1989, 1990; Durán 1991; Pierce 1992; Fowler et al. 2004; Zeitoun et al. 2010; Mallye 2011; Horwitz et al. 2012; Pelletier et al. 2017). The Plains vizcacha (*Lagostomus maximus*) is a large extant burrowing rodent from South America that occupies semiarid scrub and grasslands of the central and northern parts of Argentina, southeastern Bolivia, and southern Paraguay. Similar to other species such as the North American beaver (*Castor canadensis*) and prairie dogs (*Cynomys ludovicianus*), the Plains vizcacha are ecosystemic engineers (Jones et al. 1994; Ceballos et al. 1999; Arias et al. 2005; Nummi and Hahtola 2008). One of the particularities of the Plains vizcacha is their ability to create communal burrow systems (called 'vizcacheras'), where the family group lives. The size and depth of the vizcacheras varies according to the sedimentary characteristics, as well as the duration of occupation by the Plains vizcacha. The burrows typically range from 12 cm to 1 m diameter, and as deep as 2 m below the surface (Jackson et al. 1996). The distance between the vizcacheras and the total area also varies, with an average area of 30 m<sup>2</sup> (Arias et al. 2005). The vizcacheras are

normally located on elevated grounds, close to bodies of water. These ecological niches constructed by this rodent are usually reused by small carnivores, reptiles, and birds.

The Plains vizcacha is a soil-disturbing vertebrate capable of displacing a large volume of sediment during the construction of their burrows. The burrowing activity causes a long-term impact on the local vegetation, the denudation and infiltration of water in soils (Branch et al. 1996; Campos 1997; Arias et al. 2003, 2005), and produces changes in the chemical composition of soil, particularly associated with increased phosphorous (P) levels attributed to horizontal and vertical transport of caliche (Kelt 2011; Platt et al. 2016). They also transport locally available materials around the burrows. It is frequent to find abundant material remains such as sticks, rocks, bones, animal dung, and metallic and plastic objects used to mark their territory, elevate burrow entrance to prevent flooding, attracting mates or limiting access to other animals (Hudson 1872; Llanos and Crespo 1952; Weir 1974; Jackson et al. 1996; Villarreal et al. 2008).

Plains vizcacha fossil bones have been identified from the Middle to Late Pleistocene in Argentina and Brazil (Tonni and Fidalgo 1982; Prado et al. 1987; Vucetich and Verzi 1995; Kerber et al. 2011), and the Late Pleistocene in Uruguay (Ubilla and Rinderknecht 2016). During the Holocene, there is abundant evidence that the Plains vizcacha was a sustainable food resource for hunter-gatherer groups from the Pampas region of Argentina (Martínez and Gutiérrez 2004). In the eastern area of

the Tandilia Hills, butchering evidence in archeological sites such as Cueva Tixi, Cueva El Abra, and Lobería 1, suggests that the Plains vizcacha was a predictable resource for hunter-gatherers (Mazzanti and Quintana 2001; Quintana et al. 2003; Quintana and Mazzanti 2011). In this sector, towards the end of the Late Holocene, the faunal record indicates a change in the subsistence strategy, with an increase in the use of this prey and other small-sized animals (Quintana and Mazzanti 2001; Quintana et al. 2003; Mazzanti et al. 2010; Quintana and Mazzanti 2011, 2014). The Plains vizcacha was also exploited in the inter-sierra grasslands, however with less intensity. Archaeological sites such as Calera, Campo Laborde, Claromecó 1, Empalme Querandíes, Las Brusquillas 3, Laguna Tres Reyes, and Paso Otero 3 and 4 (Martínez et al. 2001; Salemmé and Madrid 2007; Bonomo et al. 2008; Politis and Messineo 2008; Álvarez 2009, 2014; Álvarez et al. 2013; Massigoge et al. *Forthcoming*) suggest this rodent was a complementary resource, similar to that of other small sized vertebrates such as armadillos, coypu, carnivores, and birds. In other areas of the Pampas region (North, Salado depression, and the southern Ventana Hills) there is minimal evidence of exploitation of Plains vizcacha (Escosteguy 2012).

Burrows in the fossil record are usually identified by direct (detection of chambers and tunnels during excavation) or indirect evidence (rodent bone, feces, tooth marks, etc.). For example, in the paleontology locality Puente Vanoli, Quequén Salado River (southern Pampas region), the infilling of a small cavity found in Holocene sediments contained an accumulation of mammals (marsupials and rodents) and reptiles (snakes); which, based on the taphonomic analysis of the assemblage, was interpreted as a Plains vizcacha burrow (Tomassini et al. 2016).

In an attempt to understand the effects of burrowing on the archaeological and paleontological record, researchers have undertaken actualistic studies of different mammals, including Pocket gophers *-Thomomys bottae-* (Bocek 1986,

1992; Johnson 1989), Tuco-tuco *-Ctenomys sp.-* (Durán 1991), armadillos *-Euphractus sexcintus-* (Araujo and Marcelino 2003) and *-ChaetophRACTUS villosus-* (Frontini and Escosteguy 2012), European rabbit *-Oryctolagus cuniculus-* (Pelletier et al. 2016), Badger *-Meles meles-* (Mallye et al. 2008), and Porcupine *-Hystrix sp.-* (Rabinovich and Horwitz 1994). While most authors agree that these mammals affect the spatial patterning of fossil material, others argue that faunalurbation in certain cases may promote preservation, through small spatial burial (Van Nest 2002; Morin 2006; Tomassini et al. 2016). Faunalurbation may also assist in the discovery of buried deposits; by bringing smaller artifacts upward to the surface (Pierce 1992, p. 205).

In the Pampas region, because the Plains vizcacha normally select areas for the construction of their burrows on elevated grounds close to bodies of water, settings also preferred for hunter-gatherers camp sites, vizcacheras may occasionally superimpose with archaeological sites, producing the mixture (faunalurbation) of natural and cultural remains (Salemmé 1987). In these sites, without clear evidence of human processing, determining the natural, cultural, or mixed origin of the Plains vizcacha or other small vertebrate bones can be difficult (Salemmé et al. 2012). While the Plains vizcacha role in the formation of archaeological sites of the Pampas region has been studied by previous researchers (Lanzelotti and Bonaparte 2009; Escosteguy 2012; Salemmé et al. 2012); until now, with the exception of a few preliminary studies (Curetti 2008; Bellinzoni and Kaufmann 2014), no systematic actualistic study has been available which evaluates the taphonomic action of this rodent on the fossil record. This paper presents the results of an actualistic study performed with recently abandoned vizcacheras situated in the archaeological locality Arroyo Seco, Tres Arroyos County, Province of Buenos Aires (Figure 1). The main objectives of this work are to characterise the impact that burrowing habits have in the landscape, especially in archaeological sites; to evaluate

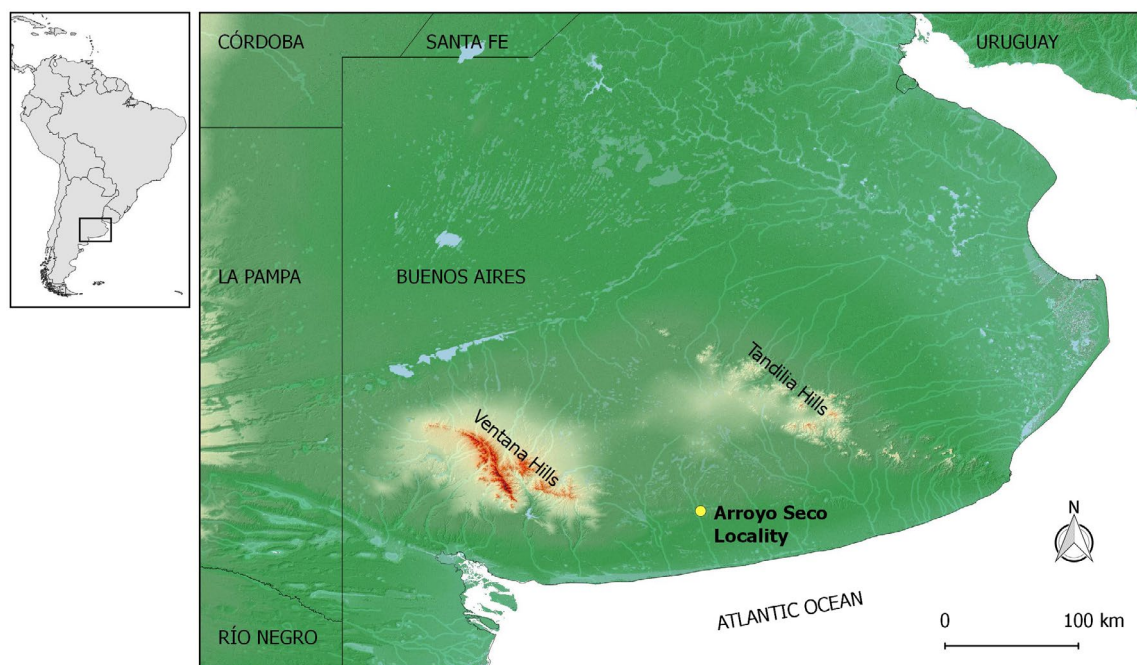


Figure 1. Map of the Pampas region of Argentina showing the location of the Arroyo Seco locality. Source: Author

how the Plains vizcacha intervenes in the accumulation, mixing and dispersion of material, and the implications of this behavior in the formation of the fossil record; and to determine relevant criteria for the identification of vizcacheras in the fossil record.

