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SPECIAL ISSUE PAPER

Differential Bone Survivorship and Ontogenetic Development in Guanaco (*Lama guanicoe)*

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ABSTRACT This paper presents the results of a taphonomic research programme conducted over the past 5years. The main objective of the programme is to investigate differential survivorship in guanaco (*Lama guanicoe*) bones, taking into account the ontogenetic development of this species and the densitometric characteristics of its skeletal parts. First, density analysis was carried out on selected bones of modern individuals corresponding to different age classes. Second, two experimental designs were conducted to explore the response of animal bone of different ages to weathering and fluvial transport. The first is a long term experiment that examines the deterioration of skeletal elements from a newborn, a juvenile and an adult modern guanaco exposed to subaerial weathering under controlled conditions. The second experiment examines the hydrodynamic sorting of dry and wet skeletal elements from a newborn, a juvenile, and an adult modern guanaco in an artificial flume under controlled current velocities (15 and 30cm/s). The main results of the research programme indicate that immature bones have higher hydric transport potential and weather at a faster rate. We propose that this differential bone behaviour is partially related to structural density, as demonstrated by density analysis. These results show age-related biases in zooarchaeological assemblages affected by taphonomic processes. Copyright © 2011 John Wiley & Sons, Ltd.

Key words: bone mineral density; differential bone preservation; fluvial transport; guanaco (*Lama guanicoe*); mortality profiles; ontogenetic development; weathering

Introduction

Early research in zooarchaeology indicated that age influences the possibilities of survival of bones in faunal assemblages (Brain, 1967; Payne, 1972; Binford & Bertram, 1977; Klein & Cruz-Uribe, 1984). Most of these studies proposed that unfused epiphyses are usually less durable than fused ones and consequently more prone to post-depositional destruction. A similar tendency was suggested for the mandibles and teeth of young individuals compared with those of adults (Payne & Munson, 1985; Munson, 2000; Steele, 2004).

Despite this early concern, actualistic research that examines the relationship between ontogenetic development and bone differential survivorship is scarce and the majority of these studies focus on the effects of carnivore ravaging (e.g., Binford & Bertram, 1977; Blumenshine, 1991; Munson & Garniewicz, 2003). Particularly, Munson and Garniewicz (2003) evaluated in detail age-mediated survivorship in ungulate mandibles gnawed by canids, as this element is the most utilised to determine age at death. However, information about age-correlated bias in the postcranial skeleton is almost nonexistent (Symmons, 2005). In addition, the consequences of other taphonomic processes on different age classes, such as fluvial transport and weathering, are just starting to be evaluated (Álvarez *et al.*, 2010; Gutiérrez *et al.*, 2010; Massigoge *et al.*, 2010; Kaufmann *et al.*, 2011).

Age-related taphonomic bias is an important issue when attempting to understand the strategies by which humans exploited animals (meat acquisition, hunting

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strategies, herd management, etc.). Different natural processes introduce changes in the original age composition of the fossil assemblages, and evaluation of the integrity of the sample is critical when interpreting mortality profiles (Marean, 1995; Steele, 2004; Lam & Pearson, 2005).

The most frequently used techniques in the estimation of the age of death on archaeological assemblages are teeth eruption/attrition and epiphyseal fusion (Klein & Cruz-Uribe, 1984). It is difficult to evaluate in practice the extent of the taphonomic bias on mortality profiles constructed with each technique when analysing zooarchaeological assemblages because of the scarcity of actualistic studies that take into account the ontogenetic development of the individuals. However, according to previous research, differential preservation may affect mortality profiles based on epiphyseal fusion and dental criteria (e.g., Binford & Bertram, 1977; Blumenshine, 1991; Munson, 2000; Munson & Garniewicz, 2003; Symmons, 2005; Kaufmann, 2009).

Aims

A taphonomic research programme investigating differential survivorship in guanaco (*Lama guanicoe*) bones in relation to the ontogenetic development of the species has been underway for the past 5 years. Because previous research has shown that bone density is an important variable influencing bone's response to many taphonomic processes (Brain, 1969; Binford & Bertram, 1977; Lyman, 1984; Lam & Pearson, 2005; Symmons, 2005), the focus of the research programme was to study the variability in this intrinsic property of bone in relation to age.

Density analysis was conducted on selected bones of modern guanacos corresponding to different age classes (Álvarez *et al.*, 2010; Gutiérrez *et al.*, 2010). In addition, two experimental designs were carried out to explore the response of bones from animals of different ages to weathering and fluvial transport (Massigoge *et al.*, 2010; Kaufmann *et al.*, 2011). These processes were selected because they are common in most open-air archaeological assemblages from our study area (the Pampean region, Argentina), and in some cases, archaeologists have argued that they are responsible for differential bone preservation (Gutiérrez & Kaufmann, 2007). Other taphonomic processes, such as carnivore gnawing and trampling, were recorded in low frequencies in bone assemblages from the study area.

In this article, we present a brief synthesis of each line of investigation in our research programme and integrate the results in order to help zooarchaeologists in the interpretation of mortality profiles affected by natural taphonomic processes. Although our results show that anatomic representation is affected by the natural processes studied here, this paper focuses on the relationship between such processes and age bias.

Guanaco reference collection

The guanaco reference collection used for these studies was gathered in the District of San Antonio (Río Negro Province, Argentina) between 2000 and 2006 (Figure 1). This collection is composed of 158 guanaco carcasses, some incomplete, derived from the same biological population. Life histories of these animals are unknown (Kaufmann, 2009).

