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Fluvial dispersal potential of guanaco bones (*Lama guanicoe*) under controlled experimental conditions: the influence of age classes to the hydrodynamic behavior

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A B S T R A C T

Hydrodynamic sorting is a taphonomic process able to transport and scatter bones deposited in archaeological and paleontological sites. This study presents the results of experimentation performed in an artificial flume with guanaco (*Lama guanicoe*) bones of different ontogenetic development, dry and saturated in water, in hydric flows velocities of 15 and 30 cm/s. The obtained results show that bone global density, the age of the individual, the dry or wet bone state, and the hydric flow velocity influence significantly bone dispersion. In this way, bones from immature individuals with unfused secondary growth centers and relatively low bulk density have better possibility of being transported than fused bones from adult individuals. Taking into account the results obtained in this experimentation and the feasibility of discriminating age categories in fossil assemblages, two bone groups with differential potential transport are presented in this paper. These transport groups constitute a methodological tool to evaluate the role hydric current may had played in the formation of a fossil assemblage.

1. Introduction

Once an animal dies and its bone remains are deposited, a great variety of natural processes begin to act which may condition the skeletal survival and original positions of the elements. Among these processes, the role of fluvial transport is remarkable because it is able to scatter and select the bones (Behrensmeyer, 1975; Boaz and Behrensmeyer, 1976; Voorhies, 1969). When performing cultural and paleoecological interpretations of archaeological and paleontological bone assemblages recovered in fluvial environments, it is appropriate to know the degree to which the taxonomic, anatomic and age representation may be biased by this natural process. Several sets of experiments are presented in this work conducted with disarticulated bones of guanaco (*Lama guanicoe*) in a flume. The main objective of this research is to contribute to the knowledge of variables intervening in hydric transport of skeletal elements of guanaco and propose a model of its differential transport. A particular objective in this study is to evaluate if the bone element dispersion is different in relation to the age of the individuals, an aspect that has not been considered in previous fluvial transport taphonomic experiments. In order to reach these objectives, elements corresponding to three guanacos with different ages, namely, newborn, juvenile and adult, were used in the experiments. The choice of this species to perform these experiments was due to the fact that the guanaco was a major resource for the hunter–gatherer groups that inhabited the different regions of the Southern Cone during the Late Pleistocene and Holocene. Consequently, it is common to find abundant remains of this ungulate in the archaeological sites of these regions (De Nigris, 2004; Madrazo, 1979; Martínez and Gutiérrez, 2004; Mengoni Goñalons, 1999; Miotti, 1998; Miotti and Salemme, 1999; Politis, 1984; Politis and Salemme, 1990; Salemme, 1987). The knowledge attained in this paper will be of particular interest to archaeologist and paleontologists studying this taxon's bone assemblages. Moreover, due to the lack of information on hydrodynamic sorting related to age, this paper will also contribute to the formation process studies in other geographic regions where *taxa* with similar characteristics to guanaco are involved.

Laboratory experiments and observations in natural environments have been made by several researchers with the aim of evaluating the consequences of water action on bone assemblages. The first studies explored the differential potential of bone hydric transport considering different variables such as hydric flow velocity and channel depth (Behrensmeyer, 1975; Boaz and

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Behrensmeyer, 1976; Dodson, 1973; Hanson, 1980; Voorhies, 1969). These studies indicated that the different intrinsic properties bone have, such as global density, shape, and size influence significantly their hydric transport potential. In later experimental studies additional variables were added such as bones in articulated state, fractured, saturated in water, and variation of the channel bed (Aslan and Behrensmeyer, 1996; Coard, 1999; Coard and Dennell, 1995; Pante and Blumenschine, 2010; Trapani, 1998); and later on, the number of *taxa* studied was increased (Frison and Todd, 1986; Kaufmann and Gutiérrez, 2004; Trapani, 1998). The most used fluvial transport model is still the one proposed by Voorhies (1969), who evaluated the potential hydric transport of different disarticulated bones of domestic sheep (*Ovis aries*) and coyote (*Canis latrans*) and proposed three skeletal groups with differential behavior.

2. Materials and methods

For this experimental study, bones corresponding to three guanaco skeletons with different fusion bone state were used; namely, newborn (0.5–3 months old) with all bone centers unfused (Fig. 1); a juvenile individual (12–19 months old) with some unfused and some fused centers and an adult individual (120–132 months old) with all its bones fused. All right elements of the appendicular skeleton were selected and for the axial, the cranium, the mandible, pelvis, atlas, axis, a cervical vertebra, a thoracic vertebra, a lumbar vertebra, the sacrum, a caudal vertebra, and a rib were considered. The total number of bone elements used in the experiment was 153, 63 of which corresponded to the newborn, 53 to the juvenile, and 37 to the adult skeletons.

To conduct the experiments, a smooth bottomed without mobility recirculating flume 0.3 m wide with a channel length of 8 m was used, with a water depth of 0.16 m. The flume was positioned horizontally and flow velocities were acquired by a pump. Each bone was placed on the surface of the water at the start of the test section (3 m long) oriented with long axes parallel to the current. Four series of three trials each were performed for each skeleton. The series included: (1) dry bones at a flow velocity of 15 cm/s; (2) dry bones at a flow velocity of 30 cm/s; (3) wet bones at a flow velocity of 15 cm/s, and (4) wet bones at a flow velocity of 30 cm/s. The total number of trials performed for the three skeletons was 36. During each trial the mode of transport of the bone was noted; *i.e.*, rolling, sliding and/or saltation along the bed, and/or floating in the water surface.

