

Beached penguins on the Atlantic Coast in the Pampas region of Argentina: Taphonomic analysis and implications for the archaeological record



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ABSTRACT

This study evaluates a modern natural deposit of Magellanic penguin remains in the coast of the Pampas region, and discusses the regional availability of this resource for prehistoric hunter-gatherer populations, as well as the potential for the natural incorporation of this species into the archaeological record. The penguin assemblage from the surveyed area, which results from beaching during seasonal migration, consists of disarticulated bones, articulated bones, and carcasses. In the skeletal representation, there is a strong predominance of limbs and shoulder girdle elements. Natural processes such as weathering, sedimentary abrasion, and predator action highly affected the preservation of specimens. Even though penguins could have been a potential prey for hunter-gatherer populations of the Pampas region, our results suggest that they were not an attractive food resource given their scarcity and poor nutritional condition. The spatial distribution of modern penguin remains and the archaeological evidence suggest that the natural incorporation of bones from this seabird into surface archaeological sites can be expected in the backshore and deflated interdunes. However, the chances of long term burial and bone preservation are low; thus, the formation of a stratigraphic archaeological site containing intrusive penguin remains in these settings is unlikely.

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1. Introduction

A recent taphonomic surface survey of modern vertebrate remains in a locality of the Atlantic coast of the Pampas region (locality Balneario San Cayetano, Buenos Aires province, Argentina), demonstrated an unexpected abundance of bones and carcasses from Magellanic penguin (*Spheniscus magellanicus*), a seabird that does not inhabit the area. The survey examined the distribution of modern vertebrate bones as well as the natural processes that condition the preservation of bone in distinct coastal environments. This actualistic research is part of a regional archaeological and taphonomic project which attempts to generate new information on prehistoric hunter-gatherer subsistence in relation to the environment. These studies are of great value not only for archaeology but for paleontology and paleobiology as well. They help recognize the natural properties of bone records, such as

spatial distribution, species representation, and bone preservation. They also provide ecological information and knowledge of possible biases that the fossil assemblages may contain.

This paper presents the analysis of penguin remains recovered during the survey. The objectives are a) to evaluate the deposition and preservation conditions of the penguin remains; b) to discuss the regional availability and quality of this resource for past human populations, on the basis of biological information and the archaeological record; and c) to evaluate the potential for intrusion of naturally deposited bones in the archaeological record.

Although no penguin breeding populations are registered in the Pampas region, individuals are occasionally spotted along the shore. In general, these penguins are forced to make landfall during seasonal foraging trips for different health reasons, or dead individuals are washed ashore by natural currents. The presence of penguins on the coast of the Pampas occurs primarily during the non-breeding season, when penguins migrate or disperse north to feeding areas during the austral fall and winter months (March to September) (Pütz et al., 2007; Stokes et al., 2014).

The skeletal structure of penguins has particularities related to its adaptation to diving (Williams, 1995), so understanding the taphonomic history of their bones can only be achieved through specific studies on this taxon. This research constitutes the first attempt to

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study the taphonomy of penguin bone remains from the Pampas region, outside this bird's preferred breeding locations. Previous evaluation of the processes governing the deposition, preservation, and distribution of penguin bones has been limited to Patagonia and Antarctica (Cruz, 2007; Emslie, 1995; Muñoz and Savanti, 1998).

2. The Magellanic penguin

Four penguin species breed along the coast of Argentina: Magellanic penguin (*Spheniscus magellanicus*), Southern Rockhopper penguin (*Eudyptes chrysocome*), Gentoo penguin (*Pygoscelis papua*), and King penguin (*Aptenodytes patagonicus*). The Magellanic penguin is the most widely distributed and has the highest population density of these species. The colonies of this seabird are distributed along the entire continental Patagonia and its islands, but the other three species are restricted to the southernmost islands of this region (Bertellotti, 2013; Schiavinni et al., 2005). The current distribution of Magellanic penguin breeding colonies ranges from Algarrobo Island on the Pacific coast of Chile to the province of Río Negro, Argentina (Fig. 1).

The Magellanic penguin is the largest species in the genus *Spheniscus*. Adults are 70 cm long and weigh between 3.5 and 4 kg. Their bodies are very robust and their wings are short and slender and are modified into powerful flippers. Unlike other diving birds, penguins propel themselves underwater using their forelimbs (Bertellotti, 2013; Habib and Ruff, 2008). The skeleton consists of denser solid bones than those of other types of birds, with reduced pneumatization (Williams, 1995; Habib and Ruff, 2008).

Magellanic penguins breed in large colonies on islands or along the mainland. The breeding season begins in September, when the first males arrive to the colony. A week or two later, the females arrive. Most penguins are born during middle and late November and remain in the nest until their independence in late February (Bertellotti, 2013). In early fall (March–April), when the breeding season ends, Magellanic penguins migrate or disperse north to feeding areas along the coastal waters and continental shelf of central Argentina, Uruguay, and southern Brazil (Pütz et al., 2007; Stokes et al., 2014).

During the seasonal migration, live or dead penguins reach the coast of the Pampas region. Different factors are responsible for the beaching of penguins, including petroleum pollution, starvation, and disease. Data from organizations that survey beached seabirds along the coast indicate that the most common cause of mortality in penguins is starvation (García-Borboroglu et al., 2010). A recent survey of dead marine animals conducted by a conservation project along the beaches of the southern coast of Buenos Aires province (covering 230 km, including the area of the present study) showed a very high frequency of Magellanic penguin. Between 2007 and 2009, 679 carcasses of sea turtles, marine mammals and seabirds were recorded. Magellanic penguin was the most common species, with a total of 544 carcasses (80%), most of them juveniles (ECOFAM Final Report, 2010).

The fossil and historical records of the Magellanic penguin indicate that, during the Late Pleistocene and Holocene, the distribution of this marine bird was restricted to Patagonia. The available data suggest that throughout the Holocene and until the eighteenth century, penguin breeding colonies were localized primarily on islands, possibly as part of a strategy for predator avoidance (Cruz et al., 2014). Historical information suggests that in recent centuries, breeding colonies of Magellanic penguins shifted further north and settled along the mainland coast (Boersma et al., 1990; Cruz et al., 2014). The increase in population and geographic range of Magellanic penguin could be due to sealing of pinnipeds (the penguins' greatest competitor and predator) during the fur trade period (Saporiti et al., 2014). In the last decades, there has also been evidence of a more northern distribution of feeding areas during the non-breeding season (Dantas et al., 2013). Since penguins are particularly sensitive to environmental and climate fluctuations, population changes throughout the Late Pleistocene and Holocene is likely to have occurred (Williams, 1995). Notwithstanding,

given that the Late Quaternary fossil record on the Atlantic coast of South America is limited, there are no known variations in the distribution of *Spheniscus* for prehistoric times.

3. Penguins in the archaeological record

In Patagonia, the large number of individuals found in predictable habitats (breeding colonies) for extended periods of time, combined with the simplicity in hunting and a high economic return-rate compared with other marine birds made the penguin an excellent prey for hunter-gatherers (Cruz, 2001; Cruz et al., 2014; Lefèvre, 1993–1994). The archaeological record from this region shows the exploitation of penguins from 6000 years BP (Borella and Cruz, 2012; Cruz, 2001, 2007; Cruz et al., 2014; Lefèvre, 1993–1994).