### The Plains vizcacha

The Plains vizcacha is an herbivorous rodent that lives in social groups integrated by 10–30 individuals. They share a communal burrow system -vizcachera- that sometimes extends over several generations (Llanos and Crespo 1952; Branch 1993). The social group is made up of female kin and immature, with just one to three adult males (Branch 1993). The female kin group resides permanently in the vizcacheras. Young individuals remain underground for several weeks, and will begin to forage with adult females shortly after they emerge from the burrow (Branch et al. 1993). The length of the head to the tail is 47–66 cm; and the length of the tale is 15–20 cm. These rodents present a remarkable sexual dimorphism that is manifested mainly in the size, coat color, and whiskers (Llanos and Crespo 1952). Females weigh up to 5 kg, and males up to 9 kg (Jackson et al. 1996; Branch et al. 1999; Chebez et al. 2014). Life expectancy for the Plains vizcacha is between 7 and 8 years (Llanos and Crespo 1952; Jackson et al. 1996).

The Plains vizcachas are nocturnal herbivores, feeding on grasses, shrubs, and seeds around the burrows. Their foraging radius can reach as much as 400 m from the central chamber. Predation is an important source of mortality; both inside and outside the burrow (Branch et al. 1993). This rodent has natural predators such as carnivores (felids and canids), reptiles (e.g. *Boa constrictor*) and birds of prey (e.g. *Bubo virginianus*) (Parera 2003). Male Plains vizcacha are particularly vulnerable

to predation during their solitary movements, and are also more prone to injury from territorial conflicts (Branch et al. 1993). Females and young individuals benefit from group protection while in the burrows and during group dispersal (Branch et al. 1993).

In the grasslands of Argentina, the Plains vizcacha is subject to eradication programs because it is considered a pest, capable of large-scale disruption of farmland, and food competitor for domestic stock; which consequently has led to a substantial decrease in population (Rendel 1990; Martella et al. 1996; Navarro et al. 1997; Branch et al. 1999; Pereira and Quintana 2009; Chebez et al. 2014). Likewise, human populations that inhabit rural sectors of Argentina continue to hunt the Plains vizcacha for meat (Escosteguy 2012).

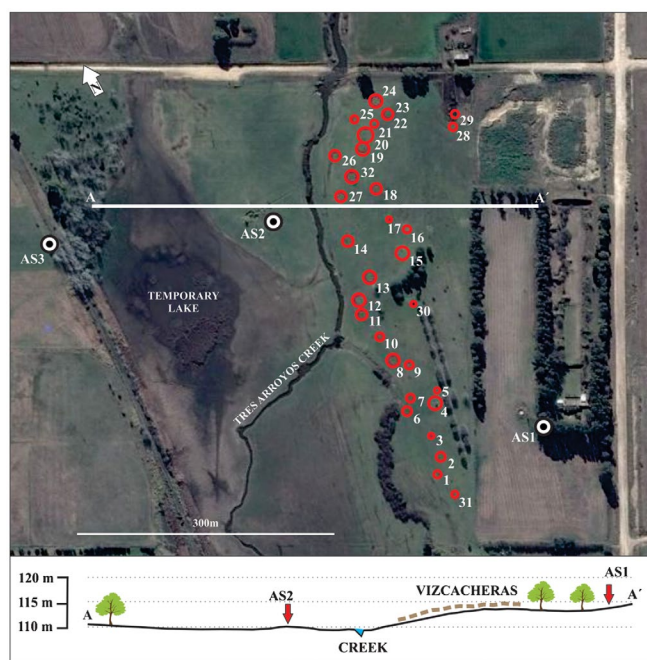
## Materials and methods

### The Arroyo Seco locality

The studied vizcacheras are located along an elongated ridge with subsurface sedimentary caliche rock, in the inter-sierra grasslands of the Pampas region. The area corresponds to municipality owned property near the archaeological locality Arroyo Seco (38°21'38"S, 60°14'39"W) (Figure 2). No agricultural activity is permitted on the land; however it is occasionally put on loan to local farmers for domestic animal grazing, specifically cows and sheep. Phytogeographically, this locality is included in the Southern Domain of the Pampean Province (Cabrera 1976) and zoogeographically, in the Pampas Domain of the Guayano-Brazilian Region (Ringuelet 1961).

The Arroyo Seco 1 site was excavated during the 1970s and 1980s, when abundant stone tools and three human burials were recovered. Systematic excavation at the site identified significant bioturbation by *L. maximus* (Politis 2014). At the Arroyo Seco 2 site, a total of 314 m<sup>2</sup> has been excavated. Here archaeological material encompasses successive episodes of occupations from the Late Pleistocene to early post-Hispanic times (Politis and Steele 2014). Archaeological bone remains at this site include 33 human burials (Politis et al. 2014), extinct Pleistocene fauna (Politis et al. 2016), and extant mammals and birds (Salemme 2014; Rafuse 2017). While 36 bone specimens of *L. maximus* were identified, there is no clear evidence of butchering for this species (Rafuse 2017). The Arroyo Seco 3 site has yet to be systematically excavated.

In 2014, a total of 37,000 m<sup>2</sup> was surveyed in an area of inactive vizcacheras. The vizcacheras were inactive as a result of a local eradication program conducted 12 months earlier than this study. Each vizcachera was spatially identified based on the presence of a central chamber and burrow entrances, and its seclusion in relation to other vizcacheras. In a first instance, the position of each vizcachera was georeferenced, the maximum length and width were measured, and the total number of burrow entrances was counted. The different materials associated with each assemblage were recorded, and all bones associated with the vizcacheras were collected for analysis in the laboratory. Two vizcacheras (#1 and #5) were selected to systematically map with a total station (Figure 2). Additionally, in one of the vizcacheras (#32), a trench measuring 3 m long, 0.5 m wide, and 1.5 m deep was excavated to explore the effect of the burrows on



**Figure 2.** The Arroyo Seco locality. Upper image: Google Earth (2016) image showing the location of vizcacheras (circles) in relation to the Arroyo Seco 1 (AS1), Arroyo Seco 2 (AS2), and Arroyo Seco 3 (AS3) sites. Lower image: Elevation profile of the Arroyo Seco locality. Topographic profile along line A–A'.

the stratigraphic profile, and to evaluate the presence of buried materials. Finally, to study if there were buried materials around the burrow entrances; a 1 m<sup>2</sup> excavation unit was dug in six of the vizcachas (#2, #5, #7, #12, #17 and #27) at a depth of 10 cm. In both the trench and the excavation units, all the sediment was water screened with a 0.5 mm sieve mesh.

### Bone analysis

#### Taxonomic determination

The bones were separated in two samples: surface and buried (including trench and excavation units); and taxonomic determination was performed for both samples. According to the local vertebrate populations (Parera 2003; Chebez et al. 2014) and the analyzed bone assemblage, three body size categories were used: small-sized vertebrates (<1 kg), medium-sized vertebrates (1–20 kg), and large-sized vertebrates (>20 kg).

#### Anatomical representation

The number of bone specimens identified by taxon (NISP) and the minimum number of individuals (MNI) was obtained for both the surface and the buried assemblages. MNI was calculated using the frequency of the most abundant anatomical element, and considering laterality and bone fusion (Andrews 1990). Additionally, we estimated the skeletal part profile of the Plains vizcacha calculating the minimum number of elements (MNE) and the relative abundance ( $R_i$ ) (Andrews 1990). For the  $R_i$ , we used the proportional relation between the number of times a determined element was present ( $N_i$ ), and the expected number of this element ( $E_i$ ) in relation to the minimum number of individuals (MNI): [ $R_i = N_i/MNI \times E_i$ ] (Andrews 1990, p. 45). A Spearman's  $r_s$  test was generated in PAST 3.16 (Hammer

et al. 2001) to first compare the relative abundance between four vizcachas in the Arroyo Seco locality, and later to discuss the results of this locality with assemblages generated by different predators, including data from two captive small-sized carnivores, *Leopardus geoffroyi* and *Lycalopex gymnocercus* (Álvarez et al. 2012; Rafuse et al. 2014), and nest accumulations of the raptor bird, *Aquila chrysaetos* (Lloveras et al. 2017). These assemblages were chosen because they represent non-ingested remains originated by native predators or foreign analogous species.