Guanaco is a wild camelid widely distributed in southern South America. For adult individuals, weight average is between 88 and 120 kg (Raedeke, 1978; Larrieu *et al.*, 1982), and sexual dimorphism is absent except in the canines and pelvises, which are different in size and morphology in females and males (Raedeke, 1978; Franklin, 1982; Cartajena, 2007; Kaufmann & L'Heureux, 2009). We focused on the guanaco as it represented one of the main faunal resources for human populations in the Pampas and Patagonia during the late Pleistocene and the Holocene (Mengoni Goñalons, 1999; Miotti & Salemme, 1999; Gutiérrez & Martínez, 2008; Politis, 2008).

Previous research

Zooarchaeologists have noted the importance of age influencing bone density for more than 3 decades (Binford & Bertram, 1977). Nevertheless, analyses are scarce and have focused on domestic animals or small samples from wild animals (Munson & Garniewicz, 2003; Symmons, 2002, 2005; Ioannidou, 2003).

Some authors have developed weathering actualistic studies (e.g., Brain, 1967; Behrensmeyer, 1978; Andrews & Cook, 1985; Fiorillo, 1989; Andrews, 1990; Tappen, 1994; Borrero, 2007). However, few have considered bone weathering differential preservation related to age. For example, based on naturalistic observations, Behrensmeyer (1978) and Fiorillo (1989) suggest that bones from younger animals usually weather faster than skeletal elements from adult individuals. Nevertheless, controlled experiments to test these observations still need to be developed.

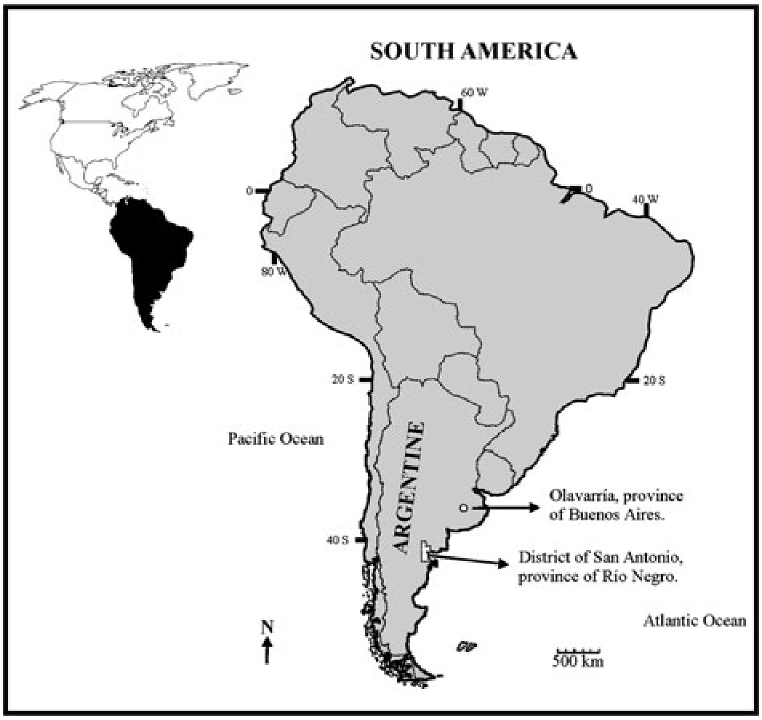

Figure 1. Map showing the provenience of the guanaco reference collection and the location where the actualistic experiments were carried out.

In relation to fluvial transport, we are not aware of previous actualistic studies that mention age as an important factor affecting hydrodynamic sorting of bones, although many other variables have been considered (e.g., taxa, flow velocity, channel depth, articulated/nonarticulated state, fragmentation, saturation in water and variation of the channel bed; Voorhies, 1969; Dodson, 1973; Behrensmeyer, 1975; Boaz & Behrensmeyer, 1976; Hanson, 1980; Frison & Todd, 1986; Coard & Dennell, 1995; Aslan & Behrensmeyer, 1996; Trapani, 1998; Coard, 1999; Pante & Blumenshine, 2010). Because of the fact that many bone properties, such as density and size, change during the ontogenetic development of animals, we expected to observe differential behaviour among elements from each age class.

Bone density

The main purpose of the density study was to obtain information about bone mineral density (BMD) variability in guanaco related to age. Two different skeletal elements from 54 guanacos were analysed. The sample was composed of 46 metacarpals and 45 femurs of different age classes, including six unborn (6 to 11 months of gestation), 14 newborn (0 to 12 months), seven juveniles (12 to 24 months), five subadults (24 to 36 months), 10 adults (36 to 84 months) and 12 senile individuals (84 to 144 months). About 41% of the sample were determined as females ($n = 22$; 40.7%), 11% males ($n = 6$; 11.1%), whereas in a large number of individuals ($n = 26$; 48.2%) it was not possible to identify sex. Bone structural densities were measured using a biphotonic X-ray densitometer, DEXA method, Norland EXCELL (Norland Corporation), and the bone mineral content of each scanned portion or complete element was divided by its volume, which was obtained independently by water displacement (Elkin, 1995). This method was considered by Lam *et al*. (2003) as a class D, as it takes into account the external and internal shape of the bone, and it is one of the more accurate ways to estimate BMD values. We used values from entire bones because this information is adequate for discussing intraspecific variation of bone mineral density. Detailed methodological description and information related to age, sex, cause of death and processing techniques for each skeleton can be found in Gutiérrez *et al*. (2010: Table 1).