In reference to the Pampas region, the evidence of penguin exploitation is not abundant in the archaeological record. In the Alfar site (Bonomo and Leon, 2010), 16 bone specimens were assigned to *Spheniscus* sp., one of which presented cut marks (humerus). None of the penguin bones were dated; however, an Eared seal (Otariidae) tooth was dated to ca. 5700 years BP (Middle Holocene). Other postcranial penguin elements, including cervical vertebrae, coracoids, scapula, ulna, radius, femur, tibiotarsus, tarsometatarsus, and phalange were recovered in the Alfar site (Bonomo and Leon, 2010). Another site in the Pampas region with penguin is El Americano II; however, researchers consider that the only bone specimen from the site (humerus recovered on the surface) is intrusive (R. Frontini, pers. com., 2014). It is important to mention that there are other archaeological sites with evidence of marine resource exploitation, including fish and seals, but only the two sites mentioned above contain penguin bones (Aldazabal et al., 2012; Bayón et al., 2012; Bayón and Politis, 2014; Bonomo et al., 2012; Conlazo, 1983; among others).

4. Study area

The Pampas coast, along the province of Buenos Aires, extends over 1,200 km and has a variety of natural environments, including sandy beaches, cliffs, dunefields, and freshwater lakes. Over the last 6000 years, this landscape has evolved under fluctuating conditions, including sea level changes and human activities (Isla et al., 2001). Since the mid-1900s, the natural ecosystem of the coast of the Pampas region has changed rapidly as a result of afforestation and urbanization.

At present, the climate for the southern coast of the Pampas region is temperate oceanic, with average annual temperature of 15 °C and average rainfall of 770 mm per year (Bértola et al., 2009). Regarding the flora, the coastal area has a mosaic of different environments: grasslands, steppes, scrublands, and dune vegetation (Celsi and Monserrat, 2008). Terrestrial mammals include several carnivores, such as the Pampas fox (*Lycalopex gymnocercus*), Common hog-nosed skunk (*Conepatus chinga*), Geoffroy's cat (*Leopardus geoffroyi*), and Lesser grison (*Galictis cuja*) (Redford and Eisenberg, 1992). Avian predators include gulls: Kelp gull (*Larus dominicanus*), and Brown-hooded gull (*Larus maculipennis*); and raptors: Southern crested caracara (*Polyborus plancus*) and Chimango caracara (*Milvago chimango*) (Darrieu and Camperi, 2001).

The locality Balneario San Cayetano (38° 45' LS; 59° 25' LW) is situated on the south-facing shore of Buenos Aires province (Fig. 2). The surveyed coastal area is located within the Southern Dune Barrier, in a transgressive dunefield that presents active dunes reaching maximum heights of 70 m (Bértola et al., 2009; Marcomini and López, 2013:520; Isla, 1989, 1997).

The area selected for the survey is positioned outside the town limits (>700 m), which minimizes the effects of human impact and the presence of dogs. During the study, four different sub-environments were surveyed (Fig. 2): 1) backshore (between the shoreline and the base of the dunes); 2) active dunes (between the backshore and approximately 1300 m off the shoreline); 3) stabilized dunes (between

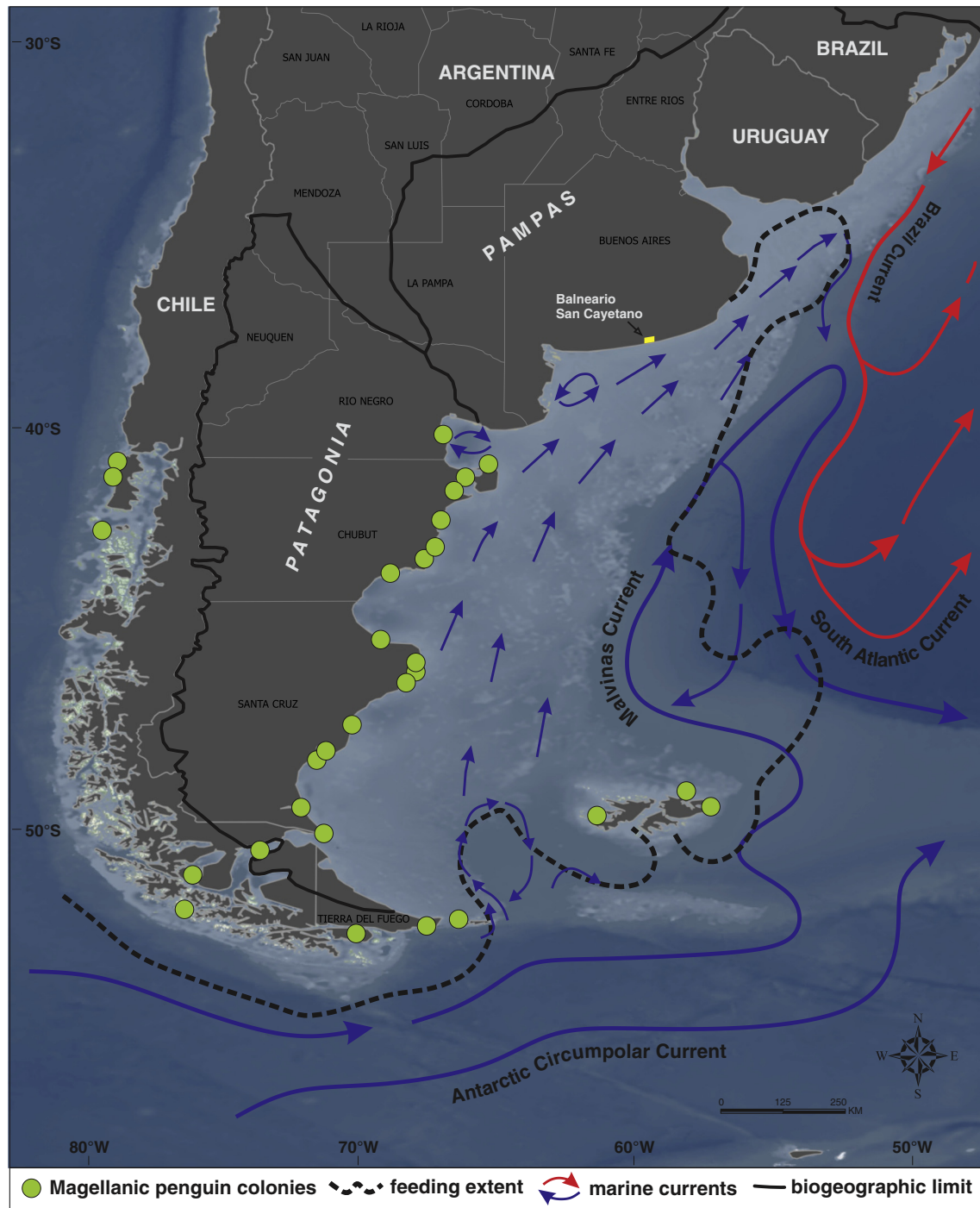


Fig. 1. Location of study area and regional colony sites of the Magellanic penguin. Feeding extent and data for colonies adapted from Falabella et al. (2009). Patagonian Sea marine currents adapted from Piola and Matano (2001). Bathimetric map from CleanTOPO2 (<http://www.shadedrelief.com/cleantopo2>).