Additionally, proportions of skeletal elements for the Plains vizcacha surface assemblage were calculated using the following ratios:

- Measurement of the proportion of cranial elements in relation to postcranial:  $PCRT/CR = [(femur + humerus)/(mandible + maxilla)] \times 100$  (Andrews 1990), and  $PCRAP/CR: [(humerus + radius + ulna + femur + tibia) \times 20/((mandible + maxilla + isolated molars) \times 10)] \times 100$  (modified from Fernández-Jalvo and Andrews 1992, considering the dental formula of the Plains vizcacha).
- Measurement of the proportion of distal limb elements in relation to proximal limb elements:  $Z/E = [(tibia + radio)/(femur + humerus)] \times 100$  (Andrews 1990).
- Measurement of the proportion of elements from the anterior limbs in relation to the posterior limbs:  $AN/PO = [(humerus + radius + ulna) \times 4/((femur + tibia) \times 6)] \times 100$  (modified from Lloveras et al. 2008).
- Measurement of the proportion of the postcranial axial skeleton in relation to the appendicular skeleton:  $AX/AP = [(vertebras + ribs) \times 10/((humerus + ulna + radius + femur + tibia) \times 71)] \times 100$  (modified from Álvarez et al. 2012).

**Table 1.** Diversity of taxa associated with vizcachas.

Taxa	Surface sample	MNI	Buried sample	MNI	Total
Small vertebrate					
<i>Corydoras paleatus</i> (Peppered catfish)	1	1			1
Anura	7	1	2	1	9
Colubridae			1	1	1
Aves	6	n/a	1	n/a	7
Passeriformes			5	1	5
Rodentia	9	n/a	12	n/a	21
Cricetidae	2	1			2
<i>Akodon azarae</i> (Grass mouse)	1	1			1
Medium vertebrate					
Canidae	1	1			1
<i>Canis familiaris</i> (Dog)	2	1			2
<i>Lagostomus maximus</i> (Plains vizcacha)	446	31	67	3	513
<i>Didelphis albiventris</i> (White-eared opossum)	1	1			1
<i>Chaetophractus villosus</i> (Hairy armadillo)	1	1			1
Large vertebrate					
<i>Bos taurus</i> (Cow)	4	1			4
<i>Lama guanicoe</i> (Guanaco)	1	1			1
<i>Ovis aries</i> (Sheep)	2	1			2
<i>Equus caballus</i> (Domestic horse)	3	1			3
Indeterminate small or medium mammal*	2	n/a	1	n/a	3
Indeterminate large mammal*	16	n/a			16
Indeterminate vertebrate*	95	n/a	39	n/a	134
Total	600		128		728

Reference: \* = Not included in taphonomic analysis. n/a = not applicable.

### Age structure

In order to establish the age structure from the Plains vizcacha bone assemblage, we used the methodology described by O'Connor and O'Connor (2000, p. 94–95), which considers the skeletal fusion state. In our analysis, we grouped the sample into an early fusion group and a late fusion group. Although there is currently no bone fusion schedule for the Plains vizcacha, the relative fusion sequence is similar for all mammals (Barone 1999). Using the established fusion schedule of European rabbit (*Oryctolagus cuniculus*) (see Jones 2006: Table 1); we considered three age groups:

- 'newborns' aged <3 months; characterised by the unfused distal epiphysis of the humerus and tibia.
- 'juveniles and subadults' aged between 3 and 9 months; characterised by the difference between the proportion of unfused elements of the late fusion group (adult to old), and the proportion of unfused elements of the early fusion group (newborn), assuming that the specimens of both fusion groups derive from the same population (O'Connor and O'Connor 2000).
- 'adults to old' aged >9 months; characterised by the full fusion of the proximal epiphysis of the humerus and tibia.

### Estimation of sex

According to Llanos and Crespo (1952; see also Rasia and Candela 2013; Ubilla and Rinderknecht 2016), the size of the skull and mandible of the Plains vizcacha shows a notable difference between males and females. Male skulls are found to be larger in most dimensions (Ubilla and Rinderknecht 2016). In order to estimate the sex-ratios of the Plains vizcacha bone assemblage, we measured the total length (TL) and the height of skull (Hsk) for both the surface and buried samples. All measurements were taken using a digital caliper (accuracy: 0.01 mm) by a single analyst. Results were compared with reference material of extant male and female *Lagostomus maximus* (Ubilla and Rinderknecht 2016: Online supplementary data 1–7).

### Taphonomy

Taphonomic variables included in this analysis are: degree of completeness of the bone (1–25, 25–50, 50–75, 75–99, and 100%), weathering stage (Behrensmeyer 1978; Andrews 1990), carnivore tooth marks -punctures, pits, scoring, crenulated edges, and furrows- (Haynes 1980; Binford 1981), sedimentary abrasion (Gutiérrez and Kaufmann 2007), bone fracture state -dry and fresh- (Johnson 1985), shape of bone fracture -helical, diagonal, steeped, irregular, transverse, and longitudinal- (Johnson 1985), lichens (Fernandez-Jalvo et al. 2002), trampling marks (Domínguez-Rodrigo et al. 2009), rodent marks (Shipman 1981; Johnson 1985), bone staining produced by the sedimentary matrix, root marks (Andrews 1990), brownish-green spots -related to the deposit of mosses and lichens-, and chemical deterioration (Gutiérrez and Johnson 2014). Taphonomic observations were conducted with the naked eye and through a stereomicroscope (10–40X). In specific cases where the bones overall structure or cortical surface was heavily damaged; the taphonomic variable was classified as indeterminate. For example, in some cases the degree of completeness was not identified

because the specimens presented a very low integrity and the original anatomical element was unknown. Another example is specimens where weathering was masked by other processes. In these cases, the weathering stage could not be estimated.

## Results

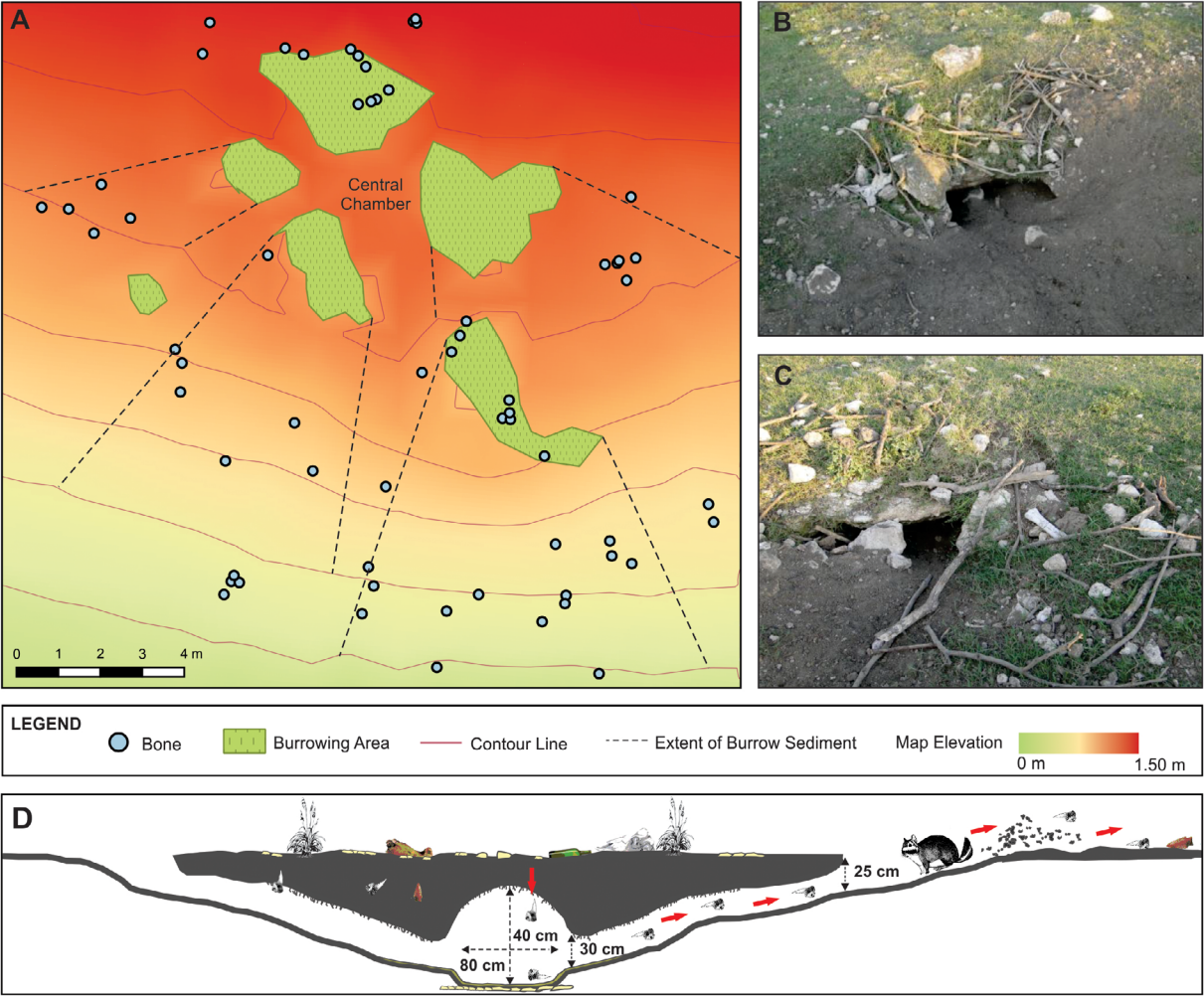
### General characteristics of the vizcacheras

A total of 32 vizcacheras were identified. The vizcacheras were integrated by 226 burrow entrances and covered a total area of 4730 m<sup>2</sup>. The average size of the vizcacheras was 149 m<sup>2</sup>, each containing on average 7 burrow entrances. Although certain variability exists in the structure of the burrows; in general, a centripetal arrangement was observed, where galleries converge into a central chamber (Figure 3). Outside the burrow entrances, slightly elevated sediment corresponds to backfill accumulated during burrow excavations by the Plains vizcacha. Many of the vizcacheras created large bare patches and dissimilar vegetation growth. In some cases, the vizcacheras were built in sectors of the landscape where the bed rock (caliche) was close to the surface. In these cases, the rocks formed part of the burrow entrance. Numerous burrows were found collapsed, forming large depressions in the landscape (Figure 4).

