

Avian and mammalian bone taphonomy in southern continental Patagonia: A comparative approach

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Abstract

In southern Patagonia, the occurrence of large seabird nesting colonies condition the features of the regional bone record, which is characterized by a large amount of bird remains, despite their small body size. Bird and mammal bones have remarkably different taphonomic histories in this region: mammal remains are less damaged by carnivores and resist weathering for long periods, whereas bird bones show a greater initial destruction by carnivore activities and faster deterioration by weathering. A comparison of these results with results from research conducted in several African parks (particularly Amboseli) shows that differences in both records are mainly due to differences in community composition and predator–prey dynamics in both ecosystems. Furthermore, while in both ecosystems bird bones weather more rapidly than mammal bones, destruction by this process is more rapid in Patagonia. Overall, the analysis reinforces the need to generate specific models to understand taphonomic histories of archaeofaunal assemblages from Patagonia.

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1. Introduction

Taphonomic processes are ecological in nature, and both faunal community composition and trophic relationships are aspects that influence the preservation of remains in a given environment. This paper presents the results of actualistic taphonomic studies conducted in southern continental Patagonia, which aimed at understanding the way natural taphonomic processes modify vertebrate remains in the region, especially avian remains. These studies consisted of the survey of the surface bone record along transects covered on foot at four localities in the region (Cruz, 1999, 2000, 2003, 2004, 2007a, b).

Patagonia is a huge peninsula in the southernmost portion of the South American continent, between 39° and 55° S. All throughout its territory, Patagonia coastal and continental habitats exhibit remarkable differences in their faunas, especially regarding bird diversity and biomass, which are particularly marked on the coast. These differences between coastal and inland communities determine the preservation and destruction of vertebrate remains, since such differences may influence, among other

factors, the rate of deposition, the places where remains will be more likely deposited, or the intensity of taphonomic agents.

Since the beginning of this research, observations were conducted within a comparative approach. First, the impact of taphonomic processes under different environmental and ecological conditions was evaluated. With the aim of evaluating the influence of the characteristics of faunal communities on bone record composition, surveys were conducted in several localities of southern Patagonia, covering important habitats in the marine coast, the steppe and inland wetlands.

Second, the way taphonomic processes, especially weathering and carnivore activities, affect avian and mammalian remains was examined in each habitat. Given the differences between the skeletons of these vertebrates, destruction and preservation factors are expected to affect them differently, even in the same environment.

Finally, the results obtained were compared with results from studies conducted in other parts of the world, with the aim of evaluating if such models are useful to understand archaeofaunistic records from Patagonia, even when they were generated under different environmental and ecological conditions. This is the case, for example, for models of carnivore activity generated in Africa and North

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America, where carnivores and ecosystems are very different from the ones in Patagonia.

To sum up, this paper characterizes the vertebrate record surveyed in southern Patagonia, indicating differences and similarities in the marine coast, the steppe and continental wetlands. Then, taphonomic features of the bones assemblages are examined, to evaluate the way weathering and carnivore activity affect avian and mammalian remains. Finally, these results are compared with those obtained in several African parks (especially Amboseli), and some of the taphonomic peculiarities of southern Patagonia are provided.

2. Environments and fauna in southern Patagonia

Southern Patagonia has many of the typical features of the entire region, where the characteristics of the relief and climate conditions determine the wide distribution of the steppe, which covers the entire plateau and portions of the Andes range (León et al., 1998; Oliva et al., 2001). However, due to the southern location, climate conditions are more severe, which in turn intensify aridity in the extreme of the continent (Mazzoni and Vázquez, 1999).