2300 m and 3500 m off the shoreline); and 4) freshwater coastal lakes (located behind the transgressive dunefield between 3500 m and 4500 m off the shoreline).

The backshore is characterized by minimal or no vegetation; sand is blown inland by wind burying most plants and forming new dunes (Fig. 3). This is a highly dynamic sub-environment. Waves occurring at exceptionally high tides and storm surges inundate this sub-environment periodically, accumulating pebbles and dead organisms from diverse origins, thus forming storm berms (Bértola et al., 2009; Marcomini and López, 2013). The active dunes are also a highly unstable

sub-environment, depending mainly on the beach aeolian activity and the availability of the sediment supply (Fig. 3). The dune ridges are characterized by sand burial and wind erosion. Vegetation is established only in the interdune areas, where the freshwater table is at or just below the sand surface (Marcomini and López, 2013). The stabilized dunes are artificial vegetated areas that contain grasses and shrubs (Fig. 3). In the interdune areas, both in the active and stabilized dunes, the high level of the freshwater table and the obstruction of rainfall drainage by the dunes cause the formation of ponds, marshes, and small temporary lakes, where abundant vegetation and fauna can

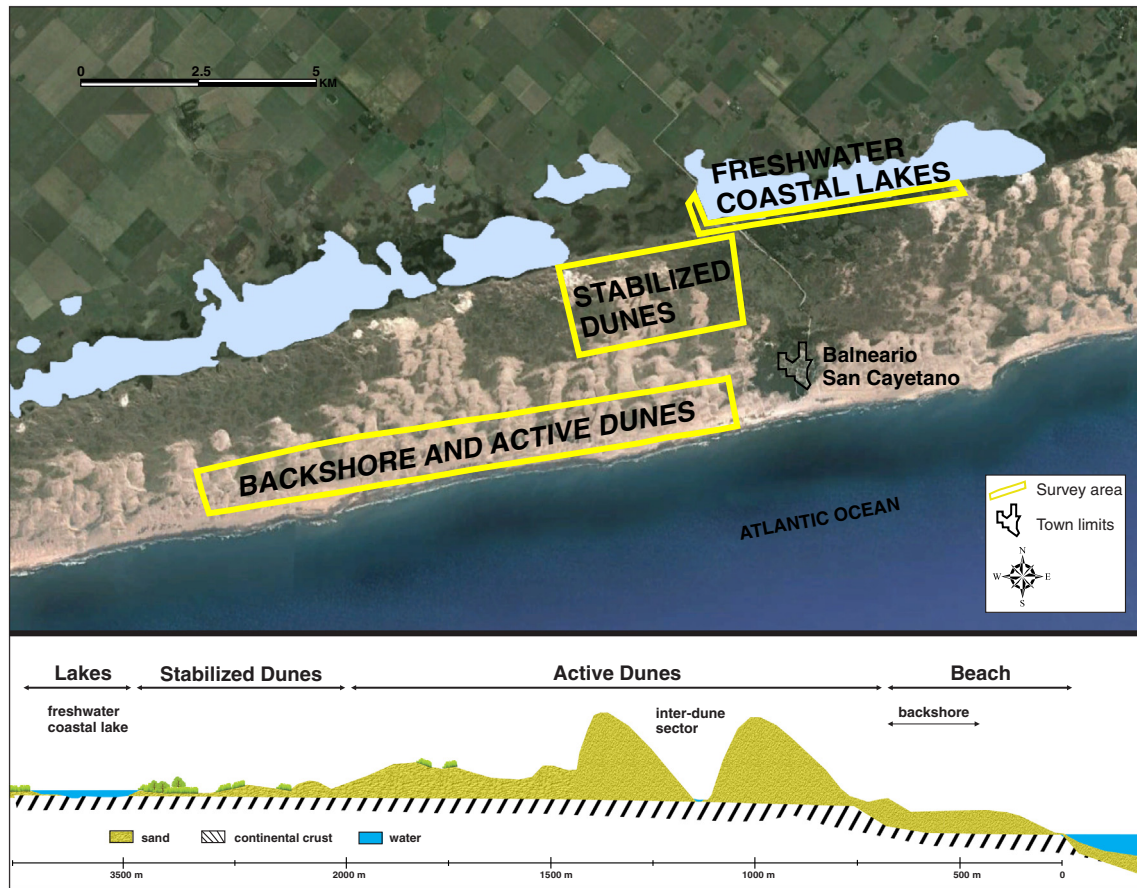


Fig. 2. The locality Balneario San Cayetano. Top image shows extent of surveyed areas (satellite image modified from Google Earth, <http://www.earth.google.com>). Bottom image shows a coastal profile for the study area (modified from Bonomo, 2005).

concentrate. Behind the dunefield, large shallow freshwater lakes are formed, as the dunes impede the drainage of the watercourses from the plains (see Frenguelli, 1931; Bértola et al., 2009) (Fig. 3).

5. Materials and methods

Transects were conducted during December 2012 in the four sub-environments, covering a surface area of 512,900 m². Systematic observations were made by shoreline-parallel transects or, in the case of lakes and ponds, following its margins. Transects were conducted on foot by two persons. Each transect was 10 meters wide, with lengths that varied depending on the environment. The transects were partitioned into samples of 50 meters in length where the following variables were registered: sediment type, slope, potential for burial of faunal material, type and distribution of vegetation, bioturbation, presence of living animals or modern human activity, archaeological materials, and visibility based on land cover (excellent visibility: without vegetation cover; very good visibility: 1–25% plant cover; good visibility: 26–50%; regular visibility: 51–75%; and poor visibility: 76–100%).

For each vertebrate remain identified in the transects, we recorded the following characteristics: 1) taxon; 2) presence of soft tissue; 3) anatomical unit; 4) bone fusion; 5) completeness (individual bone or carcass); 6) articulation between elements; 7) burial state (following Behrenmeyer and Boaz (1980), we considered a specimen buried when it was covered with more than 50% by sediment); 8) inclination; 9) stage of weathering (Behrenmeyer, 1978; Behrenmeyer et al., 2003:56), we recorded the more advanced weathering stage on a bone surface covering more than 1 cm²; and 10) other taphonomic modifications, including sedimentary abrasion, carnivore marks, rodent marks,

root etching, manganese stains, and trampling (see Behrenmeyer, 1978; Binford, 1981; Grayson, 1984; Gutiérrez and Kaufmann, 2007; Haynes, 1980; Lyman, 1994; Olsen and Shipman, 1988; Shipman, 1981).