Table 1 presents the median BMD values obtained for the different age classes of metacarpals and femurs. Considering only metacarpals, results demonstrate that significant variability in the BMD values exists, showing an increase of density values in relation to age. Unfused

Table 1. Median bone mineral density values for complete metacarpals and femurs within each age class of guanaco. The centres of ossification of both elements begin to fuse in the class subadult. For this reason, in this group of age, we can find fused and not fused elements

Skeletal element	Age class	State of fusion	№ individuals	Maximum	Minimum	Median
Metacarpal	Unborn	NF	5	0.891	0.41	0.754
	Newborn	NF	12	1.052	0.826	0.9505
	Juvenile	NF	5	1.102	0.924	1.026
	Subadult	NF-F	4	1.171	1.011	1.044
	Adult	F	10	1.233	1.091	1.1805
	Senile	F	8	1.261	1.103	1.178
Femur	Unborn	NF	2	0.93	0.855	0.8925
	Newborn	NF	12	1.054	0.839	0.906
	Juvenile	NF	5	0.889	0.826	0.856
	Subadult	NF-F	3	0.897	0.857	0.87
	Adult	F	6	1.006	0.86	0.9095
	Senile	F	12	1.02	0.784	0.916

elements are in general less dense than fused ones. The distribution of the unfused metacarpal values indicates that both diaphysis and distal end values increase as the age of the guanacos increases (see Gutiérrez *et al.*, 2010: Figure 2).

When the density values for complete metacarpals within each age class are analysed (Figure 2), variability among individuals of the same age category is clearly observed. The greatest variability occurs in the unborn class, coinciding with more rapid growth during early development of the individuals. Moreover, the median of each age class increases from younger to older individuals (except for the senile class) (Table 1).

In contrast with the metacarpal results, the increasing BMD value trend related to age is absent in each part of the unfused femur as well as in the entire fused element. Results show significant dispersion in the density values of the epiphyses. One relevant aspect of these results is that there are no significant differences between mineral density values of unfused and fused femurs, resulting in a clear overlap of femur BMD of each age class (see Gutiérrez *et al.*, 2010: Figures 4 and 5). The greatest variation was recorded in the newborn and senile categories. In contrast with the metacarpal results, femurs show no increase in the median of each age class, from younger to older individuals (Table 1; Figure 2).

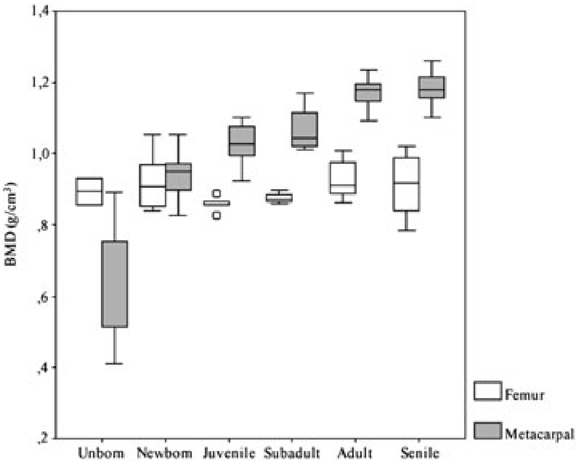

Figure 2. Box and whisker plot showing the variability in complete metacarpals and femurs density values within each age class of guanaco. The vertical lines relate to the range of bone mineral density values obtained in each age category. The boxes show the interquartile ranges and the horizontal lines within the boxes express the median values.

Our results demonstrate that metacarpals and femurs do not share the same pattern of BMD when the ontogenetic development of the guanaco is considered. The increasing linear trend in metacarpal density values related to age and the absence of such a trend in femurs is the most relevant difference between the skeletal parts. A clear pattern in mineral density is not apparent when comparing the bone elements by age classes. Femurs appear to be denser in younger individuals (the unborn age class). During the newborn age category (*ca.* 570 days), density values of metacarpals and femurs are similar. Finally, during all subsequent categories to the end of the animal's life metacarpals have, in general, higher BMD values than femurs.

Bone weathering

The second study is a long-term experiment to examine the deterioration of skeletal elements from guanacos of different ages exposed at the same time to subaerial weathering (*sensu* Behrensmeyer, 1978) under controlled conditions. Variability among different anatomical units and age classes was evaluated, although the focus of this paper is on the latter.

The sample consisted of skeletal elements from three guanacos of different ages at death: newborn (0.5–3 months); juvenile (12–19 months) and adult-senile (96–108 months). All soft tissue except the connective tissue between the bones of the skull was removed from the skeletons by boiling in water (2–4 hours) before the experiment started. According to Roberts *et al*. (2002), boiling in water produces changes in the bones that could affect its preservation including the loss of collagen and an increase in crystallinity and porosity. Nevertheless, this study also demonstrates that in bones boiled for less than 9 hours, these changes are insignificant. Although the initial conditions are not analogous to previous naturalistic studies on bone weathering (Gifford 1977; Behrensmeyer 1978; Borrero 2007), they are more similar to archaeological assemblages in which animal bones were defleshed for meat consumption.

For each skeleton, one representative element of every anatomical unit was selected; for paired bones, the right side was chosen. The sample from each carcass was composed of 22 complete skeletal elements (unfused epiphyses and diaphyses from the same element were considered as one). At the beginning of the study, the elements had a fresh appearance and did not show any sign of weathering.

Bones were placed outdoors on a sandy and well-drained substrate lacking vegetation coverage inside a fenced area with restricted access to people and animals, except for insects, birds and mammals smaller than the *ca*. 10 cm mesh. This enclosure, used for actualistic studies, is located at the University campus (UNCPBA) in the city of Olavarría (Buenos Aires Province, Argentina) (Figure 1). In this area, the weather is temperate-humid. Mean annual temperature is 14.2 °C. In January (the warmest month), the average temperature is 21ºC and in July (the coldest month), it is 6.9ºC. The precipitation pattern is irregular; mean annual precipitation is 927 mm (Sallies, 2006). The major rains occur between February and March, and October and November. The wettest month is March, receiving up to 300 mm of precipitation. The driest months are May, June and August, with less than 10 mm of rain.