The majority of the associated materials in the surface sample were located directly outside the burrow entrance. In 93.7% ( $n = 30$ ) of the vizcacheras, we recovered bones; followed by caliche (62.5%;  $n = 20$ ), large-sized domestic animal dung (50%;  $n = 16$ ), sticks (37.5%;  $n = 12$ ), small-sized carnivore feces (15.6%;  $n = 5$ ), lithic artifacts (9.4%;  $n = 3$ ), and plastic items (3.1%;  $n = 1$ ). Two bird nests were found, one from an indeterminate passerine, and another identified as Anatidae. Also, in two of the vizcacheras, we observed the presence of Burrowing owls (*Athene cunicularia*) and pellets which are currently being processed.

In the excavated trench and units, we identified substantial bioturbation, including numerous galleries at various depths (Figure 5). Only bones, caliche, and a metal piece were found in the buried sample.

A NISP of 728 bone specimens were recovered in the surveyed area, of which 82% ( $N_{taxa} = 14$ ) could be determined at the taxonomic level (Table 1). There is a higher frequency of mammals (78%;  $n = 571$ ), followed by birds (2%;  $n = 13$ ), amphibians (1%;  $n = 9$ ), fish (0.5%;  $n = 1$ ), and reptiles (0.5%;  $n = 1$ ). In terms of body size categories, specimens from all categories were recovered on the surface, while only small and medium-sized vertebrates were present in the buried sample. It is important to mention that some small sized vertebrates were identified to the Rodentia order, but given their size and shape, were not classified as *Lagostomus maximus*. These specimens likely correspond to smaller sized rodents like the grass mouse or other cricetids from the area. The majority of the bones in both the surface and the buried samples correspond to medium-sized vertebrates, given that the most frequent species was the Plains vizcacha, which represents 70% ( $n = 513$ ) of the total number of vertebrate remains, and 90% of the total number of mammals. Most of the vizcacheras (78%;  $n = 25$ ) contained at least one Plains vizcacha bone. All of the species identified in the survey area are still present in the local fauna, with the exception of the guanaco (*Lama guanicoe*), which retracted towards western and southern regions of



**Figure 3.** Vizcacheras from the Arroyo Seco locality. (A) Spatial distribution of vizcachera (#1) with multiple burrow entrances and associated bone remains. (B and C) Examples of vizcachera burrow entrances with bones, caliche, and sticks. (D) Vertical reconstruction model of a vizcachera, depicting the bone cycle, and dimensions of the galleries, and the central chamber.



**Figure 4.** Collapsed vizcacheras from the Arroyo Seco locality. Source: Author



**Figure 5.** Excavated trench. (A) trench; (B) profile of trench with intercepted burrows. Source: Author

**Table 2.** Relative frequencies of taphonomic modifications in surface sample.

Taphonomic variables	Small vertebrates ( <i>n</i> = 26)		Medium vertebrates ( <i>n</i> = 451)		Large vertebrates ( <i>n</i> = 10)		Total ( <i>n</i> = 487)	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Bone completeness								
<25%	2	7.7	85	18.8	1	10	88	18.1
25–50%	4	15.4	84	18.6	0	0	88	18.1
50–75%	2	7.7	53	11.7	2	20	57	11.7
75–99%	1	3.8	84	18.6	2	20	87	17.9
100%	12	46.2	140	31.1	3	30	155	31.8
Indeterminate	5	19.2	5	1.1	2	20	12	2.5
Weathering stage								
0	24	92.3	143	31.7	3	30	170	34.9
1	1	3.8	246	54.5	0	0	247	50.7
2	0	0	44	9.7	2	20	46	9.4
3	0	0	12	2.7	2	20	14	2.9
4	0	0	4	0.9	0	0	4	0.8
5	0	0	0	0	1	10	1	0.2
Indeterminate	1	3.8	2	0.4	2	20	5	1
Carnivore marks								
Specimens with marks	1	3.8	40	8.7	0	0	41	8.4
Puncture	1	100	7	17.5	0	0	8	19.5
Pitting	1	100	18	45	0	0	19	46.3
Scoring	0	0	32	80	0	0	32	78
Furrows	0	0	2	5	0	0	2	4.9
Crenulated edge	0	0	7	17.5	0	0	7	17
Sedimentary abrasion	2	7.7	42	9.3	0	0	44	9.03
Bone fracture								
Specimens with fractures	14	53.8	311	69	7	70	332	68
Helicoidal	1	7	4	1.3	0	0	5	1.5
Diagonal	1	7	8	2.6	0	0	9	2.7
Steeped	0	0	9	2.9	0	0	9	2.7
Irregular	8	57	234	75.2	6	86	248	74.7
Transversal	4	28.5	10	3.2	0	0	14	4.2
Longitudinal	0	0	46	14.8	1	14	47	14.2
Fresh	1	7	12	4	0	0	13	4
Dry	13	93	299	96	7	100	319	96
Lichens	1	3.8	135	29.9	4	40	140	28.7
Trampling marks	1	3.8	108	23.9	2	20	111	22.8
Rodent marks	1	3.8	21	4.7	0	0	22	4.5
Bone staining	1	3.8	27	5.9	2	20	30	6.2
Root marks	4	15.4	17	3.8	2	20	23	4.7
Brownish-green spots	1	3.8	132	29.3	1	10	134	27.5
Chemical deterioration	0	0	3	0.7	0	0	3	0.6

Reference: *n* = number of specimens.

Argentina during the Late Holocene (Tonni and Politis 1980; Politis and Pedrotta 2006; Politis et al. 2011).

### Surface sample

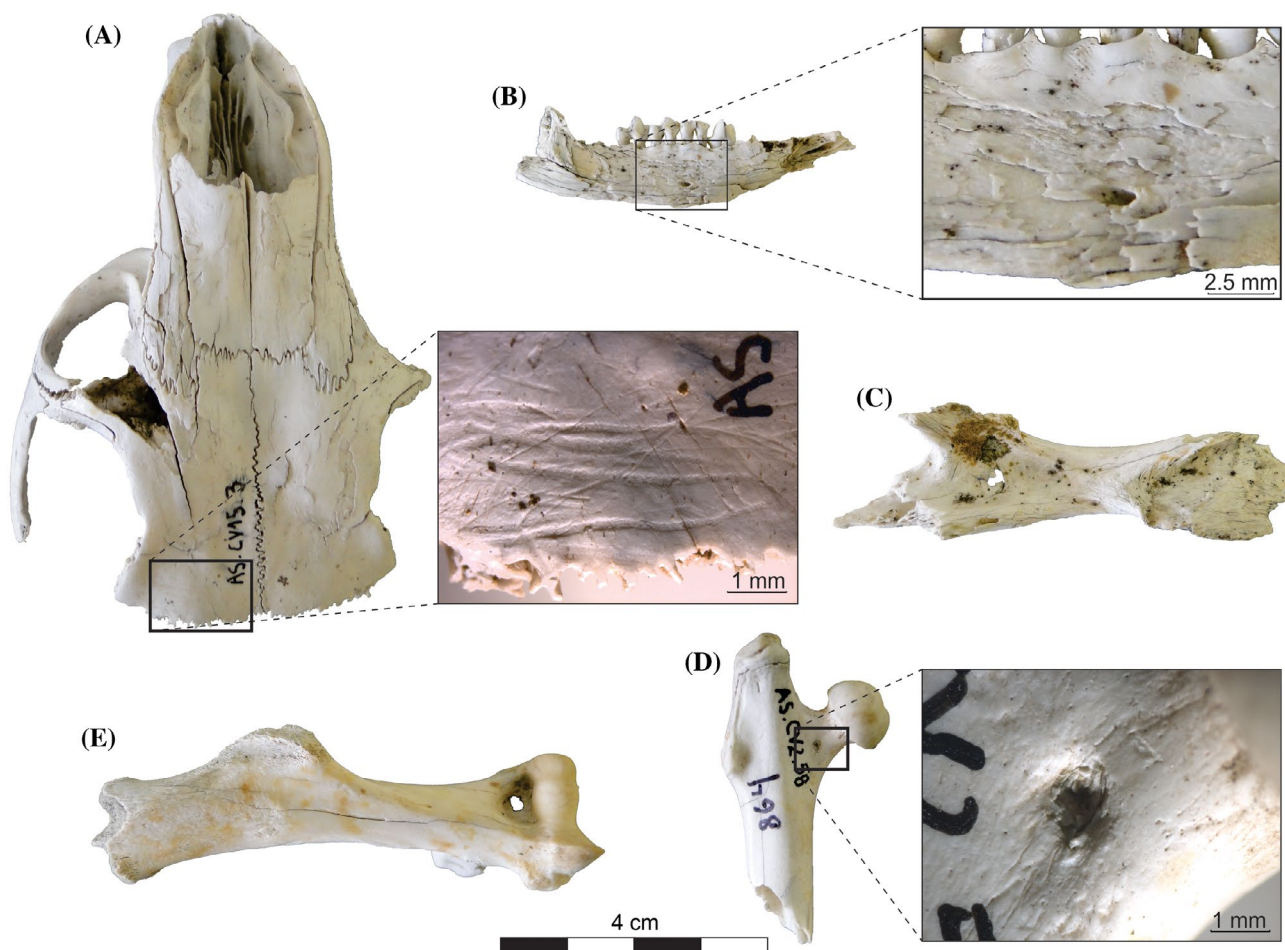
Table 2 presents the results of the taphonomic modifications observed in the surface sample. In terms of bone fragmentation, results show that 31.8% ( $n = 155$ ) are complete, while the remaining completeness percentage ranges are distributed equally between 11.7 and 18.1%. Given that the majority of specimens correspond to medium-sized taxon, this size category presented a similar pattern (31.1% complete; and completeness percentage ranges between 11.7 and 18.8%). Small-sized taxon contained a higher percentage of complete bones (46.2% complete), and a more extensive distribution of completeness percentage ranges (between 3.8 and 15.4%). The large-sized taxon presents equal percentages throughout, in both complete (30%) and fragmented bone (between 10 and 20%). In all of the size categories, 96% ( $n = 319$ ) are dry fractures, and the most frequent shape of bone fracture is irregular (74.7%;  $n = 248$ ).