Vertebrate remains were categorized as “disarticulated bone” (a bone element unrelated to another one by soft tissue), “occurrence of articulated bones” (two or more bones joined by soft tissue, involving less than 75% of the skeleton of the animal) and “carcass” (more than 75% of the skeletal elements of the animal conjoined by soft tissues). Additionally, we recorded whether the remains were scattered or formed part of a concentration. We considered a “concentration” as any set of five or more separately recorded remains (including the three categories mentioned above) from the same or different individuals distributed in a small area (around 100 m²) (Cruz, 2007). It is important to clarify that the taphonomic study was performed using the vertebrate remain as the unit of analysis; in other words, in the case of occurrences of articulated bones and carcasses, description and quantification of modifications was performed for the faunal remain, not the individual item. Similarly, individual bones from carcasses were not included in bone counts for skeletal representation.

In order to achieve the highest level of taxonomic and anatomical determination, all disarticulated bones and the majority of the occurrence of articulated bones and carcass were collected. Quantification of penguin remains was performed. The NISP is the number of identified specimens (fragments and complete bones) per taxon. The MNI is the minimum number of individuals needed to account for all the specimens identified for a particular taxonomic group. The MNE is the minimum number of a particular skeletal element necessary to account for the specimens representing that unit. The MAU is the minimum number of anatomical units identified. This value is calculated by dividing the MNE of each anatomical unit by the number of times that this

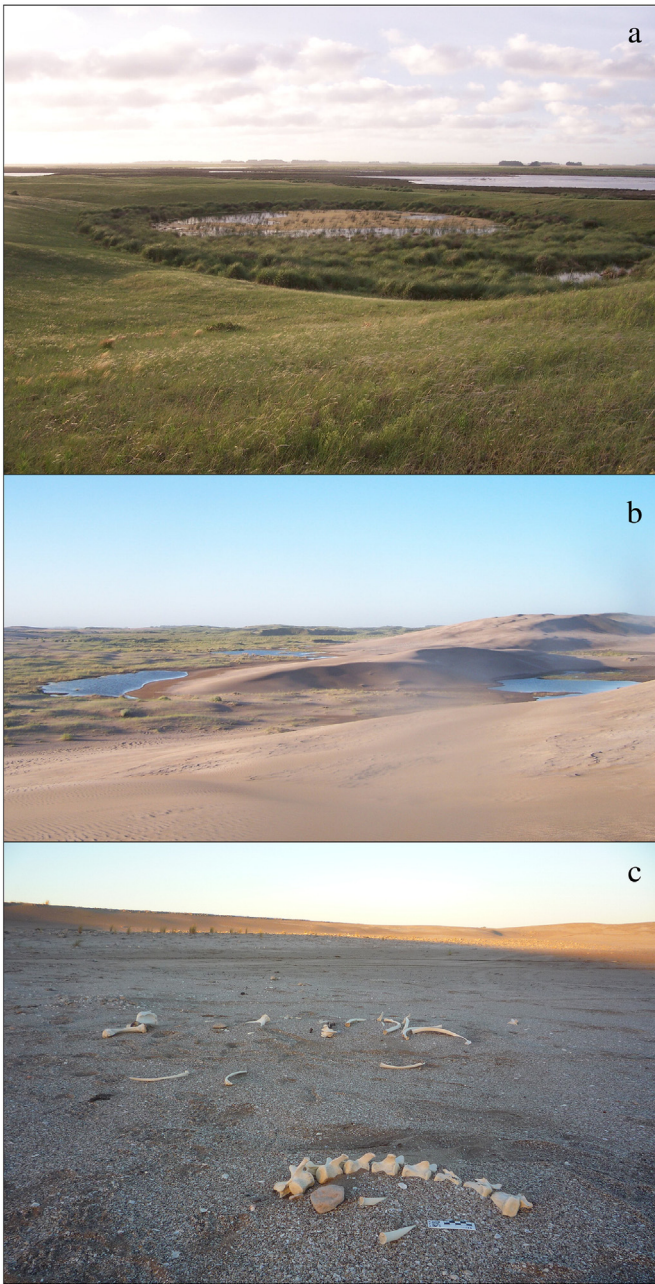


Fig. 3. Examples of surveyed sub-environments: a) foreground, a pond in the stabilized dunes; background, a freshwater coastal lake; b) active dunes and interdune lakes, c) backshore with Otariidae bones.

occurs in one complete skeleton. These numbers can be standardized by dividing all MAU values by the greatest MAU value in the assemblage (100%) (see Binford, 1978; Grayson, 1984; Klein and Cruz-Uribe, 1984; Lyman, 1994). To evaluate differential survival between anatomical regions we calculated the relative percentages of the different skeletal regions (%MNE) and compared this with the expected percentages for the whole bird. Additionally, we calculated the proportion of wing (humerus, ulna, and carpometacarpus) to leg (femur, tibiotarsus, and tarsometatarsus) bones, which allows ready comparison of skeletal parts between assemblages (see Ericson, 1987).

To determine the relative age at death of the penguin remains, we considered ossification of articular surfaces, fusion of compound skeletal elements, bone size and porosity (Cohen and Serjeantson, 1996; Tumarkin-Deratzian et al., 2006). We followed the four age categories proposed by Serjeantson (2009:46) for birds: Very young (bone

half-ossified or less); Immature (bone more than half-ossified, porous, and unfused); Subadult (bone full size and fused, with fusion line visible, and slightly porous); Adult (bone fused, and not porous). It is important to mention that these categories do not imply assumptions of sexual development or behavior (Cohen and Serjeantson, 1996; Tumarkin-Deratzian et al., 2006). The sequence and timing of skeletal development in penguins is not well known. For this study, we assumed that penguin skeletons ossify completely soon after fledging, according to the general pattern observed in other birds (Serjeantson, 2009). While biologists discriminate between juvenile and adult individuals depending on color and distribution of feathers, it was not possible to use this criterion due to the advanced degree of decay found on the carcasses.

6. Results

6.1. Environmental contexts

A total of 105 transects were surveyed in the locality Balneario San Cayetano: 75 in the backshore and active dunes, covering an area of 371,150 m²; 20 in the stabilized dunes, covering 92,750 m²; and 10 along the margins of a freshwater coastal lake, covering 49,000 m² (Table 1). The backshore and active dunes were considered together because the contact between them is irregular, causing the linear transect to intercept both sub-environments.

Along the backshore and active dunes, the overall visibility was good or excellent. In these environments, alternating sedimentation and wind erosion events occur, so the potential for bone burial is low. Bioturbation by rodents, particularly tuco-tuco (*Ctenomys* sp.) is significant, and human impact includes the circulation of off-road vehicles (see Table 1). It is important to mention that from the 743 transect samples in this environment, 2.7% (20 samples) presented archaeological materials (in particular a high proportion of knapped coastal pebbles).

In the stabilized dunes, the overall visibility is regular. There is a dominance of pedogenesis (soil formation), and the potential of bone burial is low to moderate. In this environment, rodent and armadillo burrows were frequently registered. Human action is noteworthy, particularly the presence of livestock (dung, carcasses, and tracks).