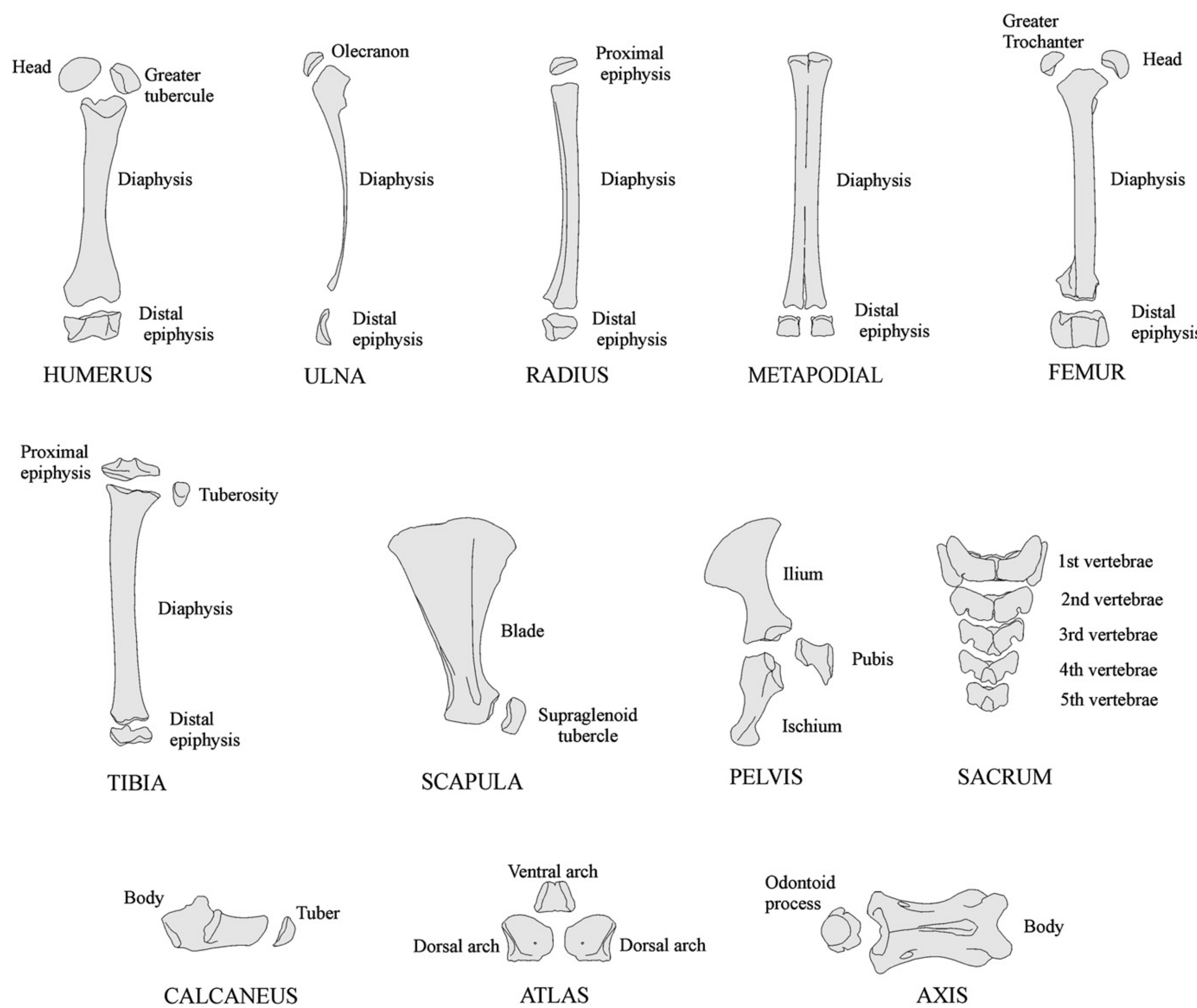

Fig. 1. Guanaco's bones showing center of fusion considered in this experiment.

According to Behrensmeyer (1975) flow velocity in natural situations are between 20 and 150 cm/seg. In our experiment, low speeds (15 and 30 cm/seg) were chosen as they would be the expectable ones for floodplains adjacent to the main current, a common setting of archaeological sites from the Pampas of the Southern Cone.

The experiment started with the dry state series. After each trial, the bones were removed from the channel and set to dry. Once dry, they were used for the following trial and the same procedure was repeated for the six series in dry state for the three individuals. To perform the series in wet state, the same bones used in the dry state series were soaked in water during 24 h. The bones were kept saturated in water between each trial series performed.