Weathering was observed in 65% ( $n = 317$ ) of the bone specimens; 79% ( $n = 247$ ) corresponds to weathering stage 1. Only the medium and large-sized taxa presents a weathering stage  $\geq 2$ , and just one large-sized specimen showed weathering stage 5 (Figure 6).

Carnivore tooth marks were identified in 8.4% ( $n = 41$ ) of the bones. With the exception of one small-sized specimen, all the carnivore marks were observed in medium-sized taxa, especially Plains vizcacha (Figure 5). The most frequent type of marks are scoring (80%;  $n = 32$ ), followed by pitting (45%;  $n = 18$ ), punctures (17.5%;  $n = 7$ ), crenulated edges (17.5%;  $n = 7$ ), and furrowing (5%;  $n = 2$ ). Lichens were found on the cortical surface of 28.7% ( $n = 140$ ) of the bones, as well as brownish-green spots in 27.5% ( $n = 134$ ). Trampling marks were observed in similar percentages (22.8%;  $n = 111$ ). The remaining modifications identified in the surface sample presented low percentages (<10%). Manganese (Mn) staining, not shown in Table 2, was recorded in <1% of sample (Figure 6).

To evaluate if it is appropriate to combine the entire surface sample for quantification of the skeletal representation, we compared the  $R_i$  of the 4 vizcacheras with the most abundant number of Plains vizcacha remains (Table 3). All correlations comparing set pairs of vizcacheras (Spearman's  $r_s$  statistic) were high and statistically significant ( $p < 0.05$ ) (Table 4). This result suggests that all the vizcacheras share a general pattern in bone survival, and validates the grouping of the entire surface sample.

Taking into consideration the fusion and laterality of the acetabulum (MNE = 60), a MNI of 31 Plains vizcachas was calculated for the surface sample (Table 5). The most abundant



**Figure 6.** Examples of taphonomic modifications identified in the surface sample. (A) Plains vizcacha skull with detailed image of trampling marks; (B) White-eared opossum hemi-mandible with detailed image of stage 3 weathering; (C) Plains vizcacha pelvis with lichens; (D) Plains vizcacha femur with detailed image of a carnivore puncture; (E) Plains vizcacha humerus with brownish-green spots.

**Table 3.** Skeletal representation from 4 of the vizcacheras.

Element	Vizcachera 4			Vizcachera 5			Vizcachera 8			Vizcachera 15		
	NISP	MNE	$R_i$	NISP	MNE	$R_i$	NISP	MNE	$R_i$	NISP	MNE	$R_i$
Skull (maxilla)	4	2	33.3	1	1	20	2	2	16.7	2	1	10
Mandible	1	1	16	2	1	20	5	4	33.3	6	6	60
Incisor	0	0	0	2	1	5	1	1	4.2	1	1	5
Vertebra	6	6	2.4	14	13	6.1	15	10	3.9	7	7	3.3
Rib	1	1	0.7	3	3	2.5	0	0	0	0	0	0
Scapula	1	1	8.3	2	2	20	0	0	0	0	0	0
Humerus	3	3	25	4	4	40	7	7	58.3	5	4	40
Radius	2	2	16.7	0	0	0	2	2	16.7	0	0	0
Ulna	4	4	33.3	2	1	10	1	1	8.3	2	2	20
Pelvis	15	11	91.7	11	8	80	9	6	50	4	4	40
Femur	7	6	50	6	5	50	8	7	58.3	6	6	60
Tibia	16	9	75	5	5	50	6	6	50	6	6	60
Calcaneus	0	0	0	3	3	30	2	2	16.7	0	0	0
Metapodial	5	5	5.9	2	2	2.8	1	1	1.2	1	1	1.4
Total	65			57			59			40		

**Table 4.** Statistical correlations comparing set pairs of vizcacheras.

	Vizcachera 5	Vizcachera 8	Vizcachera 15
Vizcachera 4	$r_s = 0.62, p = 0.016$	$r_s = 0.67, p = 0.007$	$r_s = 0.68, p = 0.006$
Vizcachera 5		$r_s = 0.74, p = 0.002$	$r_s = 0.66, p = 0.009$
Vizcachera 8			$r_s = 0.76, p = 0.001$

anatomical parts are the pelvis, femur, and tibia ( $R_i$  between 75 and 100%); followed by the humerus ( $R_i$  between 50 and 75%); mandible, skull, and sacrum ( $R_i$  between 25 and 50%). The vertebrae, metapodial, ulna, radius, scapula, astragalus, and calcaneus present  $R_i$  percentages between 1 and 25%. Bones with a  $R_i$  of <1% or absent include the phalanges, ribs, fibula, clavicles and patella.

Considering just the Plains vizcacha bones with a  $R_i$  between 50 and 100%, some differences in intra-elemental bone survival is observed. In the humerus, there is a similar representation of the shaft (56%) and distal epiphysis (42%), and a complete absence of the proximal epiphysis. The femur presents a high  $R_i$  for the shaft (84%) compared to the distal epiphysis (16%) and proximal epiphysis (13%). This pattern of differential representation is also observed in the tibia, where the shaft (89%) is more frequent than the distal epiphysis (50%) and proximal epiphysis (13%). In the pelvis, the acetabulum and the ilion present a high  $R_i$  (>95%), followed by the isquion (71%) and pubis (47%).

Table 6 shows the results of the anatomical representation indexes for the Plains vizcacha surface sample. According to the indexes that measure the proportion of postcranial to cranial elements (index PCRT/CR and PCRAP/CR), both show a representation dominated for the postcranial. In relation to the limbs, the proximal elements are more abundant than the distal elements (index Z/E), and the posterior limbs are better represented than the anterior limbs (index AN/PO). Finally, when comparing the appendicular skeleton and postcranial axial skeleton (index AX/AP), a very important loss of the axial elements are observed.

Looking specifically at the early fusion group in Plains vizcacha, there is a lower frequency of unfused distal humerus (3.6%;  $n = 1$ ) and unfused distal tibia (32.2%;  $n = 10$ ), compared to fused distal humerus (96.4%;  $n = 27$ ) and fused distal tibia (67.8%;  $n = 21$ ) (Table 7). According to the fusion schedule of *Oryctolagus cuniculus* elements, this indicates a mid to low proportion of

newborn individuals (18.6%;  $n = 11$ ). On the other hand, in the late fusion group, there is a lower frequency of fused proximal humerus ( $n = 0$ ) and fused proximal tibia (0.5%;  $n = 1$ ), compared to unfused proximal humerus (100%;  $n = 24$ ) and unfused proximal tibia (97.5%;  $n = 39$ ), which indicates a low-proportion of adult to old individuals (1.6%;  $n = 1$ ) (Table 7). The difference between the total of the two late and early fusing groups (18.6 and 98.4%) suggests the overall frequency of the Plains vizcacha surface assemblage corresponds to juvenile to subadult individuals (79.8%).