The Patagonian coast extends over 3500 km along the Atlantic Ocean, with alternating shingle or sand beaches and high cliffs, interrupted by large estuaries (Mazzoni and Vázquez, 2004). The nutrient-rich Malvinas (Falklands) current is a food source for large fish and invertebrate concentrations. Such highly productive coastal waters in Patagonia support a notable biodiversity, such as large concentrations of colonial seabirds and pinnipeds (Yorio, 1998). In southern continental Patagonia, species such as the Magellanic penguin (*Spheniscus magellanicus*) and the Imperial shag (*Phalacrocorax atriceps*) nest in colonies of thousands of individuals (Gandini et al., 1996; Albrieu and Navarro, 1997; Gandini and Frere, 1998; Malacalza, 1998; Yorio et al., 1998, among others). Besides penguins and cormorants, other characteristic birds of Patagonian coastal areas are several species of plovers, oystercatchers, gulls, petrels, and albatrosses (Frere and Gandini, 1998; Gandini and Frere, 1998, among others).

In continental lands, from the Andes range to the east, the Patagonian steppe is the predominating environment, covering a large portion in the south of the region that is characterized by the presence of huge plateaus (Mazzoni and Vázquez, 2004). Low environmental productivity and low structural diversity of habitats in the steppe, unlike those in the coast, produce a low biomass of terrestrial vertebrates (Canevari et al., 1991; Redford and Eisenberg, 1992). Compared to different regions of the world, the Patagonian steppe has low bird species diversity (Fjeldså, 1988; Vuilleumier, 1993), decreasing from north to south along with decreasing plant diversity. Hence, the open steppe in the south of the continent is where the lowest bird diversity occurs (Vuilleumier, 1993, 1995). Among the characteristic bird species of the steppe are the lesser rhea (*Pterocnemia pennata*), a large ostrich-like bird, and

tinamids (Fjeldså, 1988). Regarding mammals, the guanaco (*Lama guanicoe*), one of the wild South American camelids, is the largest herbivore in the region, whereas the puma or American lion (*Felis concolor*) is the largest carnivore. Other wild mammals characteristic of the steppe are the South American little foxes (*Pseudalopex griseus* and *P. culpaeus*), the little hairy armadillo (*ChaetophRACTUS villosus*), the “mara” or Patagonian hare (*Dolichotis patagonum*), the skunk (*Conepatus humboldti*), and other mustelids, as well as several small rodents species. In this predominantly arid environment, wetlands are especially suitable for the fauna, particularly those locally known as “mallines” or “vegas”, which are very common in Patagonia. “Mallines” are highly important for birds, some of which are directly associated with these habitats (Martín, 1984; Iglesias and Pérez, 1998). Among the characteristic bird species of Patagonia wetlands are the “cauquenes” or geese (*Chloephaga* spp.) and other Anatidae, as well as flamingos (*Phoenicopterus chilensis*), ibis (*Theristicus melanopsis*) and grebes (*Podiceps* spp.).

Although the faunal biomass in the different habitats has not been quantitatively estimated, there is consensus among authors that it is greater in the coastal area, because of the presence of hundreds of thousands of seabirds in nesting colonies (Canevari et al., 1991; Frere and Gandini, 1998; Gandini and Frere, 1998; among others) and of the predominance of large marine mammals in the south of the continent (Redford and Eisenberg, 1992).

3. Locations surveyed

Fig. 1 shows the locations where observations were performed. The environmental characteristics of these sites and transect layout in each of the habitats are as follows:

- (1) Perito Moreno National Park (47° 40' S, 72° 30' W) is located near the Andes. The landscape is mainly the result of glacial processes, where steppes, grasslands and “mallines” predominate. Transects were laid parallel to the coasts of several bodies of water (glacial lakes, permanent and temporary ponds), in plains and moraines in the steppe, as well as in several sectors of the steppe–Patagonian–Andean forest ecotone (Cruz, 2000, 2003).
- (2) Gallegos River (51° 35' S, 70° 30' W) has an extensive valley that has been shaped by fluvial, glacial and volcanic action (Mazzoni and Vázquez, 2004). Vegetation in the region is a xeric grass steppe. Transects were laid out on different terraces and the floodplain of the river valley, on several basaltic terraces, on the marine coast adjacent to the estuary, and in the nesting areas of Imperial shags (Fig. 2) and Kelp gulls (*Larus dominicanus*) on an island in the estuary (Cruz, 2007a).
- (3) Cabo Virgenes Provincial Reserve (52° 22' S, 68° 24' W) is located in the southeastern tip of the continent, near the Strait of Magellan. Beach ridges and salt marshes

alternate in this location. Grass steppe predominates, with patches of bush steppe. A colony of Magellanic penguins with about 180,000 reproductive individuals is established here. Transects covered sectors within and outside the nesting area. Three of them were placed in the area with the highest nest density, two were laid at the western boundary of the colony, ranging sectors with a smaller number of nests and farther from the sea, and the last one was located along the eastern boundary of the colony, which is the area over the sea (Cruz, 1999, 2007b).