Dry and wet global densities as well as sphericity index of the different transport groups generated by this experience were compared in order to evaluate how these bone properties could have influenced their potential transport. These data were collected in previous experimental work (Kaufmann and Gutiérrez, 2004). In order to calculate global density of each bone element, the bone weight in dry state was obtained first, and then the procedure was repeated with the bone saturated in water (Behrensmeyer, 1975). Subsequently, the volume of each element was calculated by water displacement. Thus, the global wet and dry densities of each specimen was obtained from the weight of the bone in dry and wet state and the their volume (Kaufmann and Gutiérrez, 2004). In order to estimate the sphericity index we followed the methodology proposed by Frostick and Reid (1983) by measuring three mutually perpendicular axes of each one of the analyzed bones (a: maximum dimension, b: mid dimension and c: minimum dimension) and applying the following equation: $(bc/a^2)^{0.33}$. The number obtained when applying this formula goes between 0 and 1, being 1 the one that represents greater sphericity (Kaufmann and Gutiérrez, 2004). Univariate statistical analyses such as the one-way ANOVA test and pairwise comparisons using the Tukey method were performed. Moreover, since in some cases the size of the groups was very small, the Kruskal–Wallis non-parametric test was used to verify the ANOVA results. All analyses were run using the SYSTAT program (version 10).

3. Results

After the three trials in each series were completed, each element from the three skeletons was assigned to one of the following groups, suggesting different hydric displacement possibilities and following Voorhies's (1969) proposal. Group 1: bone elements which passed through the testing section in all trials of the series. Group 2: bone elements which passed through the testing 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.

3.1. Newborn skeleton

3.1.1. Dry bones in 15 cm/s

As Table 1 and Fig. 2 show, out of the 63 anatomic elements of the newborn skeleton, 44.4% compose transport group 1, 25.4% group 2, and 30% group 3. Group 1 is mainly composed of unfused long bone epiphyses (50%), bones of the axial skeleton (25%) and podial bones and phalanges (25%). Most of these elements moved by flotation (96%). Group 2 is mostly formed by podial bones, the patellae and phalanges (62%) and axial skeleton elements (31.25%). A great diversity of modes of transport movement was observed in the elements composing the group; namely, floting (37.5%), floting–sliding (31.2%), floting–rolling (6.2%) and sliding (25%). Group 3 is formed mostly by long bone diaphyses (42%) and some axial skeleton elements, including cranium and mandible (42%).

3.1.2. Dry bones in 30 cm/s

Whereas transport group 1 comprises 69.8% of bones, group 2 accounts for 19% and group 3 for 11% (Table 1 and Fig. 2). Group 1 comprises podial bones, the patellae, and phalanges (38.6%), axial skeleton elements, including the cranium (29.5%) and unfused long bone epiphyses (31.8%). Most of the elements were transported by floting (43.2%), although the modes of transport movement within the group were diverse, including sliding, floting–sliding, rolling–sliding, floting–sliding–rolling, sliding–rolling–saltation and floting–sliding–rolling–saltation. Group 2 mainly comprises bones of the axial skeleton (including the mandible) (50%) and unfused long bone epiphyses (25%). Most of these elements moved by sliding (66.7%). Group 3 comprises almost exclusively long bone diaphyses (85.7%).

3.1.3. Wet bones in 15 cm/s

As Table 1 and Fig. 2 show, most of the elements are within group 3 (96.8%). The only elements transported, both by sliding, were the first tarsal (group 1) and the pisiform (group 2).

3.1.4. Wet bones in 30 cm/s

In this series, 20.6% of the bone elements make up group 1; 53.9% group 2 and 25.4% group 3 (Table 1 and Fig. 2). Group 1 consists of elements of the axial skeleton, including the cranium (38.5%), unfused epiphyses (32.3%) and some podial and third phalanx bones (30.8%). Most of these bones moved by sliding-rolling (84.6%). Group 2 consists of axial skeleton (32.4%), unfused epiphyses (32.4%) and podial bones, patellae and second phalanx (35.3%). An important number of these elements were transported by sliding (35.3%) and by sliding–rolling (52.9%). Group 3 consists mainly of long bone diaphyses (43.8%) and axial skeleton elements, including the mandible (25%).

3.2. Juvenile skeleton

3.2.1. Dry bones in 15 cm/s

As Table 2 and Fig. 2 show, 20.8% of the elements belong to group 1, 13.2% to group 2, and 66% to group 3. Group 1 consists of unfused long bone epiphyses (54.5%) and axial skeleton bones (45.5%). Almost all the elements that make up this group were transported by floting (90.9%). Group 2 mostly consists of bones of the axial skeleton (57.1%). The mode of movement observed in this group were sliding (57.1%) and floting (42.9%). Group 3 consists of a great diversity of elements, including the podial ones (40%), the long bone diaphyses (17.1%), some unfused epiphyses (17.1%), axial skeleton bones (including cranium and mandible) (14.3%), phalanges (8.6%), and the scapula.

3.2.2. Dry bones in 30 cm/s

In this series, the 34% belong to group 1, 41.5% to group 2 and 24.5% to group 3 (Table 2, Fig. 2). Group 1 consists mainly of axial skeleton bones (50%) and epiphyses of unfused long bones (27.8%). An important percentage of the elements of this group was transported by floting (55.6%). Group 2 consists mainly of podial elements (40.1%), unfused epiphyses (27.3%) and axial skeleton bones, including the cranium (22.7%). The most frequent type of transport mode movement registered among the elements of this group was sliding (59.1%). Group 3 consists of long bone diaphyses (38.5%), some podial elements (23.1%) and unfused epiphyses (15.4%), the first phalanx, mandible, and scapula.