### Buried sample

Table 8 presents the results of the taphonomic modifications observed in the buried sample. In the medium size vertebrates, 50.7% ( $n = 34$ ) of the specimens are complete; while in the small size vertebrates, 66% ( $n = 33$ ) of the bones are incomplete. The majority of the bones (28.5% small vertebrates, 19.4% medium vertebrates) present a bone completeness of <25%. The totality of incomplete bones presents dry fractures. The most frequent type of fracture are irregular shaped (87.2%;  $n = 41$ ).

Weathering stage 1 was observed in a low percentage (3.4%;  $n = 3$ ), and only in the medium-sized vertebrate (i.e. Plains vizcacha). Regarding the carnivore tooth marks, one specimen of Plains vizcacha was identified with pitting and scoring. A total of 53% ( $n = 43$ ) of the buried bones presented differential color produced by the sedimentary matrix. Root marks were observed in 30.7% ( $n = 27$ ) of the bone specimens. Other modifications, such as trampling, chemical deterioration, and rodent marks were identified in low percentages (<10%).

Taking into consideration the fusion and laterality of the tibia (MNE = 3), a MNI of 3 was calculated for the Plains vizcacha buried sample. The most abundant anatomical parts of the Plains vizcacha (between 25 and 50%) are the sacrum, scapula, radius, pelvis, patella, tibia, fibula, and skull (Table 5). The remaining elements present a low  $R_i$  (<25%) or are completely absent (i.e. carpal/tarsal). Given the low abundance of anatomical parts in the buried sample, there are no significant differences shown in the intra-elemental bone survival. In spite of the low number of bones, we recovered elements that were not identified on the surface sample, such as patella, clavicle, and fibula. Looking specifically at the early fusion group in the buried sample (Table

**Table 5.** Plains vizcacha skeletal representation: surface sample and buried sample.

Element	Abbreviation	MNE surface sample	R <sub>s</sub> surface sample	MNE buried sample	R <sub>b</sub> buried sample
Skull (maxilla)	SK	23	37.09	2	33.33
Mandible	MAND	27	43.64	1	16.66
Incisors	INC	6	4.83	1	8.33
Molar	M	0	0	1	2.08
Atlas	AT	2	6.45	0	0
Axis	AX	3	9.67	0	0
Cervical	CE	3	1.93	3	20
Thoracic	TH	8	2.15	2	5.5
Lumbar	LU	24	11.05	1	4.76
Sacrum	SA	8	25.8	1	33.33
Caudal	CAU	0	0	5	8.33
Rib proximal	RI-P	6	0.8	9	12.5
Rib shaft	RI-S	7	0.94	8	11.11
Rib distal	RI-D	5	0.67	4	5.55
Clavicle	CLA	0	0	1	16.66
Scapula glenoid cavity	SP-GC	7	11.29	1	16.66
Scapula body	SP-B	5	8.06	2	33.33
Humerus proximal	HU-P	0	0	0	0
Humerus shaft	HU-S	35	56.45	1	16.66
Humerus distal	HU-D	26	41.93	1	16.66
Radius proximal	RA-P	3	4.83	0	0
Radius shaft	RA-S	7	11.29	2	33.33
Radius distal	RA-D	2	3.22	1	16.66
Ulna proximal	UL-P	12	19.35	0	0
Ulna shaft	UL-S	15	24.19	1	16.66
Ulna distal	UL-D	4	6.45	1	16.66
Pelvis ilion	IN-IL	59	95.16	1	16.66
Pelvis isquion	IN-IS	44	70.96	1	16.66
Pelvis pubis	IN-PU	29	46.77	2	33.33
Pelvis acetabulum	AC	60	96.77	1	16.66
Femur proximal	FE-P	8	12.9	0	0
Femur shaft	FE-S	52	83.87	0	0
Femur distal	FE-D	10	16.12	1	16.66
Patella	PA	0	0	2	33.33
Tibia proximal	TI-P	8	12.9	1	16.66
Tibia shaft	TI-S	55	88.7	3	50
Tibia distal	TI-D	31	50	1	16.66
Fibula proximal	FIB-P	0	0	2	33.33
Fibula distal	FIB-D	0	0	2	33.33
Astragalus	AS	1	1.61	0	0
Calcaneum	CA	9	14.51	0	0
Carpal/Tarsal	C/T	0	0	0	0
Metapodial proximal	MET-P	14	3.22	3	7.14
Metapodial shaft	MET-S	19	4.38	4	9.52
Metapodial distal	MET-D	12	2.76	3	7.14
Phalanges	PH	2	0.15	9	7.14

7), although the number of selected elements for this methodological criterion is minimal, we observed a slightly higher count of newborn specimens (67%;  $n = 2$ ) with respect to juvenile to subadult (33%,  $n = 1$ ) and adult specimens ( $n = 0$ ).

### Sex ratio

Finally, based on the completeness of the Plains vizcacha skulls, a total of eight elements could be measured for sex estimation. The height of skull (Hsk) measurements ranged between 23.15 and 33.6 mm; and the skull total length (TL) ranged between 95.99 and 133.79 mm (Supplemental online material Table 1). When we plot this data with extant *Lagostomus maximus* reference material (Figure 7) we see how 7 skulls are in the range of subadult/adult female and subadult male individuals, and only 1 skull corresponds to an adult male.

### Discussion

The results obtained throughout the study of 32 vizcacheras showed that these rodents can severely impact the soil and

modify the landscape by burrowing and moving several types of materials. Additionally, a very important consequence of the Plains vizcacha activity for the formation of the archaeological and paleontological records is the accumulation of bones. In our study, numerous bones were recovered from the vizcacheras, including animals of different body size categories. All of the small-sized vertebrates, with the exception of the Peppered catfish likely occupied the vizcacheras. Along with the Plains vizcacha, some medium-sized vertebrates identified in the bone assemblage, including white-eared opossum and hairy armadillo may have also occupied the vizcacheras. However, while a high taxonomic richness was identified, the remains of Plains vizcacha dominate the sample. Taphonomic modifications were recorded both in the surface and buried samples. The most frequent types of modifications in the surface sample were fractures (especially in dry state) and weathering, which was recorded in an important percentage of the bones, although in low stages. On the other hand, in the buried sample the percentage of fractured bones was high, but still lower than in the surface assemblage. Except for differential color and root marks, other modifications were recorded in low percentages.

**Table 6.** Anatomical representation indexes for the Plains vizcacha surface sample.

Indexes	%
PCRT/CR	174
PCRAP/CR	656
Z/E	71.3
AN/PO	35.5
AX/AP	4.7

Note: Abbreviations are provided in the methods section.

**Table 7.** Fusion of selected Plains vizcacha elements.

Fusion group	Surface sample				Buried sample			
	Unfused		Fused		Unfused		Fused	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
<i>Early fusion</i>								
Distal humerus	1	3.6	27	96.4	1	100	0	0
Distal tibia	10	32.2	21	67.8	1	50	1	50
Total	11	18.6	48	81.4	2	67	1	33
<i>Late fusion</i>								
Proximal humerus	24	100	0	0	1	100	0	0
Proximal tibia	39	97.5	1	0.5	4	100	0	0
Total	63	98.4	1	1.6	5	100	0	0

The sample of vizcacha remains indicated that, for the surface assemblage, the anatomical profile is dominated by the pelvis, femur, and tibia; followed by the humerus, mandible, skull, and sacrum. Some of the bones (e.g. long bones) were better represented by denser sections. The age profile was dominated by juvenile to sub-adult individuals, with a mid to low proportion of newborns and a low proportion of adults to old individuals. In the case of the buried sample, the most abundant anatomical parts were the sacrum, scapula, radius, pelvis, patella, tibia, fibula, and skull. In this assemblage, there are a slightly higher number of newborn specimens, in relation to juvenile to subadult. Skull measurements from both the surface and buried sample indicate that the assemblage is made up of mostly female and subadult male individuals.

Our actualistic research helps support previous studies conducted with the Plains vizcacha (Branch et al. 1996; Campos 1997; Arias et al. 2003, 2005; Curetti 2008; Bellinzoni and Kaufmann 2014), which indicate that these rodents generate a significant impact to the local landscape. The Plains vizcacha constitutes an important ecosystemic engineer in the Pampas grasslands, with a similar role to that of other burrowing mammals that inhabit different environments around the world (Reichman and Seabloom 2002; Eldridge et al. 2006; Mallye et al. 2008; Wilkinson et al. 2009; Pelletier et al. 2016). During the construction and maintenance of their communal burrows, the Plains vizcacha produces soil mixing, redistributes the sediment within the soil profile, and accumulates soil at the surface. Moreover, these bioturbation processes become more complex when these rodents begin to carry different kinds of objects from peripheral areas.

In the following sections we discuss a series of criteria that can be used for the identification of vizcacheras in the archaeological and paleontological record.