- (4) Punta Medanosa (48° 06' S, 65° 55' W) is an area of considerable environmental variability, with a conse-

quently higher diversity in marine and coastal avian species (Gandini and Frere, 1998), such as Magellanic penguins and several species of cormorants. Several transects were set at different distances from the present-day marine coast as well as on Quaternary beach ridges. Transects also were laid out in two inland ponds with the aim of monitoring the habitat of aquatic and terrestrial birds in the area (Cruz, 2003, 2004, 2007b).

4. Methodology

Similarly to other researchers that have conducted modern observations aimed at understanding several aspects of vertebrate taphonomy (e.g., Behrensmeyer and Dechant-Boaz, 1980; Blumenschine, 1989; Behrensmeyer, 1993; Sept, 1994; Tappen, 1995), the surveys were done by direct observation of the superficial bone record, along several 10 m-wide foot transects of varying length. A thorough and intensive bone search was performed walking along each transect, and the recorded data included: type of substrate, species and skeletal parts identified, distribution of bone remains, bone articulation, carcass completeness, weathering stage, burial condition, and bone modifications (fractures, predator damage, etc.). The results presented in this paper correspond to the bones surveyed. Results from carcasses were presented elsewhere (Cruz, 1999, 2003, 2004, 2007a, b; Cruz and Fernández, 2004).

The minimal number of elements (MNE) was estimated on the basis of the degree of completeness of elements, anatomical portions present, size, proximity, and possibility of assemblage. Based on field evaluations, it was considered that specimens present in different transects came from different individuals (following Behrensmeyer and Dechant-Boaz, 1980; Blumenschine, 1989; Sept, 1994; Behrensmeyer et al., 2003) and therefore from different

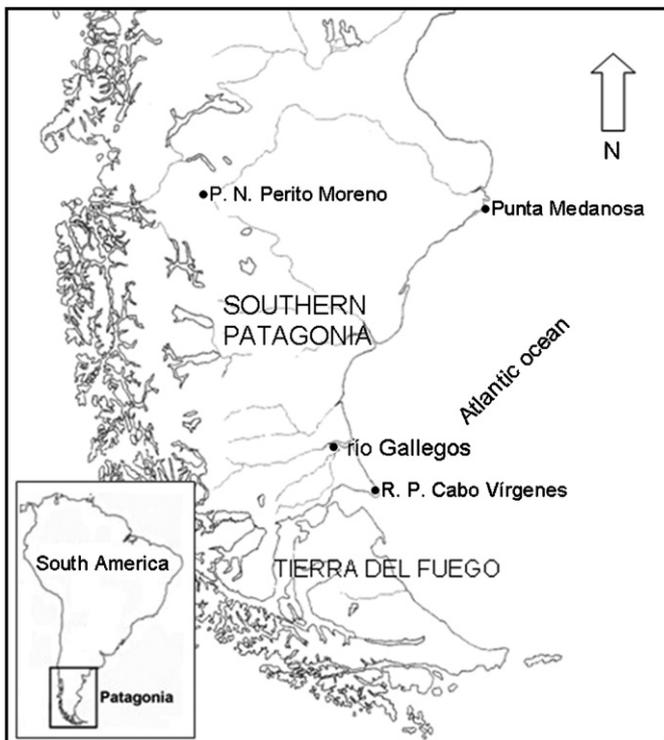


Fig. 1. Location of the four localities surveyed.