In the margins of the freshwater coastal lake, the visibility was regular or bad. In this environment, some sectors presented a dominance of pedogenesis and others of lacustrine sedimentation. Therefore, the potential for burial is high in some samples, and low in others. Animal burrowing occurs, but with less intensity than in the dune environments. In reference to human action, livestock also has a significant impact on this environment.

6.2. Vertebrate assemblage

In the locality Balneario San Cayetano, we identified a total of 1236 disarticulated bones, 34 occurrences of articulated bones, and three carcasses. The greatest density of vertebrate remains was registered in the backshore and active dunes (Table 1). The highest density of bone remains in these sub-environments may be influenced in part by visibility, which, as mentioned above, was excellent in some areas.

A high diversity of taxa was recorded in the locality (see Supplementary data Table A). Of the total surveyed area, 88% of the bones were assigned to a taxonomic category. There is a higher frequency of mammals (56%), followed by birds (28%), and fish (3.5%). Only one amphibian specimen was identified, and no reptiles were found. While the mammal bones dominate the assemblage, the most frequent species is *Spheniscus magellanicus*, which represents 17% of the total number of vertebrate remains from the locality and 59% of the total number of birds.

Table 1
Environmental context and density of faunal remains.

	Backshore and active dunes	Stabilized dunes	Freshwater coastal lakes	Total
Visibility	Excellent to very good	Regular	Regular to bad	
Dominant natural processes	Rodent burrowing	Rodent burrowing and vegetation	Vegetation	
Dominant anthropic processes	Vehicles circulation	Cattle farming	Vehicles circulation and cattle farming	
Transects	75	20	10	105
Samples	743	187	98	1028
Sampled area (m ²)	371150	92750	49000	512900
Disarticulated bones	1073	90	73	1236
Density (m ⁻²)	0.0029	0.0010	0.0015	0.0024
Occurrence of articulated bones	28	4	2	34
Density (m ⁻²)	0.000075	0.000043	0.000041	0.000066
Carcasses	3	0	0	3
Density (m ⁻²)	0.0000081	0	0	0.0000058

6.3. Magellanic penguin sample

From the four sub-environmental settings, only the backshore and active dunes presented penguin remains. A total of 213 penguin remains were identified in this area. The most frequent type were disarticulated bones without soft tissue (NISP = 201; MNE = 195¹), followed by occurrences of articulated bones (n = 9; MNE = 59), and carcasses (n = 3) (Fig. 4 and Supplementary data Fig. A). Of the penguin remains identified to age (n = 80), 72.5% were from adult and 27.5% from subadult individuals. It is important to mention that 62% of the bone remains (n = 133) could not be assigned to any age category. The main reason for this problem was that the extensive surface abrasion precluded the systematic recording of bone porosity. Considering the disarticulated bones, we estimated a MNI of 13 (based on the left humerus); however, if we consider the elements present in the occurrences of articulated bones and the complete carcasses, the MNI increases to 18 (based on the left humerus and both coracoids).

The estimated density for this area is 0.00054 disarticulated bones/m²; 0.000024 occurrences of articulated bones/m²; and 0.0000081 carcasses/m². The majority of the penguin remains were found directly on the surface (93%), or slightly covered by sediments (6.6%). Only one of the penguin remains was identified as buried (0.4%). The backshore and active dunes present an important internal variation (micro-environments). The majority of the remains (n = 198; 93%) were registered in the beach berms and deflated interdune sectors, while the rest were around interdune ponds, marshes, and small temporary lakes (n = 15; 7%). The penguin remains were isolated (n = 96) or formed part of a concentration (n = 117, distributed in 10 concentrations). In the majority of the concentrations, the identified elements probably correspond to a single individual (MNI = 1); however, in one of the concentrations, at least three individuals (MNI = 3) were quantified.

In reference to the spatial location of the penguin remains, a decrease in the frequency was observed in relation to the distance from the shoreline (see Supplementary data Table B). The correlation between these two variables is statistically significant (Spearman rho = -0.66; p = 0.027). The highest density of remains was observed in transects between 0 and 400 meters from the shoreline (0.001 remains/m²). This sector of the coast corresponds to the backshore and the beginning of the dunefield. An interesting feature observed was the presence of penguin remains more than 1000 m from the shoreline. The outermost finding occurred at 1065 m off the shoreline, on the edge of an interdune lake, and corresponds to an occurrence of articulated bones (pectoral girdle and wing).

6.3.1. Skeletal part representation

Among the disarticulated bones and the occurrences of articulated bones, elements from all the anatomical skeletal regions were identified, although some regions, such as limbs and pectoral girdle were over-represented (Table 2; Supplementary data Fig. B). The pectoral girdle was the best represented anatomical region, with coracoids as the most abundant element (MNE = 30; %MAU = 100). The wings



Fig. 4. Two penguin carcasses gnawed by carnivores recovered at 410 m from the shoreline along an interdune lake in the active dunes.

¹ The similarity between the MNE and NISP is due to the fact that most of the penguin bones were found complete (79%); or in cases of incomplete bones, the portion which survived was generally the same (e.g., coracoids facets of the sternum; proximal portion of the scapula).

Table 2
Anatomical representation of Magellanic penguin.

Anatomical region	Anatomical unit	DB		OAB		TOTAL		
		MNE	%MAU	MNE	%MAU	MNE	%MAU	MNI
Axial skeleton	Cranium	2	17.4	1	25	3	20	3
	Mandible	1	8.7	1	25	2	13.3	2
	Cervical vertebrae	22	12.8	4	6.8	26	11.5	2
	Thoracic vertebrae	7	8.7			7	6.7	1
	Vertebrae indet.	3				3		
	Pygostyle	1	8.7			1	6.7	1
	Ribs	12	5.8	16	22.2	28	10.4	1
	Sternum	5	43.5	1	25	6	40	6
	Furcula	2	17.4	1	25	3	20	3
	Pectoral girdle	Scapula	9	39.1	8	100	17	56.7
Coracoid		22	95.6	8	100	30	100	15
Wing	Humerus	23	100	5	62.5	28	93.3	15
	Radius	13	56.5	2	25	15	50	8
	Ulna	12	52.2	2	25	14	46.7	9
	Ulnar carpal	1	4.3	1	12.5	2	6.7	2
	Carpometacarpus	6	26.1			6	20	4
Pelvic girdle	Hemi-pelvis	5	21.7			5	16.7	3
	Synsacrum	7	60.9			7	46.7	7
Leg	Femur	22	95.6	2	25	24	80	12
	Tibiotarsus	15	65.2	3	37.5	18	60	11
	Fibula	3	13	3	37.5	6	20	3
	Tarsometatarsus	2	8.7	1	12.5	3	10	2
Total		195		59		254		

DB: disarticulated bones; OAB: occurrence of articulated bones.

were represented mainly by the humerus (MNE = 28; %MAU = 93.3), and the legs by the femur (MNE = 24; %MAU = 80). The proportion of wing and leg elements were similar (wing = 51.6%; leg = 48.4%). Some limb bones were infrequent or absent, particularly distal elements such as carpometacarpus, carpals, tarsometatarsus, and phalanges (Table 2). Elements from the axial skeleton were under-represented. The most frequent element from this region was the sternum (MNE = 6; %MAU = 40). Only three incomplete skulls, two mandibles, and few vertebrae and ribs were recorded.