Table 1
Experimental data obtained for the newborn skeleton (n = 63).

Newborn	Dry bones-15 cm/s			Dry bones-30 cm/s			Wet bones-15 cm/s			Wet bones-30 cm/s		
	G1	G2	G3	G1	G2	G3	G1	G2	G3	G1	G2	G3
Skull	–	–	X	SL-R	–	–	–	–	X	SL-R	–	–
Mandible	–	–	X	–	SL	–	–	–	X	–	–	X
Atlas ventral arch	–	–	X	–	SL	–	–	–	X	–	SL	–
Atlas dorsal arch	F	–	–	F	–	–	–	–	X	–	SL-R	–
Axis vert. body	–	F-R	–	F-SL-R	–	–	–	–	X	–	SL-R	–
Axis odont. process	F	–	–	F	–	–	–	–	X	SL-R	–	–
Cervical vert.	–	F	–	–	F-SL	–	–	–	X	–	SL-R	–
Thoracic vert.	–	SL	–	SL-R	–	–	–	–	X	SL	–	–
Lumbar vert.	–	–	X	SL-R	–	–	–	–	X	–	–	X
1st sacral vert.	–	F-SL	–	–	SL-R	–	–	–	X	–	SL	–
2nd sacral vert.	F	–	–	F-SL	–	–	–	–	X	–	SL	–
3rd sacral vert.	F	–	–	F-SL	–	–	–	–	X	–	SL	–
4th sacral vert.	–	–	X	F-SL	–	–	–	–	X	–	SL	–
5th sacral vert.	–	F-SL	–	SL-R-S	–	–	–	–	X	SL-R	–	–
Caudal vert.	F	–	–	F	–	–	–	–	X	SL-R-F	–	–
Sternum	F	–	–	F	–	–	–	–	X	–	SL-R	–
Ilium	–	–	X	–		X	–	–	X	–	–	X
Pubis	F	–	–	F-SL-R	–	–	–	–	X	–	SL-R	–
Ischium	–	–	X	–	SL	–	–	–	X	–	–	X
Rib	–	–	X	–	SL	–	–	–	X	–	SL	–
Scapula	–	–	X	–	SL	–	–	–	X	–	–	X
Scapula tubercle	F	–	–	F-SL-R	–	–	–	–	X	SL-R	–	–
Hum. diaph.	–	–	X	–	SL	–	–	–	X	–	–	X
Hum. head	F	–	–	F	–	–	–	–	X	–	SL-R	–
Hum. great. tub.	F	–	–	F	–	–	–	–	X	–	SL-R	–
Hum. ds epiph.	F	–	–	F	–	–	–	–	X	–	SL	–
Radius diaph.	–	–	X	–	–	X	–	–	X	–	–	X
Radius px epiph.	F	–	–	–	SL	–	–	–	X	–	SL	–
Radius ds epiph.	F	–	–	F	–	–	–	–	X	–	SL-R	–
Ulna diaph.	–	–	X	–	–	X	–	–	X	–	–	X
Ulna olecranon	F	–	–	F-SL	–	–	–	–	X	–	SL-R	–
Ulna ds epiph.	F	–	–	F-SL	–	–	–	–	X	–	R	–
Metacarp. diaph.	–	–	X	–	–	X	–	–	X	–	–	X
Metacarp. ds epiph.	F	–	–	F	–	–	–	–	X	–	SL-R	–
Pisiform	F	–	–	F	–	–	–	SL	–	SL-R	–	–
Lunate	–	F	–	SL	–	–	–	–	X	–	–	X
Cuneiform	–	F	–	SL-R	–	–	–	–	X	–	SL	–
Scaphoid	–	–	X	SL-R	–	–	–	–	X	–	SL	–
Unciform	–	F	–	SL-R-S	–	–	–	–	X	–	SL-R	–
Magnum	–	SL	–	SL-R-S	–	–	–	–	X	–	R	–
Trapezoid	–	F-SL	–	F-SL-R-S	–	–	–	–	X	SL-R	–	–
Femur diaph.	–	–	X	–	–	X	–	–	X	–	–	X
Femur head	F	–	–	F	–	–	–	–	X	SL-R	–	–
Femur great. troch.	F	–	–	F	–	–	–	–	X	SL-R	–	–
Femur ds epiph.	F	–	–	F	–	–	–	–	X	–	–	X
Patella	–	F	–	F	–	–	–	–	X	–	R	–
Tibia diaph.	–	–	X	–	–	X	–	–	X	–	–	X
Tibia tub.	–	–	X	–	SL-R	–	–	–	X	–	SL-R	–
Tibia px epiph.	–	F-SL	–	SL-R	–	–	–	–	X	–	–	X
Tibia ds epiph.	–	–	X	–	SL	–	–	–	X	–	SL-R	–
Astragalus	–	SL	–	SL	–	–	–	–	X	–	SL-R	–
Calcaneus	–	SL	–	SL	–	–	–	–	X	–	SL-R	–
Calcaneus tuber	F	–	–	F	–	–	–	–	X	–	SL	–
Cuboid	F	–	–	F	–	–	–	–	X	–	R	–
Navicular	F-SL	–	–	SL	–	–	–	–	X	–	SL	–
Ext. cuneiform	F	–	–	SL	–	–	–	–	X	–	SL-R	–
Lat. malleolus	–	F-SL	–	SL	–	–	–	–	X	–	SL-R	–
First tarsal	F	–	–	F	–	–	SL	–	–	SL-R	–	–
Metatars. diaph.	–	–	X	–	–	X	–	–	X	–	–	X
Metatars. ds epiph.	F	–	–	F	–	–	–	–	X	SL-R	–	–
1st phalanx	–	F	–	–	SL-R	–	–	–	X	–	–	X
2nd phalanx	F	–	–	SL-R	–	–	–	–	X	–	SL-R	–
3rd phalanx	F	–	–	F	–	–	–	–	X	SL-R	–	–
n	28	16	19	44	12	7	1	1	61	13	34	16