## Burrows and bioturbation

One of the more conspicuous signs of Plains vizcacha activity in the landscape is the presence of communal burrows. These underground dwellings are integrated by several galleries that generally converge into a central chamber of larger dimension. The depth of the burrows varies depending on the sedimentary characteristics of each area, sometimes reaching more than 2 m deep (Jackson et al. 1996). The sediment that these rodents extract is accumulated in mounds, which form a fan-shaped area, where the pre-existing soil is buried. As our study has shown, this sediment may contain bones of Plains vizcacha or other animals that died inside the burrows. Usually, animal trampling, gravity, and water circulation leads to the collapse of these structures over time, generating a mixture of sediments that break the original stratigraphy. At the same time, the materials deposited around the central chamber can sink and bury.

The burrows of Plains vizcacha present characteristics that would help to differentiate them from other local burrowing mammals in the sedimentary matrix. For example, burrows generated by the tuco-tuco (*Ctenomys*) consist of branched tunnels and an intermediate main chamber (Durán 1991; Antinuchi and Busch 1992). The tuco-tuco burrows occupy, on average, an area of 8 m<sup>2</sup>, with tunnels that have an average diameter of 8 cm and reach a depth of 49 cm (Antinuchi and Busch 1992). This rodent also has the ability to displace materials, however significantly smaller than the Plains vizcacha; on average less than 5 cm in length (Durán 1991). Another burrowing mammal from the Pampas region is the Hairy armadillo (*Chaetophractus villosus*). The complex burrows of this armadillo can reach 4.85 m in length and depths of 1 m (Abba et al. 2005). The burrows also have the potential to be colonised by different predators (Frontini and Escosteguy 2012).

## Taxonomic diversity

As the result of the Plains vizcachas burrowing behavior and the re-occupation of the burrows by other animals (e.g. frogs, snakes, mice, small carnivores, and birds), remains from numerous species are deposited in a small area. In general, a local bird of prey, the Burrowing owl, colonise the vizcacheras and deposit pellets containing the remains of their prey, adding complexity to this type of assemblage (Machicote et al. 2004; Villarreal et al. 2005). No beak marks were identified; nonetheless birds of prey such as the Burrowing owl may be responsible for some bone modifications. The bones that do present tooth marks are likely from small mammals such as Pampas fox (*Lycalopex gymnocercus*), Lesser grison (*Galictis cuja*), or domestic dogs. These carnivores could have been involved in the transport of some specimens and the differential destruction of less dense elements, such as vertebrae and ribs. Larger-sized fauna remains are also expected due to the Plains vizcacha behavior of accumulating objects from the surrounding area. Here, we observed large cow and horse bone specimens dragged to the vizcacheras by the Plains vizcacha.

Another factor which contributes to the accumulation of faunal remains is the subterranean formation of vizcacheras and their geomorphological evolution. The vizcacheras act as a type

**Table 8.** Relative frequencies of taphonomic modifications in buried sample.

Taphonomic variables	Small vertebrates (n = 21)		Medium vertebrates (n = 67)		Total (n = 88)	
	n	%	n	%	n	%
Bone completeness						
<25%	6	28.5	13	19.4	19	21.5
25–50%	4	19.1	10	14.9	14	16
50–75%	2	9.5	6	8.9	8	9.1
75–99%	2	9.5	4	5.9	6	6.8
100%	4	19.1	34	50.7	38	43.2
Indeterminate	3	14.3	0	0	3	3.4
Weathering stage						
0	21	100	63	94	84	95.5
1	0	0	3	4.5	3	3.4
Indeterminate	0	0	1	1.5	1	1.1
Carnivore marks						
Specimens with marks	0	0	1	1.5	1	1.1
Pitting	0	0	1	100	1	1.1
Scoring	0	0	1	100	1	1.1
Sedimentary abrasion	0	0	7	10.4	7	8
Bone fracture						
Specimens with fractures	14	66.6	33	49.2	47	53.4
Irregular	11	78.6	30	90.9	41	87.2
Transversal	3	21.4	1	3	4	8.5
Longitudinal	0	0	2	6	2	4.3
Dry	14	100	33	100	33	70.2
Trampling marks	0	0	6	8.9	6	6.8
Rodent marks	1	4.8	4	6	5	5.7
Bone staining	0	0	46	68.6	46	53
Root marks	7	33.3	20	29.8	27	30.7
Chemical deterioration	0	0	1	1.5	1	1.1

Reference: n = number of specimens.

of negative topographic feature (e.g. fissures, caves, sinks, and slopes), which trap small vertebrates or remains of animals affected by natural processes, such as water transport (Behrensmeyer and Hook 1992; Pardiñas 1999). The animals and carcasses can attract predators and scavengers, who may also become trapped (Behrensmeyer and Hook 1992). During cyclical flood events such as those that characterise the hydrological dynamics of the Pampas region, the negative topographic features in the landscape, such as the vizcacheras, may become the concentrators of biological remains (e.g. animal carcasses, bone specimens, pellets, and feces from predators, etc.) deposited in the surrounding environment (Pardiñas 1999; Pomi and Scanferla 2005; Scheifler et al. 2012).

### Skeletal representation and taphonomic processes

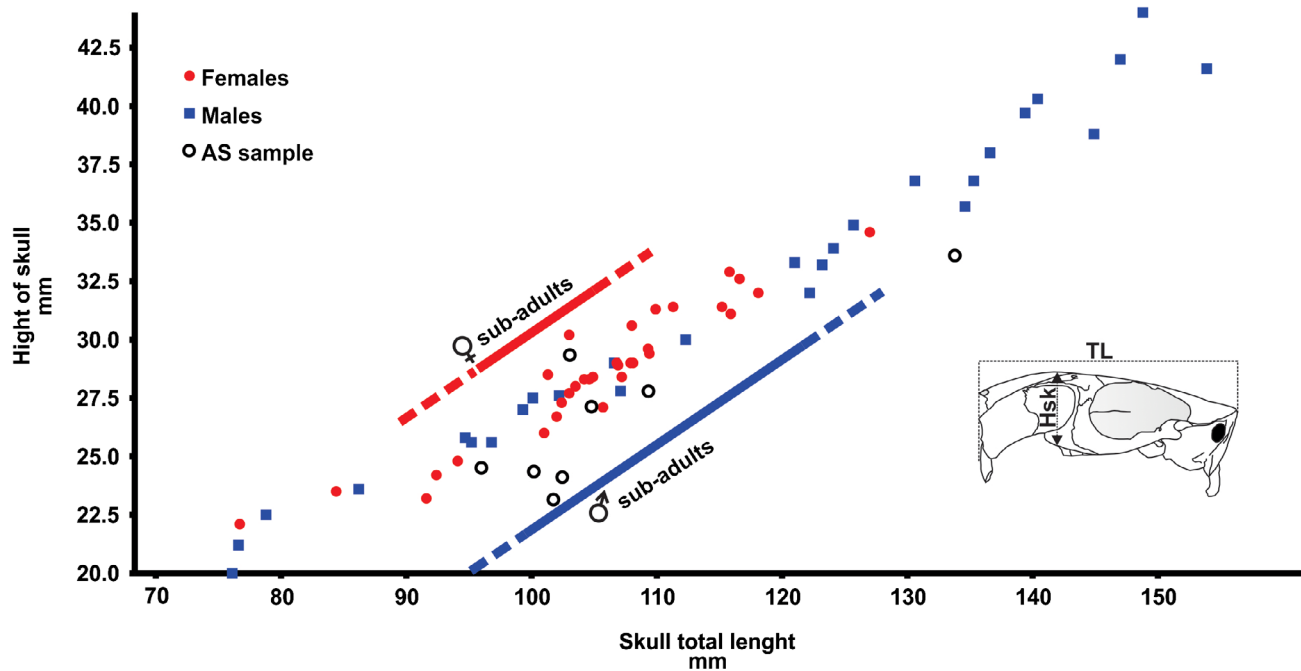
In the surface sample of the vizcacheras, there is dominance of the pelvis and some elements of the hind limb, such as the femur and tibia. The carpals/tarsals, phalanges, ribs, vertebrae, and clavicles are absent or have very low representation. When comparing the relative proportions of distinct skeletal elements in the surface sample, we observe a greater frequency of the postcranial skeleton, a greater frequency of posterior limbs, and an important loss of the axial elements. The skeletal representation of the buried sample is similar to that of the surface (see Figure 8); including the absence or near absence of molars, and carpal/tarsal.