6.3.2. Taphonomic modifications on disarticulated bones

Considering that the action of some taphonomic processes is directly related to the micro-environment, it is important to mention that the majority of the disarticulated bones were found in the backshore and deflated interdune sectors (n = 191) and the rest were found around interdune ponds, marshes, and small temporary lakes (n = 10). One process that highly affected penguin specimens was sedimentary abrasion (75%) (Table 3). Varying degrees of abrasion were recorded, from a slight cortical polished surface to a complete loss of cortical tissue and the exposure of underlying cancellous tissue.

Also important are the effects of weathering (51%) (Table 3; Fig. 5). The majority of the weathered specimens were identified in stage 1. The most advanced stage observed was 4, but only in a small proportion of the sample. On the other hand, breakage affected 21% of the bones.

Table 3
Relative frequencies of taphonomic modifications on Magellanic penguin remains.

Taphonomic variables	DB	OAB	C
Sedimentary abrasion	74.6	33.3	0
Weathering	Stage 0	49.2	88.9
	Stage 1	26.4	11.1
	Stage 2	10	0
	Stage 3	11.9	0
	Stage 4	2.5	0
Breakage	21.9	n/a	n/a
Root etching	1.5	11.1	0
Predator marks	13.4	66.7	100

DB: disarticulated bones; OAB: occurrence of articulated bones; C: carcasses; n/a: not applicable.

The percentage of weathering is higher in the fractured bones (73%) compared to the complete elements (45%), suggesting that this process had an important role in breakage. Root etching was registered in only a few remains, while rodent and trampling marks were completely absent.

Predator action was registered in 13% of the specimens (Table 3). Marks were identified on elements of all anatomical portions, the pelvic girdle portion being the most affected. The most frequently identified type of modification were perforations (77%), which could be attributed both to birds of prey or mammalian carnivores. Also identified were carnivore pits (65%), scoring (42%), and crenulated edges (19%) (Fig. 6).

6.3.3. Taphonomic modifications in occurrences of articulated bones and carcasses

The total number of carcasses and conjoined bones was low (n = 12); therefore, only a general characterization of taphonomic modifications was made. Given that many of the bone elements were protected by soft tissue, sedimentary abrasion and weathering were lower compared with the disarticulated bone sample (Table 3). A prominent feature was the high frequency of remains affected by carnivores (n = 9). Carnivore modifications were observed in both the soft tissue and on some exposed bone elements (Fig. 4).

7. Discussion

7.1. Deposition and accumulation of Magellanic penguin remains along the coast of the Pampas region

Magellanic penguin remains dominate a modern vertebrate assemblage from the coast of the Pampas region. In the locality Balneario San Cayetano, penguin bones and carcasses considerably outnumber the remains from other terrestrial and aquatic birds inhabiting this coastal ecosystem. The abundance of penguin remains is related to the beaching of this seabird during seasonal migration. As expected in non breeding locations, remains of very young and immature individuals were not identified. The penguin remains were determined mainly as adult and secondly as subadult. Nevertheless, the minimal number of subadult individuals cannot be precisely estimated since some of the remains determined as adult could correspond to bones from younger individuals that mature early.

Most of the penguin remains were disarticulated bones. Only a few occurrences of articulated bones and three carcasses were recorded. The presence of penguin remains in different stages of decay – from complete carcasses to isolated bones in advanced weathering stages – suggests that the assemblage from this locality is attritional. Time averaging can inflate the abundance of species with more robust skeletal elements. In this sense, the particular structure of penguin bones could favor a late decay and contribute to its higher frequency compared with other vertebrates (Cruz, 2007).

Penguins arrived to the coast as floating carcasses or near-death individuals. Animals which died in the ocean probably presented some degree of decomposition because of aquatic decay and scavenging by seabirds. Once the carcasses were deposited on the beach, further natural processes contributed to soft tissue decay, disarticulation, and spatial dispersal of bones. Tides and waves displaced the remains from the original deposition, causing carcass accumulation in particular locations, such as storm berms along the backshore, where the highest density of remains was recorded. Predators were also responsible for disarticulation and dispersal of carcasses. Additionally, they contributed to bone damage, conditioning the pattern of skeletal representation. During the survey, no live predators were directly observed feeding on remains, so it was not possible to determine the exact species involved in the modification of penguin carcasses. The best candidates are the Pampas fox, and local birds of prey, such as gulls and raptors. Previous studies of natural bone accumulations in penguin colonies from Patagonia suggested these predators regularly scavenge carcasses (Cruz, 2007).

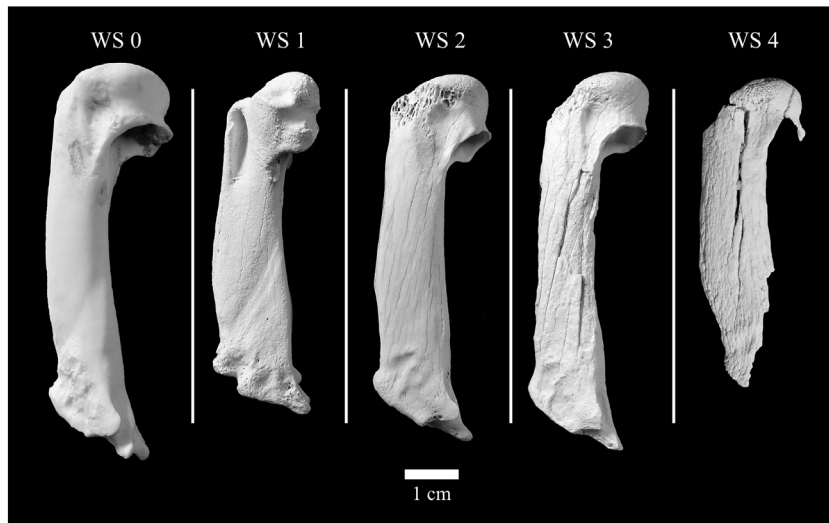


Fig. 5. Examples of stages of weathering (WS) in disarticulated penguin humerus.

In this region, the action of gulls and raptors was the most common, although the bone modifications were scarce and located mainly on the sternum and ribs. Foxes were also observed feeding on the penguin carcasses, acting mainly on the hindlimbs. Other important observation from this study was that while bird predation and scavenging took place *in situ*, foxes occasionally transported carcasses or bone portions (Cruz, 2007). In our study, foxes were probably responsible for the inland transport of carcasses and body portions, in some cases long distances from the shoreline (Gutiérrez et al., 2015). The three penguin carcasses recorded during the survey were likely transported by this predator from the beach to vegetated interdune areas. This location would have been selected by the carnivores for its vegetation cover which provides protection from competitors. Predator modification of carcasses is higher in the Balneario San Cayetano, compared with the samples from

Patagonia. Cruz (2007) claims that the high penguin mortality, which is temporally and spatially concentrated in the colonies, along with the low levels of carnivore competition, promotes light carcass utilization.