Fig. 2. Nesting area of Imperial Shags (*Phalacrocorax atriceps*) in the Gallegos River estuary.

elements. For operative reasons, within a transect it could only be determined that two specimens corresponded to the same element within a reasonable spatial proximity range, which results in a possible overestimation of the elements present in each transect.

Following Behrensmeyer and Dechant-Boaz (1980), a bone was considered buried when 50% or more of its surface was covered by sediments. Weathering was evaluated using the stages proposed by Behrensmeyer (1978). Morphological criteria used to define damage by carnivores are those defined by Binford (1981). Fractures include those produced by trampling or by indeterminate causes. Fractures produced by carnivores are included in damage by carnivores, whereas those associated with weathering are included in the corresponding stages, as indicated by Behrensmeyer (1978).

5. Results and discussion

5.1. Characteristics of the modern bird and mammal bone records

Table 1 summarizes some characteristics of the surveys conducted. Other details of the research in each site have already been published elsewhere (e.g. Cruz, 1999, 2000, 2004, 2005, 2007a,b; Cruz and Elkin, 2003). Transects covered a different area in each locality, accommodating to the need for covering habitat diversity in each location. There is no direct relationship between the size of the area surveyed and the amount or density of remains. The two locations with the smallest areas surveyed (Cabo Vírgenes and Punta Medanososa) exhibited higher bone density per spatial unit.

MNE values obtained per habitat type in each site are listed in Table 2. The spatial distribution of organic remains and the association with specific environmental features are related to organisms' use of space and to preservation or destruction factors that vary in space. In southern Patagonia, coastal habitats comprise 60% of the remains. This high percentage is related to the great

mortality of chicks and juveniles occurring in the nesting areas of seabirds (Cruz, 1999, 2004, 2007b). This great amount and concentration of available carcasses results in lesser destruction of individual carcasses by carnivores in coastal habitats (Cruz, 2003, 2004, 2007b). It can thus be argued that, notwithstanding the body size, avian bones have high preservation potential in this ecological setting.

The wetlands contain 31% of the remains. In environments like those in Patagonia, wetlands are the portion of the landscape where predator–prey activities are concentrated, and therefore they are also loci with a relatively higher number of remains. In steppe habitats, however, deposition opportunities are lower and/or decay is higher (Cruz, 2003, 2007a); hence, the number of observed remains was the lowest (9%).

Table 3 lists the taxonomic composition of the modern bone record relative to habitat type. Avian bones are concentrated on the marine coast, whereas they are

Table 2
Bone distribution by habitat (only bones of birds and mammals)

Habitat	P.N.P.M.	R.G.	C.V.	P.M.	Total MNE ^a	% MNE
Marine coast	–	103	2095	1451	3649	60
Steppes	386	131	–	–	517	9
Wetlands	1649	85	–	171	1905	31
Total					6071	100

P.N.P.M.: Parque Nacional Perito Moreno (Perito Moreno National Park); R.G.: Gallegos River Valley; C.V.: Cabo Vírgenes Provincial Reserve P.M.: Punta Medanososa.

^aMNE includes only bones of birds and mammals.

Table 3
Taxonomic representation by habitat

	Marine coast MNE = 3649(%)	Steppes MNE = 517(%)	Wetlands MNE = 1905(%)
Birds	93	9	11
Mammals	7	91	89

Table 1
Characteristics of the bone samples

	P.N.P.M.	R.G.	C.V.	P.M.
Habitats	Steppes Wetlands	Steppes Wetlands	– –	– Wetlands
Surface surveyed	213.400 m ²	371.242 m ²	47.700 m ²	81.262, 5 m ²
Total MNE ^a	2035	319	2125 ^a	1628 ^a
MNE/m ²	0.009	0.0009	0.04	0.02
MNE mammals	1961	183	69	228
% MNE mammals	96.4	57	3.3	14
MNE birds	74	136	2026	1394
% MNE birds	3.6	43	95.4	85.5
MNE Mammals and birds	2035	319	2095	1622

^aTotal MNE includes bones from all recorded taxa (birds, mammals and fishes). P.N.P.M.: Parque Nacional Perito Moreno (Perito Moreno National Park); R.G.: Gallegos River Valley; C.V.: Cabo Vírgenes Provincial Reserve P.M.: Punta Medanososa.

remarkably scarce in wetlands and the steppe. In contrast, mammalian remains were recorded mainly in wetlands and the steppe, whereas in coastal habitats they were less represented.