G1 = Group 1; G2 = Group 2; G3 = Group 3; F = flotation; SL = sliding; R = rolling; S = saltation; X = non transported; vert. = vertebra; odont. = odontoid; Hum. = humerus; diaph. = diaphysis; great. = greater; tub. = tuberosity; ds = distal; epiph. = epiphysis; px = proximal; Metacarp. = metacarpal; troch. = trochanter; Ext. = external; Lat. = lateral; Metatars. = metatarsal.

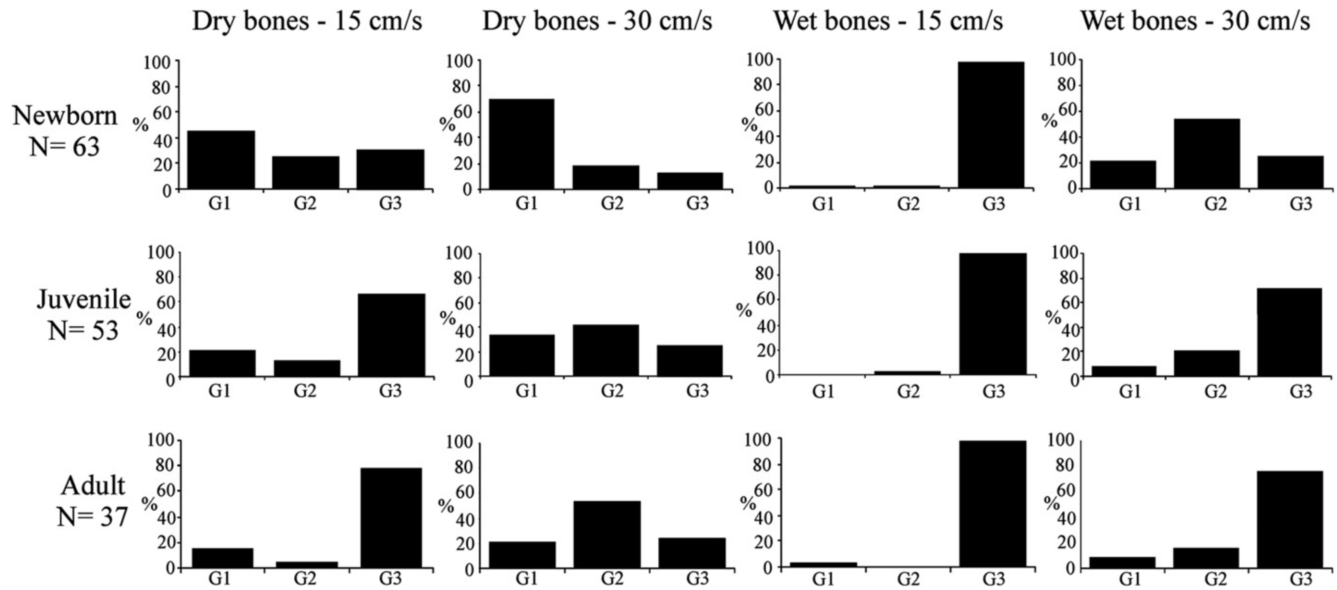

Fig. 2. Percentage of guanaco elements per group, considering age, bone state and speed of current.

3.2.3. Wet bones in 15 cm/s

Almost all the elements belong to group 3 (98.1%) (Table 2, Fig. 2). The only element outside this group is the cranium, which was transported by sliding in some of the trials and belongs to group 2.

3.2.4. Wet bones in 30 cm/s

In this series, 7.5% of the elements belong to group 1, 20.8% to group 2, and 71.7% to group 3 (Table 2, Fig. 2). Group 1 consists of the caudal vertebra, sternebra, ulna olecranon and trapezoid. These elements moved by rolling and sliding. Group 2 consists mainly of elements of the axial skeleton, including the cranium (54.5%). The typical mode of movement for bones in this group were sliding and rolling. Group 3 consists of a great diversity of elements, including podial bones (34.2%), unfused epiphyses (26.3%), axial skeleton bones, among them the mandible (18.4%), long bone diaphyses (13.2%), phalanges (5.3%), and scapula (2.6%).