After soft tissue decay, weathering and sedimentary abrasion affected the bones. The penguin sample shows weathering stages from 0 to 4, prevailing fresh or slightly weathered bones. Several authors noted that a low frequency of bones in high weathering stages may result from a quicker disintegration after reaching stage 1 (Behrensmeier et al., 2003; Cruz, 2007; Muñoz and Savanti, 1998). In the case of bones deposited along the backshore, the continual variation in moisture associated with tides and the precipitation of salts from the underlying substrate could accelerate weathering (Behrensmeier, 1978). On the other hand, a high frequency of fresh remains could be the result of an increase in the number of beached penguins shortly before the survey. In relation to this, it is important to point out that the survey made by the conservation project already mentioned showed an uneven monthly distribution of Magellanic penguin, with two peaks in March and July (ECOFAM Final Report, 2010).

Sedimentary abrasion was very common in the sample of disarticulated bones. Considering that the majority of bones were recorded in the backshore and deflated interdune areas, this was probably caused by sand particles transported by water and wind. The predominance of erosion processes in the backshore and active dunes precluded the long term burial of penguin remains. On the surface, the combined action of water, predators, weathering, and physical abrasion on penguin remains promoted a fast decay of carcasses and bones. Consequently, even though the surface assemblage is time averaged, the period of time implicated in the accumulation was probably short (in year or decadal scale).

Natural processes involved in the formation of the penguin bone assemblage in the Pampas are similar to those acting in the colonies. However, an important difference is the high impact of trampling in the breeding locations, where penguins go from nests to the sea daily by using the same paths (Cruz, 2007). This process produces disarticulation and burial of remains but it is also one of the main causes of fragmentation.

In relation to the skeletal part representation in the penguin assemblage, limbs (primarily humerus and femur) and pectoral girdle elements (mainly coracoids) are the most abundant. The proportions of wing and leg elements are approximately equal, and for both regions, distal elements are scarce. Bones from the axial skeleton, in particular cranium, mandibles, vertebrae, and ribs are infrequent. The differential representation of penguin skeletal elements could result from a

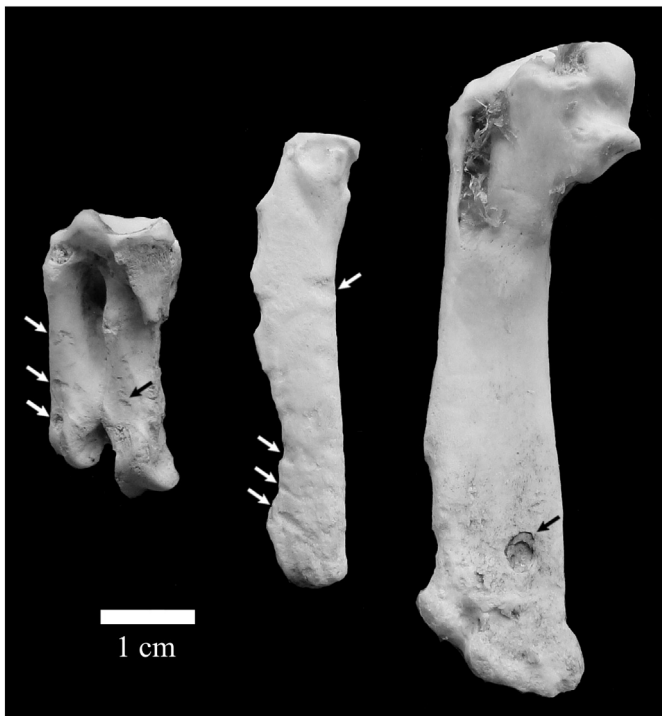


Fig. 6. Examples of carnivore modifications in penguin bones. From left to right: tarsometatarsus with multiple pitting; radius with scores and crenulated edges; humerus with puncture.

combination of different factors, such as the structural bone properties, the disarticulation sequence, and the action of natural taphonomic processes.

Structural bone properties are considered of great importance because they can affect bone survivorship (Cruz, 2007; Higgins, 1999; Livingston, 1989; Serjeantson, 2009). Although bone density data is not available for penguins, other characteristics of their limb bones could partly explain their over-representation in our sample. The penguin limb bones, adapted for diving, present a reduced pneumatization and a thicker cortical wall compared to those of other birds (Triche, 2007). These properties could make them more resistant to destructive taphonomic processes. The element survival could also be related to the time of disarticulation because this process increases the exposure of elements. The abundance of wing and pectoral girdle elements in the sample of articulated bones suggest that these portions were the last to disarticulate. This observation agrees with the natural disarticulation pattern for bird skeletons observed under varied conditions. The cranium, the cervical vertebrae, and the ribs are the first to disarticulate, followed by the legs from the pelvis, the synsacrum from the thoracic unit, the scapula, coracoid, and the wing elements (Cruz, 2007; deFrance, 2005; Serjeantson, 2009).

Predator action and weathering were probably the main taphonomic processes affecting skeletal part representation in the locality Balneario San Cayetano. The combined action of birds of prey and foxes could partly explain the low representation of axial and distal limb elements. Nevertheless, the low frequency of distal limb bones could also be a consequence of methodological bias against smaller bones which present less visibility.

Despite differences in origin and processes involved in the formation of the bone assemblages, the pattern of penguin skeletal part representation from Balneario San Cayetano shows similarities with the element survival in modern and abandoned breeding colonies. The study conducted by Cruz (2007) at two active Magellanic penguin breeding colonies (Cabo Virgenes and Punta Medanosa) in Patagonia shows an abundance of limb and pectoral girdle elements and a low frequency of axial elements (see Supplementary data Table C). The skeletal part distribution from San Cayetano is not significantly different from Cabo Virgenes ($X^2 = 8.04$; $P = 0.090$) but is significantly different from Punta Medanosa ($X^2 = 18.77$; $P = 0.0008$). The main difference between the Balneario San Cayetano and the Patagonia samples is the lower proportion of axial elements in the later. This could be related to a higher incidence of predation by birds in the samples from Patagonia. Another factor that could affect the survival of axial elements in the colony samples is the recurrent trampling by penguins, which plays an important role in carcass disarticulation and bone fracture (Cruz, 2007).

A similar pattern of element survival was also recorded by Emslie (1995) at modern and abandoned rookeries of pygoscelid penguins in Antarctica. In both samples, elements from the limbs and the pectoral girdle were the most abundant, and axial elements were scarce. Nevertheless, some differences exist between our sample and those studied by Emslie (1995); in particular, the higher proportion of tibiotarsus and furcula in his sample. This difference could be related to the specific ecological and environmental conditions of Antarctica (e.g., absence of mammal predators) which probably conditioned the taphonomic history of the penguin bone assemblages.

The similarity in the pattern of skeletal part representation between our sample and the samples from the colonies is noteworthy considering that the age representation in both types of samples is different. Colony samples are dominated by juveniles, which represent more than 70% in Emslie (1995) samples; while in our sample all the bones correspond to subadults and adults. This suggests that age distribution did not considerably affect the skeletal part representation.