This paper summarises the results obtained from the first 4 years of exposure. During the first 3 years, systematic bone weathering observations and data collecting were conducted at 6 month intervals. Observations during the fourth year were conducted once per year and will continue at the same time interval for the remainder of the experiment. During the observations, bone weathering stages, as proposed by Behrensmeyer (1978), were used as a descriptive tool because the weathering features within each stage are known and accepted worldwide and were the same as those observed in our sample (cracking, flaking and mosaic cracking, among others). Even so, we do not consider the weathering stages to have any connotation in terms of time of exposure. A detailed description of the results from the first 2 years can be found in Massigoge *et al*. (2010).

Figure 3 shows the changes through time in the weathering profiles for the individual skeletons. After 4 years of exposure (48 months) the three skeletons exhibit differential representation of weathering stages. At this point in time, the juvenile skeleton presents a higher percentage of elements in weathering stages 3 and 4, and is the only one with at least one bone at stage 5. As Figure 3 shows, the elements of all carcasses weathered progressively, but the bones in the juvenile skeleton weathered at a faster rate, reaching stage 2 at 6 months and stages 3 and 4 at 18 months after exposure.

Comparison of the frequency distributions of the weathering stages shown by the three skeletons at 48 months indicates that the only statistically significant difference is observed between the juvenile and the adult (Kolmogorov–Smirnov two-sample statistics are: newborn to juvenile, $Z = 1.234$, $p = 0.095$; newborn to adult, $Z = 0.463$, $p = 0.983$; juvenile to adult, $Z = 1.697$, $p = 0.006$).

Particularly important for our research are the effects of weathering on skulls, mandibles and teeth because of the widespread use of dental criteria in zooarchaeology to construct mortality profiles (Klein & Cruz-Uribe, 1984; Stiner, 1990). After 4 years of exposure, the skull and mandible of the newborn and juvenile skeletons were among the elements at the most advanced weathering stage (newborn: skull stage 4 and mandible stage 3; juvenile: skull stage 5 and mandible stage 4) (Figure 4). In contrast, the skull and mandible of the adult weathered at a lower rate, reaching stage 3 and 2, respectively.

After 6 months of exposure, the deciduous premolars of the newborn skeleton were fractured, with some fragments scattered around the skull and mandible, and the incisors were dislodged from their alveoli. After 18 months of exposure, the cusps of all premolars were broken and only the roots remained in their alveoli. After 36 months, the root of Pd_4 was no longer in its alveolus (Figure 4).

The juvenile skeleton showed no changes in dental integrity prior to the 18 months inspection, at which point we observed that most of the incisors were out of the broken alveoli. Forty-eight months after exposure superior and inferior premolars and molars still survived in their alveoli and only one cheek tooth was fractured (Figure 4).

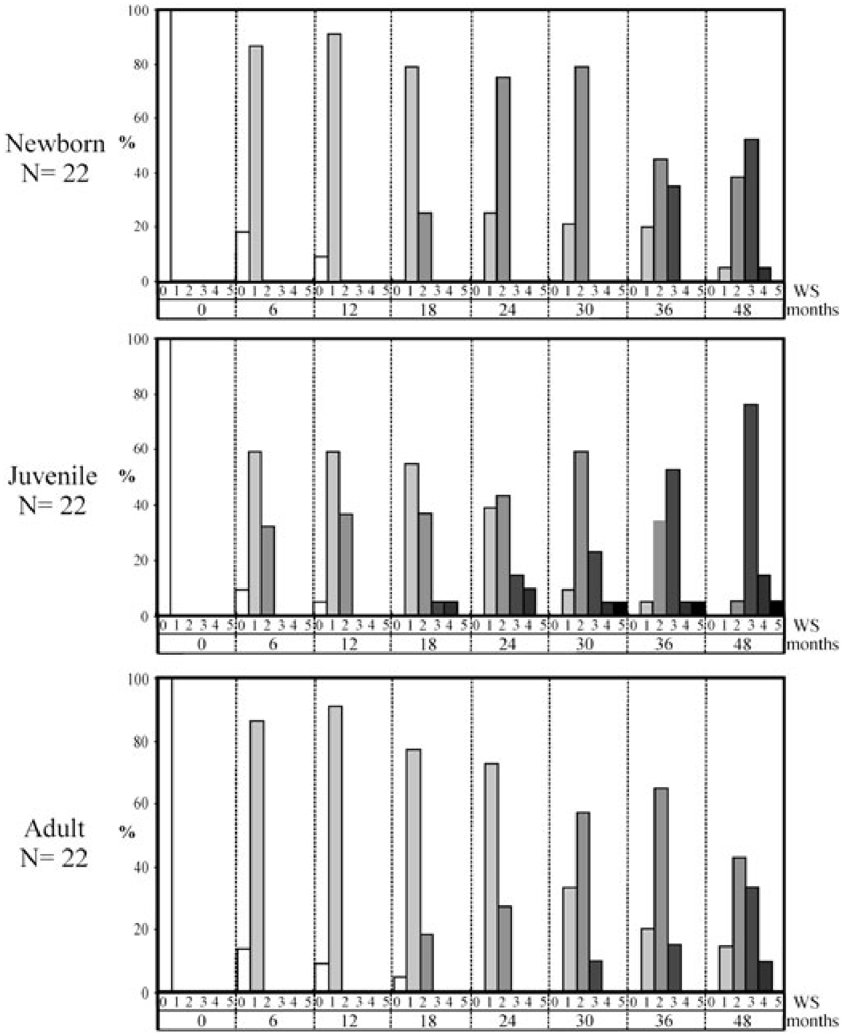

Figure 3. Weathering profiles for guanaco carcasses with different age at death. Reference: WS: weathering stages.