3.3. Adult skeleton

3.3.1. Dry bones in 15 cm/s

As Table 3 and Fig. 2 show, 16.2% of the elements belong to group 1, 5.4% to group 2 and 78.4% to group 3. Group 1 consists mainly of elements of the axial skeleton (83%). Most of the elements of this group were transported by floting (66.7%). Group 2 consists of the pelvis and patellae which moved by sliding. Group 3 consists of elements of the appendicular skeleton (79.3%) as well as the axial, including the cranium and mandible (20.7%).

3.3.2. Dry bones in 30 cm/s

Group 1 is formed by 21.6% of the elements, group 2 by 54.1%, and group 3 by 24.3% of the bones (Table 3, Fig. 2). Most of the elements composing group 1 correspond to the axial skeleton (75%). Although diverse modes of movement were observed, the most frequent was floting (50%). Group 2 is mainly composed of podial bones (55%) and of the axial skeleton, including the cranium (25%). A great percentage of the elements moved by sliding (55%). Group 3 is composed of long bones (44.4%) and podial bones (33.3%), a phalanx and the mandible.

3.3.3. Wet bones in 15 cm/s

Most of the elements belong to group 3 (97.3%). The only transported element was a caudal vertebra (group 2) which moved by sliding and rolling (Table 3, Fig. 2).

3.3.4. Wet bones in 30 cm/s

In this series, 8.1% of the elements belong to group 1, 16.2% to group 2 and 75.7% to group 3 (Table 3, Fig. 2). Group 1 consists of the thoracic vertebra, caudal vertebra and the rib, which moved mainly by sliding. Group 2 consists mostly of axial elements, including the cranium (66.7%). The most frequent type of movement mode was sliding. Group 3 consists almost totally of elements of the appendicular skeleton (82.1%) and some elements of the axial, including the mandible.

4. Discussion

The results of the conducted experiments show that the different bones that compose the guanaco skeleton present varied hydrodynamic behavior. Many factors influence bone transport potential in water. Among them, the intrinsic bone properties, such as shape, weight, volume and density; their state; *i.e.*, whether they are articulated, disarticulated, dry, saturated in water, fresh or weathered; and different variables related to the natural environment where the transport is taking place; *e.g.*, flow velocity, water depth, the nature of the substrate and bedforms (Aslan and Behrensmeyer, 1996; Behrensmeyer, 1975; Boaz and Behrensmeyer, 1976; Coard and Dennell, 1995; Hanson, 1980; Trapani, 1998). Considering the experiments performed with the three guanaco skeletons, it was observed that the greatest percentages of transported elements were obtained from dry bones under a flow velocity of 30 cm/s (Fig. 2). On the contrary, the smallest quantity of transported elements was obtained from the series performed with saturated bones at a flow velocity of 15 cm/s (Fig. 2). Under these conditions, only one element from each of the newborn and adult skeletons was transported; the first tarsal and the caudal vertebra, respectively, whereas no element from the juvenile skeleton was transported. On the other hand, dry bones submitted to a flow velocity of 15 cm/s and wet bones submitted to a flow velocity of 30 cm/s presented intermediate displacement compared to the conditions previously mentioned (Fig. 2).

Table 2
Experimental data obtained for the juvenile skeleton ($n = 53$).