Overall, the modern vertebrate bone record in southern Patagonia is characterized by the presence of greater numbers and relative densities of remains in the marine coast, whereas in the inland steppes and wetlands, remains and respective densities are lower. In the coastal area avian remains predominate, whereas in the inland steppe and wetlands they represent a very small part of the record. On the other hand, mammalian remains comprise the greatest part of remains in the continental region studied, especially in the wetlands. Considering all habitats together (Table 4), avian remains predominate, representing 60% of the total surveyed.

5.2. Taphonomic processes on avian and mammalian bones

With the aim of comparing how taphonomic processes are expressed in avian and mammalian remains, four of the variables evaluated—weathering, modifications by carnivores, fractures and burial—are summarized in Table 5.

Weathering is one of the most important processes leading to destruction of bones deposited on the land surface (Lyman, 1994). In southern Patagonia, weathering profiles of birds and mammals show different taphonomic histories (Fig. 3). Avian remains have a profile biased towards the lowest stages, with predominance of unweathered or slightly weathered bones and with higher stages scarcely represented or not represented at all. In contrast, the profile corresponding to mammalian remains includes all the stages, with 30% of the cases being included in the highest stages (3, 4 and 5).

Weathering is a historical process that implies the passage of taphonomic time, weathering stages representing points along the continuous process of bone decay. In general, destruction produced by weathering takes longer than other processes, such as carnivore activity. In Patagonia, the lack of bird specimens at the highest stages indicates rapid destruction mediated by this process. In contrast, mammalian bones show longer survival on the land surface, indicated by the presence of the higher stages.

Carnivore modifications are scarce in the remains of both vertebrates, but the percentage is higher in mammalian remains. Taphonomic studies conducted in Patagonia revealed that regional carnivores do not affect ungulate carcasses significantly, both because of predators' habits

Table 5
Modifications in bird and mammal bones

	Birds	Mammals
Unweathered	51%	27%
Stage 1	40.5%	23%
Stage 2	7%	21%
Stage 3	1%	22%
Stage 4	0.5%	6%
Stage 5	–	1%
Modifications by carnivores	1%	8%
Fractures	25%	42%
Buried	18%	14.5%
MNE	3630	2441

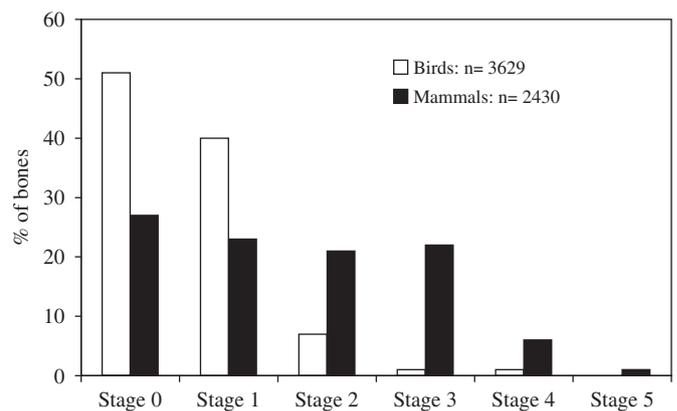


Fig. 3. Comparison of bones in different weathering stages for birds and mammals in the samples from Patagonia.

and limited bone damaging capacity (Borrero, 1989, 1990, 2000). However, due to their small body size and particular bone structure, birds constitute a special type of prey and when hunted and/or consumed by carnivores, destruction of their bones is almost complete (e.g. Bickart, 1984; Oliver and Graham, 1994; Cruz, 2000). Those bones that have not been destroyed often have few carnivore modifications. Hence, traces attributable to carnivore activity are scarce.