The taphonomic and contextual information suggests that the bones collected in this work would have been deposited in an attritional way, and could include some episodes of mass death resulting from human poisoning (see Section *Sex and age of death distributions*). Lichen colonisation on some remains (28%) indicates a certain exposure time to weathering (Borella 1994). However, the assemblage shows a weathering profile dominated by stages 0 and 1, with a very low percentage of bones reaching

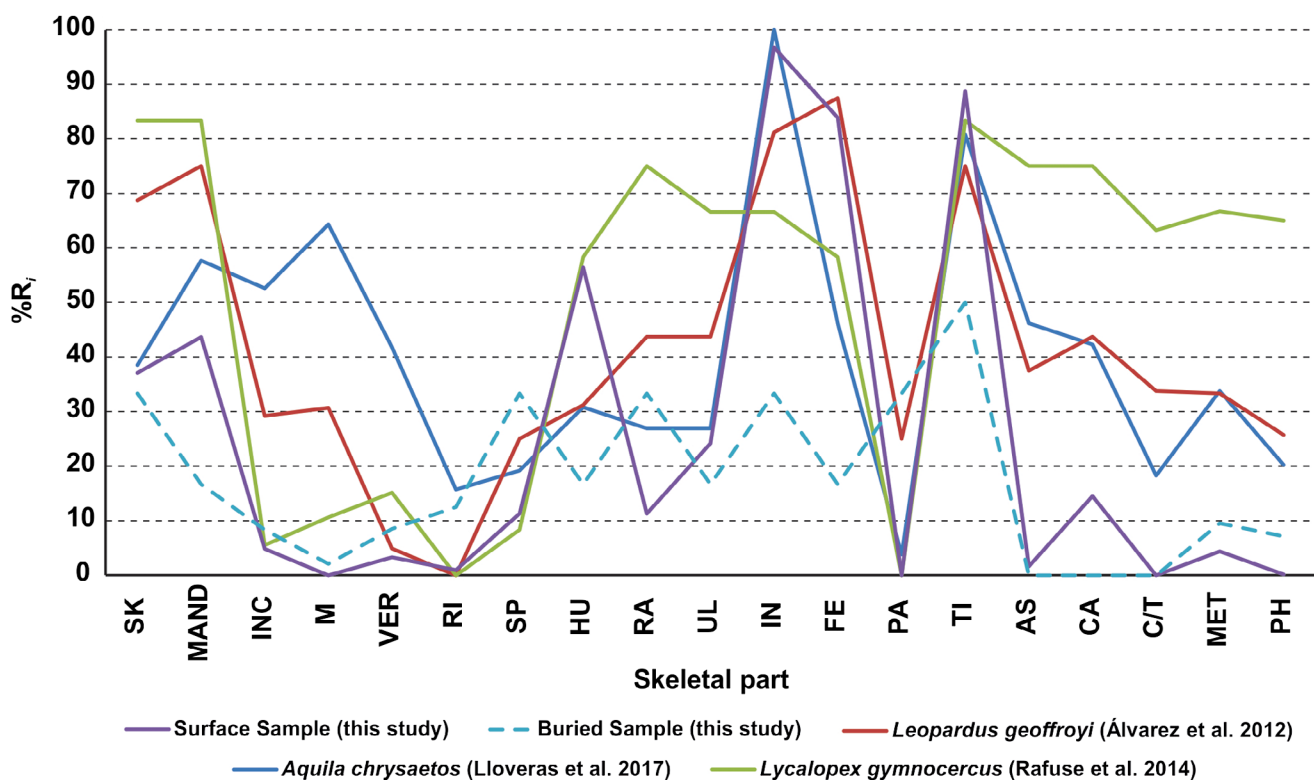
stages 3 and 4. It is also noteworthy the high percentage of dry bone fractures (96%), as well as the abundance of trampling marks (23%). Both of these modifications could have been caused by cattle or horse and perhaps even the Plains vizcacha.

In relation to the taphonomic modifications in the buried assemblage, as expected, there are a higher percentage of bones with root marks and differential color, as well as a lower proportion of fractured bones (49%), trampling marks (7%), weathering (3%), and carnivore marks (1%). The differences in the anatomical representation between the surface and the buried samples could be due to differences in the intensity in which these processes acted in both contexts. Other factors that could have influenced in the configuration of the assemblage are differential burial and recovery methods.

In order to further examine the pattern of anatomical representation, Figure 8 compares the Plains vizcacha bone assemblage from the vizcacheras with non-ingested leporid bones from two feeding experiments with Geoffroy's cat (*Leopardus geoffroyi*) and Pampas fox (*Lycalopex gymnocercus*), and from a Golden eagle (*Aquila chrysaetos*) nest (Supplemental online material Table 2). Leaving the buried sample aside because of its small sample size, some clear overlapping is evident; specifically, the higher frequency of the innominate, femur and tibia; and the lower frequency of vertebrae, ribs and patella. A Sperman's  $r_s$  test shows a positive correlation between the surface sample and the Golden eagle ( $r_s = 0.50$ ;  $p = 0.021$ ), Geoffroy's cat ( $r_s = 0.74$ ;  $p = 0.0003$ ) and Pampas fox ( $r_s = 0.49$ ;  $p = 0.029$ ). Additionally, when comparing the relative proportions of distinct skeletal elements in these assemblages (Supplemental online material Table 3); similar proportions are present in all four samples, suggesting that the Plains vizcacha skeletal pattern cannot be easily distinguished from that generated by other predators. This could be related to the participation of predators in the accumulation of



**Figure 7.** Plotted skull measurements from the Plains vizcacha sample and reference material of male and female extant *Lagostomus maximus* (Ubilla and Rinderknecht 2016). Skull diagram modified from Ubilla and Rinderknecht (2016): Figure 2.



**Figure 8.** Comparative chart of relative abundance of non-ingested leporid from three predators, and the Plains vizcacha surface and buried assemblages. (For color, see online version.)

bones in the vizcachas; a theory which is supported by the presence of tooth marks.

### Sex and age of death distributions

In the surface assemblage, our results show an age of death distribution highly dominated by juvenile to subadult individuals,

with a mid to low proportion of newborn, and a close to absent number of adults to old individuals. In the buried assemblage, there is a slightly higher count of newborn individuals. The measurements from the skull elements in both the surface and the buried samples also indicate an assemblage dominated by female and subadult male individuals and a low number of adult males. This age of death distribution and sex estimation

could correspond principally to one or various catastrophic events of death (Klein and Cruz-Urbe 1984; Lyman 1987; Stiner 1990; Lubinski 2000; Steele and Weaver 2002; Discamps and Costamagno 2015). As mentioned above, the Plains vizcacha is subject to eradication programs which include the use of pesticides (Rendel 1990; Branch et al. 1999; Chebez et al. 2014). This type of local extermination is present in the Arroyo Seco area, however, we cannot assess the date and frequency of this action, but this may explain in part the age of death distributions and sex. The lower representation of newborn individuals in the surface sample can be explained by post-depositional processes, including the impact of carnivores, which could have affected the smallest individuals in the Plains vizcacha population with greater intensity. The slightly higher count of newborn individuals in the buried sample, suggests that these individuals died inside the burrows and in some cases were later extracted and differentially altered with respect to the juvenile to subadult individuals by post-depositional processes.

## Conclusions

The Plains vizcacha is an important agent in the postdepositional history of the fossil record. These rodents are ecosystematic engineers capable of accumulating, mixing, and fragmenting different materials. The vizcachera data presented in this paper provides information which can be used to help predict the extent of this alteration. When the origin of the Plains vizcacha is suspicious, or when burrowing activity is present, some relevant criteria for the identification of vizcacheras in the fossil record can be applied. The most pertinent criteria are the presence of burrows or bioturbation, some of which may contain remains of Plains vizcacha and bones of animals that inhabited the burrow. Another diagnostic feature is a high taxonomic diversity, although a clear dominance of Plains vizcacha bone remains should be expected. Additionally, the age and sex composition of the Plains vizcacha bone assemblage can be a pertinent criterion. In this case, the predominance of juvenile to subadult (male and female) and a low count of adult male individuals could indicate the presence of vizcacheras. In reference to the anatomical representation of parts, the similarities found with the anatomical patterns produced by natural predators on prey of similar size to Plains vizcacha indicate that this is not a useful criterion for identifying vizcacheras. Furthermore, in archaeological sites of the Pampas region where the Plains vizcacha were processed for meat, leather and marrow; the pattern of anatomical representation is variable (Martínez et al. 2001; Quintana and Mazzanti 2011; Álvarez 2012), coinciding in some cases with the observed naturalistic study. For this reason, we propose that this characteristic taken in isolation does not allow determining the origin of an assemblage.

While most archaeological sites are disturbed to some degree because of postdepositional processes, the objective is to determine to what extent assemblages are mixed (Morin 2006, p. 257). In the particular case of faunalurbation, this alteration will depend on interrelated factors such as geomorphic context, burrowing animal population size, and the type of archaeological/paleontological assemblage (Pierce 1992, p. 189). Our results suggest that the Plains vizcacha produces a high impact on the fossil record with multiple consequences at a taxonomic, anatomic,

taphonomic, and spatial level. However, their action can be identified if the criteria proposed in this paper are taken into account, and meticulous field methods, such as tight point-province control of artifacts, skillful sediment excavation methods for isolating burrows, and a robust zooarchaeological and taphonomic analysis are used. In environments where vizcacheras and hunter-gatherer sites superimpose on the landscape, archaeologist must take into consideration the strong possibility of a natural incorporation of Plains vizcacha bone and the transported material by this rodent. In cases where fossil vizcacheras are clearly present, both the vertical and horizontal movement of materials in the site assemblage, as well as the natural incorporation of material (bones and other materials) not related to the human occupation is likely. In these cases, inferences of subsistence practices involving the Plains vizcacha should be exclusively based on direct evidence of butchering.

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