Juvenile	Dry bones-15 cm/s			Dry bones-30 cm/s			Wet bones-15 cm/s			Wet bones-30 cm/s		
	G1	G2	G3	G1	G2	G3	G1	G2	G3	G1	G2	G3
Skull	–	–	X	–	SL	–	–	SL		–	SL	–
Mandible	–	–	X	–	–	X	–	–	X	–	–	X
Atlas	–	–	X	SL	–	–	–	–	X	–	SL-R	–
Axis	–	SL	–	SL	–	–	–	–	X	–	SL-R	–
Cervical vert.	–	SL	–	–	SL	–	–	–	X	–	–	X
Thoracic vert.	F-SL	–		SL	–	–	–	–	X	–	–	X
Lumbar vert.	–	–	X	SL	–	–	–	–	X	–	–	X
1st + 2nd sacral vert.	–	F	–	–	F-SL	–	–	–	X	–	–	X
3rd sacral vert.	F	–	–	F	–	–	–	–	X	–	SL-R	–
4th sacral vert.	F	–	–	F	–	–	–	–	X	–	SL	–
5th sacral vert.	F	–	–	F	–	–	–	–	X	–	SL	–
Caudal vert.	F	–	–	F	–	–	–	–	X	SL-R	–	–
Sternum	F	–	–	F	–	–	–	–	X	SL	–	–
Innominate	–	–	X	–	SL	–	–	–	X	–	–	X
Rib	–	SL	–	–	SL	–	–	–	X	–	–	X
Scapula	–	–	X	–	–	X	–	–	X	–	–	X
Hum. diaph. + ds epiph.	–	–	X	–	SL	–	–	–	X	–	R	–
Hum. head	F	–	–	F	–	–	–	–	X	–	R	–
Hum. great. tub.	F	–	–	F	–		–	–	X	–	–	X
Radius–ulna diaph.	–	–	X	–	–	X	–	–	X	–	–	X
Ulna olecranon	F	–	–	F	–	–	–	–	X	R	–	–
Radius–ulna ds epiph.	–	–	X	–	SL-R	–	–	–	X	–	R	–
Metacarp. diaph.	–	–	X	–	–	X	–	–	X	–	–	X
Metacarp. ds epiph.	–	–	X	–	SL-R	–	–	–	X	–	–	X
Pisiform	–	–	X	–	SL	–	–	–	X	–	–	X
Lunate	–	–	X	–	R	–	–	–	X	–	–	X
Cuneiform	–	–	X	–	SL-R	–	–	–	X	–	–	X
Scaphoid	–	–	X	–	SL	–	–	–	X	–	–	X
Unciform	–	–	X	–	SL-R	–	–	–	X	–	–	X
Magnum	–	–	X	–	SL	–	–	–	X	–	–	X
Trapezoid	–	–	X	R	–	–	–	–	X	R	–	–
Femur diaph.	–	–	X	–	–	X	–	–	X	–	–	X
Femur head	–	F	–	–	SL	–	–	–	X	–	–	X
Femur great. troch.	F	–	–	F	–	–	–	–	X	–	–	X
Femur ds epiph.	F	–	–	F	–	–	–	–	X	–	–	X
Patella	–	SL	–	SL-S	–	–	–	–	X	–	R	–
Tibia diaph.	–	–	X	–	–	X	–	–	X	–	–	X
Tibia tuberosity	–	–	X	–	–	X	–	–	X	–	–	X
Tibia px epiph.	–	F	–	–	SL	–	–	–	X	–	–	X
Tibia ds epiph.	–	–	X	–	SL	–	–	–	X	–	–	X
Astragalus	–	–	X	–	–	X	–	–	X	–	–	X
Calcaneus	–	–	X	–	–	X	–	–	X	–	–	X
Calcaneus tuber	–	–	X	–	SL-R	–	–	–	X	–	–	X
Cuboid	–	–	X	–	–	X	–	–	X	–	–	X
Navicular	–	–	X	–	SL	–	–	–	X	–	–	X
Ext. cuneiform	–	–	X	–	SL-R	–	–	–	X	–	–	X
Lat. malleolus	–	–	X	–	SL	–	–	–	X	–	–	X
First tarsal	–	–	X	R	–	–	–	–	X	–	–	X
Metatars. diaph.	–	–	X	–	–	X	–	–	X	–	–	X
Metatars. ds epiph.	–	–	X	–	–	X	–	–	X	–	–	X
1st phalanx	–	–	X	–	–	X	–	–	X	–	–	X
2nd phalanx	–	–	X	–	SL-R	–	–	–	X	–	–	X
3rd phalanx	–	–	X	SL-R	–	–	–	–	X	–	SL	–
n	11	7	35	18	22	13	0	1	52	4	11	38

G1 = Group 1; G2 = Group 2; G3 = Group 3; F = flotation; SL = sliding; R = rolling; S = saltation; X = non transported; vert. = vertebra; odont. = odontoid; Hum. = humerus; diaph. = diaphysis; great. = greater; tub. = tuberosity; ds = distal; epiph. = epiphysis; px = proximal; Metacarp. = metacarpal; troch. = trochanter; Ext. = external; Lat. = lateral; Metatars. = metatarsal.

It is noteworthy that regarding flow velocity in particular, when velocity was increased from 15 cm/s to 30 cm/s, the number of transported bone elements increased (group 1) and the number of non-transported elements decreased (group 3). This change was observed in the three skeletons, both in dry and water-saturated bones (Fig. 2). Due to the channel technical limitations, it was not possible to experiment with greater velocities. However, the velocities reached can account for transport groups in both low and medium energy flows.

With respect to the bone state, dry or wet, important changes were observed when bones passes from dry to saturated states maintaining the same velocity. In fact, the most marked change was observed in the newborn skeleton under a velocity of 15 cm/s. In this series, this skeleton passed from 44.4% transported elements (group 1) and 30% non transported bones (group 3) in the dry state series, to 1.6% transported elements (group 1) and 96.8% non transported elements (group 3) in the saturated state series (Fig. 2). Last, this type of change was also observed in the newborn skeleton under a flow velocity of 30 cm/s as well as in the other two individuals under both velocities, although it was less marked (Fig. 2).

Regarding the bone elements susceptibility to transport and the age of the individuals, it was observed that out of the three guanaco

Table 3
Experimental data obtained for the adult skeleton ($n = 37$).