The percentage of bone fractures is greater in mammal bones than in bird bones. Fractures may be the direct result of weathering or because more advanced stages promote or facilitate fracturing by other mechanical processes. The number of fractures may be the result of the amount of time elapsed since deposition. The longer the time elapsed, the higher the probability of taphonomic processes producing fractures. In southern Patagonia, trampling is very intense and is one of the main causes of destruction of ungulate (Borrero, 1989, 1990, 2007) and bird bones (Cruz, 2000, 2007a, b). Therefore, this process is likely to be the main cause of the fractures observed. As bird bones that survive this and other taphonomic processes are scarce, the bones surveyed have a lower number of fractures than mammal bones. Regardless of the process leading to fracturing, the number of fractures indicates that

Table 4
Bird and mammal representation

	MNE	% MNE
Birds	3630	60
Mammals	2441	40
Total	6071	100

mammalian remains have longer taphonomic histories than those of birds.

Because of their smaller size, bird bones are expected to be covered by sediments earlier than mammal bones. Table 5 shows that the percentage of bird bones buried is higher. However, burial mainly depends on the substrate where bones are deposited (Borrero, 1989; Lyman, 1994, among others). Of the localities surveyed, only Punta Medanosa has sandy sediment, which is suitable for remains to be covered through several processes, including aeolian sediment transport, trampling, or burrow digging by birds (Cruz, 2007b). In general, bird bones will be destroyed before being buried, except in some particular loci like rocky shelters or sectors where sediment accumulation prevails (Cruz, 2000, 2007a). Mammal bones, however, are more resistant to taphonomic processes and therefore are more likely to be covered by sediments under different contextual conditions (Cruz, 2003, 2007a).

The results obtained indicate that in southern Patagonia, bones of birds and mammals have different taphonomic histories. Destruction of mammal bones is the result of a long period of exposure and is mainly produced by weathering. In contrast, depending on the environment of deposition (see Cruz, 2004), bird bones are subject to more complete initial destruction by carnivores, and the bones that survive this process remain on the surface for a shorter period because other taphonomic processes at work rapidly destroy them.

5.3. Comparison with Amboseli and other African parks

Taphonomic models widely used in zooarchaeological analyses have been generated on the basis of observations performed in several fauna reserves in Africa (e.g. Behrensmeyer, 1978, 1993; Behrensmeyer and Dechant-Boaz, 1980; Blumenschine, 1989; Sept, 1994; Tappen, 1995; Behrensmeyer et al., 2003). The results obtained in southern Patagonia present some differences and similarities with respect to those obtained in the African parks. This paper addresses only two aspects: the amount of small vertebrate remains observed and the effect of weathering on destruction of avian and mammalian bones.

One of the topics of greatest interest in paleoecological studies is the differential preservation of diverse taxa, especially those of different body sizes. This is an important aspect because, as Behrensmeyer and Dechant-Boaz (1980) state, a more detailed knowledge of the manner in which taphonomic processes affect different-sized organisms will contribute to a better understanding of some aspects of the community structure in the past.

The studies conducted in Africa revealed that in those ecosystems body size has important effects on the survival and collection of bones of small-sized animals. In Amboseli, remains of birds (Behrensmeyer et al., 2003) and of other small vertebrates (Behrensmeyer and Dechant-Boaz, 1980) represent a small portion of the bones surveyed. Similar results have been reported for the Serengeti (Blumenschine,

1987, 1989) and Virunga National Park (Sept, 1994; Tappen, 1995). In contrast, at a regional level, results of the survey in Patagonia show a predominance of bird bones. This large amount of bird remains is related to the particular taphonomic dynamics of breeding colonies. These colonies are loci where remain deposition is high and in which carnivores mainly consume and modify soft tissues of seabird carcasses (Cruz, 1999, 2003, 2004, 2007b). This case shows that, under ecological conditions different from those in the African parks, remains of small vertebrates are more likely to be preserved.