In the adult skeleton, we observed that some incisors and canines were dislodged after 6 months of exposure, but premolars and molars were held in place and in good condition at 48 months (Figure 4).

Fluvial transport

The third study examined the hydrodynamic sorting of dry and wet skeletal elements from guanacos of different ages in an artificial flume under controlled current velocities (15 and 30 cm/s). Wet bones consisted of fresh bones soaked in water for 24 hours. Dry bones were the same elements used in the wet series, but not soaked in water. The main objective of the study was to evaluate if the bone element dispersion by fluvial action differs in relation to age of the individuals.

Bones corresponding to three guanaco skeletons (not those used in the weathering experiment) with different states of fusion were used: a newborn (0.5–3 months) with all bone centres unfused ($n = 63$); a juvenile (12–19 months) with some unfused and some fused centres ($n = 53$); and an adult-senile (120–132 months) individual with all bones fused ($n = 37$). The selected elements from the appendicular skeleton were all right bones, and for the axial skeleton, one representative skeletal part of each anatomical unit was selected.

To conduct the experiment, a 0.3 m wide smooth-bottomed recirculating flume, with a channel length of 8 m, and a water depth of 0.16 m was used. Flow velocities were controlled by a pump. For each skeleton, four series of three trials were conducted: (i) dry bones at a flow velocity of 15 cm/s; (ii) dry bones at a flow velocity of 30 cm/s; (iii) wet bones at a flow velocity of 15

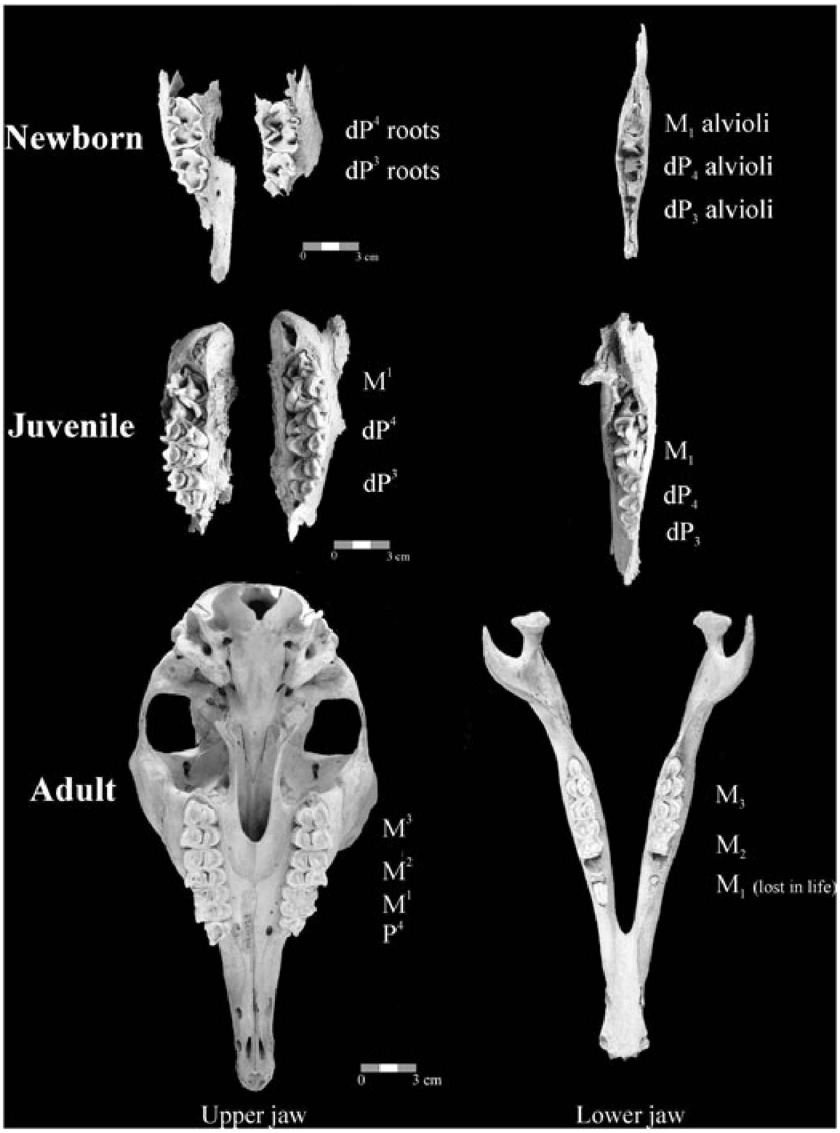

Figure 4. Guanaco skulls and mandibles after 4years of exposure.

cm/s; and (iv) wet bones at a flow velocity of 30 cm/s (see details in Kaufmann *et al.*, 2011).

After the three trials in each series were completed, each element was classified according to the following groups. Group 1: bone elements which passed through the testing section (3 m long) in all trials of the series. Group 2: bone elements which passed through this section in at least one trial of the series, but not all. Group 3: bone elements which did not pass through the testing section in any trial of the series.