The comparison between the bone assemblages reveals a distinct pattern in penguin element survival, despite important differences in age structure, type of location (breeding versus non breeding site), ecological and environmental context (e.g., predators populations),

and the time involved in the formation of the deposit. Our study corroborates the proposal by Cruz (2007), that the element survival in penguin is different from other types of birds. The few available studies of natural avian assemblages suggest that wing elements dominate in flying birds, whereas leg elements dominate in flightless birds (Cruz, 2011; Muñoz and Savanti, 1998). On the other hand, bones from both limbs are equally represented in the natural accumulation of penguin bones. If element survival is related to the functional anatomy, as some authors propose (Cruz, 2007; Livingston, 1989; Muñoz and Savanti, 1998), a similar pattern could be found in other birds like penguins that propel themselves in water primarily using their forelimbs.

In summary, the taphonomic evidence presented here indicates that although Magellanic penguin dominates a natural modern assemblage from the Pampas region, it has a low chance of becoming part of the fossil record. Natural processes such as weathering, and modification from predators prompts the fast dispersion and destruction of the penguin remains. Additionally, many of the bone concentrations were located on storm berms or deflated interdune areas, micro-environments that do not favor burial. Due to the high-energy sediment reworking of these coastal sub-environments, the chances of complete burial of carcasses, articulated bones, or a dense concentration of bones is very low; therefore, the formation of a bonebed containing penguin remains in this particular setting is not expected. There are however other micro-environments that could favor the preservation of vertebrate remains for longer periods of time. These are the interdune ponds, marshes, and small temporary lakes, where the diminished erosion (due to the more extended vegetation coverage) and the lacustrine sedimentation could contribute to the burial of the remains. Furthermore, in this type of setting, weathering proceeds more slowly because vegetation coverage decreases the effects of destructive environmental processes (Behrensmeyer, 1978).

7.2. Implications of the natural deaths of Magellanic penguin for the archaeological record of the Pampas region

Faunal remains from archaeological deposits can have a cultural or a natural origin. As archaeologists, one of our main interests in taphonomy is to determine if people were responsible for incorporating these remains. In the Pampas region, penguin bones are present in a few coastal archaeological sites. Our study of a modern assemblage of Magellanic penguin remains from natural deaths provides useful information to evaluate the probability of natural incorporation of bones from this species into archaeological deposits. Additionally, archaeological data combined with biological information on modern penguin distribution, migration patterns, and mortality allow us to derive expectations on regional availability and quality of penguins for past human populations.

The archaeological record from the Pampas coast consists of mostly surface assemblages of lithic artifacts in the active dune sector and a few deposits in stratigraphy (Bonomo, 2005). The few bones recovered in these assemblages constitute the only evidence to evaluate the importance of faunal coastal resources for the subsistence and technology of hunter-gatherer populations. Our results indicate that the natural incorporation of modern penguin bones into these archaeological sites can be expected, especially in the surface assemblages located close to the present shoreline. The finding of both lithic artifacts and penguin remains in a few transects during our survey supports this idea. Archaeologist working in surface sites should strongly consider the possibility of a natural origin in case of occurrence of penguin bones, mostly elements of higher survival potential (e.g., humerus and coracoids), without human modifications. The isolated penguin bone recovered in the site El Americano II is a good example of this situation. The intrusion of naturally deposited penguin bones in surface assemblages could also have occurred in the past, assuming that the biological and geological conditions controlling the deposition of penguin remains were similar to the present ones. However, the taphonomic analysis presented

here indicates low chances of burial in the backshore and deflated interdunes, where the surface archaeological evidence usually occurs (Bonomo, 2005). Accordingly, buried archaeological contexts in ancient beach and dune deposits containing intrusive penguin bones are unlikely.

Nevertheless, there are particular settings in the coastal environment where penguin remains were recorded, which do favor bone preservation and burial: interdune ponds, marshes, and small temporary lakes. As proposed above, carnivores could transport penguin remains to these places, sometimes moving the bones long distances from their original deposition site (Gutiérrez et al., 2015). It is important to point out that ponds, marshes, and lakes were also selected for campsites by hunter-gatherers in the past because of the presence of fresh water and faunal resources (Bonomo and Leon, 2010; Blasi et al., 2013; Bayón et al., 2012). Therefore, penguin bones transported by carnivores could be mixed with culturally deposited materials. In this type of context, an examination of the bones for the presence of cultural and carnivore modifications is needed to determine their origin. These results call attention to the problem of two common criteria used to sustain human consumption in the absence of cultural modifications on the bones: the spatial association between remains and archaeological artifacts; and the occurrence of remains far away from the natural habitat of the species, frequently attributed to human transport. In sum, interpretation on penguin exploitation in archaeological sites should be based on detailed taphonomic analyses of the bones together with taxon-dates.

Despite the limited faunal evidence in the Pampas coast, one stratigraphic site shows the human exploitation of penguin. The presence of a few penguin remains in the Alfar site suggests the procurement of solitary individuals at least during the Middle Holocene. As mentioned above, there is no data on the location of breeding colonies in the Pampas region during prehistoric times. Thus, if the penguin feeding areas were at or close to the current location, it is likely that the occurrence of these birds along the coast was a consequence of beaching during migration periods as is currently observed. On the other hand, the southernmost distribution of the breeding colonies and the absence of petroleum pollution and overfishing in the past, suggest that these marine birds beached in a lower frequency in this area. Even though penguins could have been a potential resource for hunter-gatherer populations of the Pampas region during prehistoric times, this seabird would have been scarce. While the beaching of penguins along the coast is seasonal they are available in a broad range of time. Additionally, considering that most individuals arrive at the beach in bad health, they were probably not an attractive food resource. The skeletal remains could have also been used as raw material for bone tools, as observed in archaeological contexts from Patagonia (e.g., Tivoli, 2014); however, evidence for tool manufacture in the Pampas is lacking.

8. Conclusions

In this paper we analyzed an attritional bone assemblage from the coast of the Pampas region formed as a result of the beaching of Magellanic penguins during seasonal migration. This study allowed us to characterize a natural deposit generated outside breeding locations and compare it with assemblages from colonies. Our data contributes to the interpretation of the archaeological record from this region and similar environmental settings. As we have shown, the natural incorporation of bones from this seabird into archaeological sites located in non-breeding areas can be expected but would not be frequent. In this case, our study provided useful information to identify natural versus anthropic bone deposits. The combination of biological and archaeological information showed that penguins were not an attractive food resource for past human populations in the Pampas region given their scarcity and poor nutritional condition.

Additionally, our results help to identify if a fossil assemblage corresponds to a breeding or non-breeding penguin location, which is useful

for paleobiogeographical reconstructions. Some of the properties previously proposed to characterize a colony assemblage, such as the higher representation of penguin bones over other taxa, and the skewed anatomical representation toward limb and pectoral girdle elements are shared with our sample. The main differences between both types of deposits are the spatial density of remains and the age class profile. Finally, further research on this topic will contribute with the knowledge of ecology and biology of the Magellanic penguin, particularly in relation to mortality, nutrition, and predator-prey interaction.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at <http://dx.doi.org/10.1016/j.palaeo.2015.06.045>. These data include Google map of the most important areas described in this article.

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