Knowing how and to what degree carnivores affect remains deposited helps us understand the different representation of small vertebrates. In the African parks, the high initial destruction of remains is basically an effect of carnivores, which in general are large-sized, have a great ability to destroy bones, and often hunt in group. These conditions are completely different in Patagonia, where carnivores are medium to small-sized (Redford and Eisenberg, 1992), usually have a lower capacity of destruction than carnivores from the northern hemisphere, do not process bones with the same intensity as do some African carnivores, and in general hunt alone or in pairs (Borrero, 1989, 2000, 2007).

However, the effects of weathering in Amboseli (Behrensmeyer et al., 2003, Fig. 4) and in southern Patagonia are similar. In both places, weathering profiles of bird bones are biased towards the lowest stages, whereas profiles of mammal bones present higher percentages in the higher stages.

In Amboseli, bones of both birds and mammals show a unimodal distribution in terms of weathering stages (Behrensmeyer et al., 2003). However, a distribution peak in stage 2 characterizes mammalian bones, whereas bird bones peak in stage 1. It appears that after reaching stage 2, weathering accelerates, rendering examples of stages 4 and 5, relatively rare: only 9% of avian bones, as opposed to 21% of mammalian bones. According to Behrensmeyer et al. (2003), the dominance of avian bones in stage 1 is the result of their tendency to weather more rapidly than bones of adult mammals. Based on the weathering profiles presented in Table 5, this conclusion is valid for remains surveyed in Patagonia (Cruz, 2000, 2003, 2004). However, the comparison of weathering profiles of avian bones from Patagonia (Fig. 3) and from Amboseli (Behrensmeyer et al., 2003, Fig. 4) shows that in Patagonia destruction of bird bones produced by weathering is more rapid. The same was observed in ungulate bones in Tierra del Fuego (Borrero, 2007). Here, the differences observed with respect to Amboseli are a result of fluctuations in temperature and humidity prevailing in Tierra del Fuego, especially the importance of freeze–thaw cycles (Borrero, 2007). Regarding bird remains surveyed in southern Patagonia, the presence of large amounts of juvenile remains in nesting colonies may also be important because, as Behrensmeyer (1978) states, juvenile remains may be destroyed by weathering more rapidly.

6. Concluding remarks

Taphonomic studies conducted in Patagonia allowed characterization of the modern bone record of birds and mammals, and association of these records with aspects of the ecology in the region. Unlike records from other regions of the world, the Patagonian record shows a prevalence of avian remains despite the birds' small body size (less than 5 kg). This greater bird bone representation varies in different habitats, as their bones predominate mainly in the coastal region as a consequence of the important diversity and biomass of seabirds in coastal communities and of the low carnivore activity on remains of these vertebrates.

The processes responsible for the modifications recorded in both bird and mammal remains are the same in all the habitats: mainly weathering and carnivore activity. Variations are related to the relative importance of each process and the way they combine to produce a given bone record in each habitat. Carnivore activity in the Patagonian steppe is different from that in the marine coast due to variations in bird bone deposition between habitats. This means that the rate of deposition is a factor that strongly influences the following stages of the taphonomic history of a bone or assemblage of bones. Due to the greater number of bird carcasses available during the breeding season, avian remains in the marine coast will be less modified and, unless they are rapidly covered by sediments, their destruction will be produced by the action of weathering. In contrast, in the steppe carnivore activity will be the main factor of destruction and modification of avian remains and only the few bones surviving this process will be exposed to weathering or will be likely to be preserved.

At a regional level, bones of birds and mammals have markedly different taphonomic histories. Mammal bones are generally less affected by carnivores and resist weathering during longer periods than avian remains in the same environment. Bird bones have shorter taphonomic histories, even in those habitats where deposition is very important, due to a greater initial destruction by carnivores and to the early weathering destruction. Comparison of the results obtained in Patagonia with those from studies conducted in African parks shows that the differences are mainly a product of community composition and predator–prey dynamics of both ecosystems. However, in both cases the effects of weathering are similarly expressed in bird and mammal bones. Overall, all the aspects analyzed reinforce the need to generate specific models to interpret the archaeofaunistic records of Patagonia in a more accurate and significant way in terms of the processes involved.

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