In comparing the three individuals, great variability in the hydrodynamic behaviour of the bones was observed (Figure 5). Details for each skeletal element can be found in Kaufmann *et al.* (2011: Tables 1–2). This experiment showed that in general, bones from the newborn skeleton were the most affected by hydrodynamic action (highest percentage of elements in group 1). A Kolmogorov–Smirnov two-sample test was performed to compare the frequency distributions of the transport groups among the skeletons (Table 2). The results indicate that significant differences exist between the newborn and the other skeletons in all the series except the wet series at 15 cm/s. The unfused long bone epiphyses, vertebrae, phalanges and podial bones from the newborn were the most transported elements in all the series. The skull was only transported in the series at 30 cm/s flow velocity and in no case was the mandible in group 1.

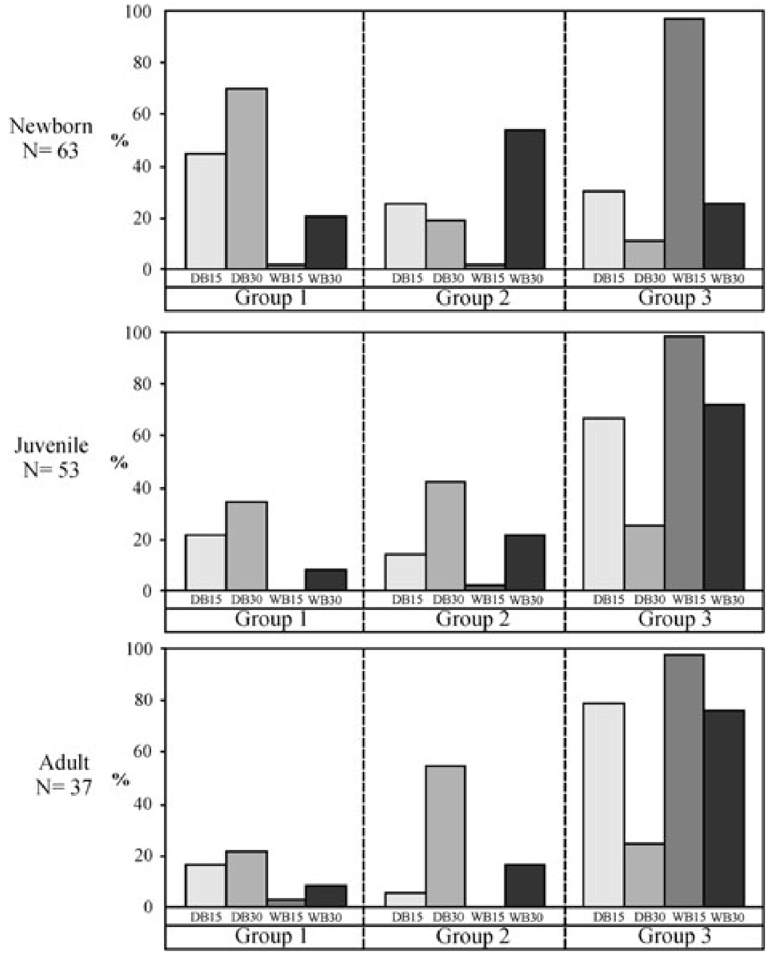

Figure 5. Percentages of skeletal elements from a newborn, a juvenile and an adult guanaco in the three transport groups under variable speed of current and bone state. References: DB: dry bone; WB: wet bone.

Table 2. Results of the Kolmogorov–Smirnov two-sample tests comparing the frequency distributions of the transport groups between the skeletons

Serie (15cm/s)	Age class	Juvenile	Adult
Dry bones	Newborn	$Z=1.925$ $p=0.001$*	$Z=2.328$ $p=0.000$*
	Juvenile		$Z=0.576$ $p=0.894$
Dry bones	Newborn	$Z=1.925$ $p=0.001$*	$Z=2.328$ $p=0.000$*
	Juvenile		$Z=0.576$ $p=0.894$
Wet bones	Newborn	$Z=0.085$ $p=1.000$	$Z=0.054$ $p=1.000$
	Juvenile		$Z=0.126$ $p=1.000$
Wet bones	Newborn	$Z=2.484$ $p=0.000$*	$Z=2.427$ $p=0.000$*
	Juvenile		$Z=0.186$ $p=1.000$

*Significant difference

The juvenile skeleton showed slightly more transportability than the adult in the dry bone series, but no statistically significant differences in the frequency distribution of the transport groups between these two skeletons were found in any series (Table 2). In the juvenile, unfused long bone epiphyses and post-cranial axial elements were the most transported bones. The skull was transported in a few occasions, whereas the mandible was never displaced. For the adult individual, the majority of transported elements corresponded to the post-cranial axial skeleton (principally vertebrae). The skull and mandible behaved in the same way as those from the juvenile individual.

For all skeletons, the greatest percentages of transported elements were obtained in the series of dry bones under a flow velocity of 30cm/s. Conversely, the smallest quantity of transported elements was obtained in the series performed with saturated bones at a flow velocity of 15cm/s. In this series, only one element from the newborn and adult skeletons was transported, and no elements from the juvenile skeleton were displaced. When flow velocity was increased from 15 to 30 cm/s the number of transported bones for each skeleton rose. This behaviour was observed both in dry and water-saturated elements.

Discussion and conclusions

Our study contributes new evidence about potential age-related taphonomic bias in faunal assemblages. As shown by density data, metacarpals from immature animals are clearly less dense than those from mature animals. According to the widely accepted premise that bone preservation is partially related to its structural density, we can hypothesise that the former would be more prone to density-mediated destruction/selection. However, as the results from femurs indicate, the tendency for fused bones to be denser than unfused ones does not apply for all skeletal elements and needs to be further investigated through experimental studies. Consequently, in the absence of a deeper understanding of how BMD varies as a function of age in anatomical units other than the ones studied here, we cannot conjecture the response of such anatomical units to processes mediated by this bone property.

Although age is an important factor determining BMD values, other aspects such as nutritional and health status, lactation, genetics, sex and exercise, and so on contribute to the variability in this bone property and consequently should also be considered (Symmons, 2002, 2005; Ioannidou, 2003; Lam & Pearson, 2004; Álvarez *et al.*, 2010). As Symmons (2005) points out, these other factors can obliterate the influence of age on bone density; unfortunately, measuring most of these variables in the archaeological assemblages is methodologically impossible. Our results, although concerning only two skeletal elements, show the same trend described by this author: great variability in bone density values among individuals as well as within age classes. Moreover, our study demonstrates that the high level of interindividual variability in bone density detected in domestic populations is also present in a temporally and spatially restricted population of a wild species. Clearly, the nature of the interactions of the broad spectrum of factors affecting BMD remains uncertain and requires further analyses. Existing bone density data sets which take into consideration ontogenetic development (Symmons, 2005; Gutiérrez *et al.*, 2010) do not allow us to make fine-grained predictions about density in bones from individuals of different ages and consequently to anticipate the chances of survivorship of different age groups in archaeological assemblages.

One difference observed in our results that transcends age is that between the epiphyses of long bones and their corresponding diaphyses, the former always being with are less dense. This suggests that the diaphyses have a greater chance of survival than the epiphyses in assemblages affected by density-mediated post-depositional processes, an aspect corroborated by other actualistic studies on carnivore ravaging (Marean & Cleghorn, 2003). As discussed in the following, our fluvial transport experiment also supports this premise. Unfused epiphyses were more frequently transported than diaphyses in newborn and juvenile individuals.

The bone weathering results show that over a short period of time, a marked difference in the degree of modification among the skeletons of different age classes was recorded. In general terms, we observed that bones from younger individuals weathered faster than those from older individuals. This could partially be explained by age-related changes in different bone properties, such as bone mineral density. As such, in accordance with the previous research, our density data show that some bones from immature animals are less dense than the mature ones and consequently more prone to density-mediated attrition. However, as was previously mentioned, the trend of unfused bones being less dense than fused ones was not observed in the femurs. An unexpected result was that the juvenile skeleton weathered at a faster rate than the newborn. Although the exact causes of this situation are unknown, we can venture to suggest that it is related to the high variability that exists in BMD among individuals because of factors other than age (e.g., nutrition, health). As shown in Figure 2, the BMD ranges of metacarpals and femurs from newborn and juvenile guanacos overlap, indicating that some juvenile individuals exhibit the same or even lower density values than some newborn individuals. Unfortunately, because we do not know the life history of the juvenile individual, we cannot relate its response to weathering to the previously mentioned factors. An alternative explanation is that the more advanced weathering profile in the juvenile skeleton could be related to differences in other bone properties not investigated here but that are known to affect the mechanical properties of bone. According to other authors, bone structural organisation (amount and distribution of compact and cancellous bone) and bone tissue microstructure (such as the number, size and orientation of collagen fibres and their degree of cross-linking) are important bone properties influencing bone response to taphonomic processes (Lyman, 1994; and references therein). Recent studies on bone weathering of superficial archaeofaunal assemblages recovered from dunes found that bone elements from large mammals with low density survived better than those with high density. Based on these results, the authors proposed that the repeated heating, cooling, wetting and drying characteristics of this particular depositional environment favour the destruction of thick cortical bone, which is more brittle; whereas cancellous bone, with better insulative properties, is less affected (Belardi *et al.*, 2010; Conard *et al.*, 2008). These results show that bone properties other than density should be considered when studying differential bone preservation. Changes in these bone variables in relation to the ontogenetic development in guanaco should be considered in future work in this field. In addition, taking into account the high interindividual variability in bone density and other bone properties, future experiments using a larger sample of skeletons of each age class need to be developed for better understanding weathering variability related to age.

A significant result from our experiment is the great difference in the survivorship of the dental material from the three skeletons after 4years of exposure. Contrary to Klein & Cruz-Uribe's (1984: 43) assumption that the teeth from individuals of different ages do not differ in their durability and that dental age profiles are less prone to selective post-depositational destruction bias, we observed that the rows of cheek teeth from younger guanacos were more affected by weathering than those from older individuals. These differences were remarkable in relation to the conditions of preservation of the teeth, because premolars from newborns were rapidly fragmented by exposure to atmospheric agents. This fact could be favoured by the inmature roots and the lack of flexibility in the recently formed dentine, which are characteristic of the early phase of tooth eruption (Hillson 1986). Besides, skulls and mandibles from the newborn and juvenile skeletons showed higher weathering stages, which contributed to the loss of teeth.

These results suggest that in zooarchaeological assemblages exposed to weathering for a time period comparable with the one in our experiment, the effects will be more intense on the elements of the immature individuals, generating an important bias in the archaeofaunistic mortality profiles (Binford & Bertram, 1977; Munson & Garniewicz, 2003; Steele, 2002). However, this does not necessarily mean that all elements are going to be underrepresented, because post-cranial specimens, although affected, are not completely destroyed. The teeth of newborns, however, will be in an advanced state of destruction.

Additionally, great variability in weathering stages was recorded even in bones from the same individual. We believe that this variability is partially related to skeletal element differences in bone density, as has been proposed by other authors (Lyman & Fox, 1989 and references therein). With the objective of testing this idea, we correlated weathering stages data with density values. Because we have density values for only two guanaco skeletal elements, we used values for adult camelids from Elkin (1995). Because of the limitation of the density data, we could evaluate the relation between weathering stages and density for the adult skeleton only. We correlated both variables through Spearman's rho. The results indicated a negative correlation ($rs = -0.466$; $p = 0.059$; $n = 17$), which means that the more weathered bones are the less dense ones. Although this correlation was not significant, it shows that the trend is in accordance with our proposal, that density is one of the factors influencing bone weathering.

Accordingly, in the fluvial transport experiment, bones from the newborn skeleton were the most affected by hydrodynamic sorting. We suggest that this fact is partially related to the lower density of bones from younger individuals. In a previous study, Kaufmann & Gutiérrez (2004) calculated both dry and wet density of each element used in the present experiment from the weight of the bones in dry and wet states and their volumes. The authors observed that, in general, density values for the newborns were lower than those from the two other age classes. Other authors note the importance of density in the fluvial transport of bones, although in relation to the differential transportability of skeletal elements. Lyman (1984: 279) indicates that bulk density is an important factor mediating fluvial transport potential in dry bones because spongy bones have more buoyancy owing to the greater volume of air-filled pore space. Furthermore, Behrensmeyer (1975: 499) links the variability in bone transport to density, although she also emphasises that other factors, such as size and shape, contribute to bone dispersion potential. In our experiment, bulk density of the different anatomical units was an important factor mediating fluvial dispersal; but, particularly for long bones, transportability was also significantly affected by fusion state. As such, unfused epiphyses presented high fluvial dispersal, but once fused to their corresponding diaphyses (which are denser), their transport potential diminished in accordance with the higher density of the element as a whole.

The lower transportability registered in the wet trials indicated that bone state was also an important variable conditioning fluvial transport. When bones were saturated, the air pore space filled with water and the density of the wet bones became greater than that of water (*ca*. 1 g/cm^3). Consequently, buoyancy ceased to be a significant factor affecting bone displacement by water. Similar results were obtained experimentally by Coard (1999) using bones from three different mammal species.

Kaufmann *et al*. (2011) indicate that there are no significant differences in the sphericity index between adult, juvenile and newborn guanaco bones. However, they find statistically significant differences between each transport groups for each of the series with respect to this index, especially between groups 1 and 3, and groups 2 and 3. Bones of juvenile and newborn individuals are more frequent in groups 1 and 2 (Figure 5). These results support the idea that shape is another bone property that contributes to bone transport.

Finally, our fluvial experiment confirmed previous evidence from other actualistic studies that skulls and mandibles are some of the elements less affected by fluvial transport (Voorhies, 1969; Coard, 1999). Moreover, our results indicate that this occurs even in individuals of different ages.

The general conclusions from our ongoing research programme that should be taken into account in the construction and interpretation of mortality profiles are:

- Generally, whenever archaeological assemblages are affected by taphonomic processes such as weathering and fluvial transport, a bias against the representation of the youngest individuals is expected. This is a consequence of the differences in some bone properties resulting from the ontogenetic development of the individuals. In particular, we suggest that bone mineral density, state of fusion and shape influenced the responses of the skeletal elements in our experiments;
- Although in general terms the post-depositional processes studied generate bias against the immature animals in mortality profiles, it is important to note that weathering and fluvial action affected the skeletal profiles of each individual in different ways. The unfused epiphyses of long bones and different post-cranial axial elements were the most transported bones of the newborn and juvenile skeletons. Moreover, the skulls and the mandibles were some of the less affected elements, a situation that was also observed for the adult skeleton. On the contrary, in the weathering experiment, the skulls and mandibles of the newborn and the juvenile individuals were more weathered than those of the adult. The high degree of destruction of the mandible of the newborn skeleton would prevent its correct identification in archaeological contexts (analytical absence *sensu* Lyman & O'Brien, 1987). Considering the differential effects of both post-depositational processes, we suggest that:
- In archaeological assemblages affected by weathering (even in cases of low intensity), newborn individuals not be considered in mortality profiles based on dental criteria and complementary profiles be conducted based on bone fusion. However, this last proposal will not be useful for assemblages affected by other processes that selectively destroy cancellous bone (such as carnivore gnawing), which is prevalent in epiphyses and metaphyses, hence diminishing the evidence of fusion. Although in the Pampean region, carnivores are small and affect bone assemblages in very low proportions, this fact should be taken into account when following this guideline in other areas;
- In archaeological assemblages modified by fluvial action, mortality profiles should be constructed on the basis of dental criteria and, in cases where they are based on bone fusion, that the epiphyses of the long bones not be included in the fusion groups but rather the corresponding diaphyses.

Final remarks

Results obtained in this study demonstrate the possibility of underrepresentation of immature individuals in zooarchaeological assemblages affected by hydrodynamic sorting and/or weathering as well as other processes mediated by bone density. In particular, our research draws attention to age-related biases in mortality profiles from such assemblages. The occurrence of such biases has been assumed in the zooarchaeological literature but not quantified for wild animal populations. Our investigation, although in an initial stage, constitutes an advance in this field.

Finally, it is worth mentioning that because of the experimental nature of these studies, variables were isolated to study their effects on bone elements. Nevertheless, we are aware that in the archaeological record, taphonomic processes are interrelated and, consequently, their effects are more complex. This should be taken into account when applying our suggestions to archaeological assemblages. We recognise that our sample is limited and that the influence of other variables on the behaviour of bones remains to be explored. In addition, not knowing the life histories of the animals was a limitation when it came to interpreting the differential behaviour of bones from different individuals, which is why it is desirable to include samples containing this information in future work. Nevertheless, our investigation is one of the first in experimentally evaluating the differences in bone preservation of individuals of different ages in relation to two taphonomic processes that are common at many archaeological sites.

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