Adult	Dry bones-15 cm/s			Dry bones-30 cm/s			Wet bones-15 cm/s			Wet bones-30 cm/s		
	G1	G2	G3	G1	G2	G3	G1	G2	G3	G1	G2	G3
Skull	–	–	X	–	SL	–	–	–	X	–	R	–
Mandible	–	–	X	–	–	X	–	–	X	–	–	X
Atlas	–	–	X	–	SL	–	–	–	X	–	–	X
Axis	–	–	X	–	R	–	–	–	X	–	SL	–
Cervical vert.	–	–	X	–	SL	–	–	–	X	–	–	X
Thoracic vert.	F-SL	–	–	F-SL	–	–	–	–	X	SL	–	–
Lumbar vert.	SL	–	–	SL-R	–	–	–	–	X	–	SL	–
Sacrum	F	–	–	F	–	–	–	–	X	–	F-SL	–
Caudal vert.	F	–	–	F	–	–	SL-R	–	–	SL-R	–	–
Sternum	F	–	–	F	–	–	–	–	X	–	–	X
Pelvis	–	SL	–	–	SL	–	–	–	X	–	–	X
Rib	–	–	X	R	–	–	–	–	X	SL	–	–
Scapula	–	–	X	–	SL	–	–	–	X	–	–	X
Hum.	–	–	X	–	F-SL	–	–	–	X	–	–	X
Radius–ulna	–	–	X	–	–	X	–	–	X	–	–	X
Metacarp.	–	–	X	–	–	X	–	–	X	–	–	X
Pisiform	–	–	X	–	R	–	–	–	X	–	–	X
Lunate	–	–	X	–	SL	–	–	–	X	–	–	X
Cuneiform	–	–	X	–	SL	–	–	–	X	–	–	X
Scaphoid	–	–	X	–	SL-R	–	–	–	X	–	–	X
Unciform	–	–	X	–	SL	–	–	–	X	–	–	X
Magnum	–	–	X	–	–	X	–	–	X	–	–	X
Trapezoid	–	–	X	–	SL-R	–	–	–	X	–	–	X
Femur	F	–	–	F	–	–	–	–	X	–	–	X
Patella	–	SL	–	SL-S	–	–	–	–	X	–	SL-R	–
Tibia	–	–	X	–	–	X	–	–	X	–	–	X
Astragalus	–	–	X	–	SL	–	–	–	X	–	–	X
Calcaneus	–	–	X	–	–	X	–	–	X	–	–	X
Cuboid	–	–	X	–	–	X	–	–	X	–	–	X
Navicular	–	–	X	–	R	–	–	–	X	–	–	X
Ext. cuneiform	–	–	X	–	SL-R	–	–	–	X	–	–	X
Lat. malleolus	–	–	X	–	SL	–	–	–	X	–	–	X
First tarsal	–	–	X	–	SL-R	–	–	–	X	–	SL-R	–
Metatars.	–	–	X	–	–	X	–	–	X	–	–	X
1st phalanx	–	–	X	–	–	X	–	–	X	–	–	X
2nd phalanx	–	–	X	–	SL-R	–	–	–	X	–	–	X
3rd phalanx	–	–	X	–	SL	–	–	–	X	–	–	X
n	6	2	29	8	20	9	0	1	36	3	6	28

G1 = Group 1; G2 = Group 2; G3 = Group 3; F = flotation; SL = sliding; R = rolling; S = saltation; X = non transported; vert. = vertebra; Hum. = humerus; Metacarp. = metacarpal; Ext. = external; Lat. = lateral; Metatars. = metatarsal.

skeletons studied in the experiments, the newborn individual presented the greatest hydric transport potential (Fig. 2). For instance, for the flow speed 30 cm/s series with dry state bones, the newborn skeleton presented 69.8% of the specimens, the juvenile 34%, and the adult 21.6%, all in group 1.

The results discussed so far confirm that flow velocity and bone state; *i.e.*, dry or saturated in water, are important variables conditioning fluvial transport (Coard, 1999). Moreover, experiments show that the age of the individual is another factor influencing potential transport. The relevance of other important variables conditioning transport and their relation to the already mentioned factors; such as, flow velocity, state and age, will be discussed next.

The experiment showed that in different trials the bones moved by flotation, saltation, rolling, and sliding, experimenting many of specimens more than a type of movement (Table 4). Flotation was very important in trials with dry bones, in which the global density of many of them was smaller to water density. Some of the bones began trials floating and then, once they incorporated water continued the displacement by sliding, rolling, and saltation. Also, some bones passed the test sector moving through sliding, rolling, and saltation. On the contrary, flotation was not registered in the trials with wet bones, standing out the sliding and the rolling as the mode of transport (Table 4).

As one can observe in Fig. 3, the dry and wet bone density value range in the different skeletons is ample (values taken from Kaufmann and Gutiérrez, 2004). On the one hand, in the newborn individual, dry density ranges between 0.63 g/cm^3 and 1.6 g/cm^3, being 1.00 g/cm^3 the median; it ranges from 0.66 g/cm^3 to 1.63 g/cm^3 and the median is 1.27 g/cm^3 for the juvenile one; and for the adult skeleton, dry density ranges from 0.55 g/cm^3 to 1.88 g/cm^3 and the

Table 4
Modes of transport movements for bones in group 1 and group 2.

Dry bones				Wet bones			
15 cm/s		30 cm/s		15 cm/s		30 cm/s	
G1	G2	G1	G2	G1	G2	G1	G2
41 F 3 F-SL 1 SL	9 F 5 F-SL 1 F-R 10 SL	33 F 6 F-SL 3 F-SL-R 1 F-SL-R-S 11 SL 3 SL-R-S 8 SL-R 2 SL-S 3 R	3 F-SL 32 SL 4 R 15 SL-R	1 SL	2 SL 1 SL-R	1 F-SL-R 3 SL 12 SL-R 3 R	18 SL 23 SL-R 9 R 1 F-SL

G1 = Group 1; G2 = Group 2; F = flotation; SL = sliding; R = rolling; S = saltation.

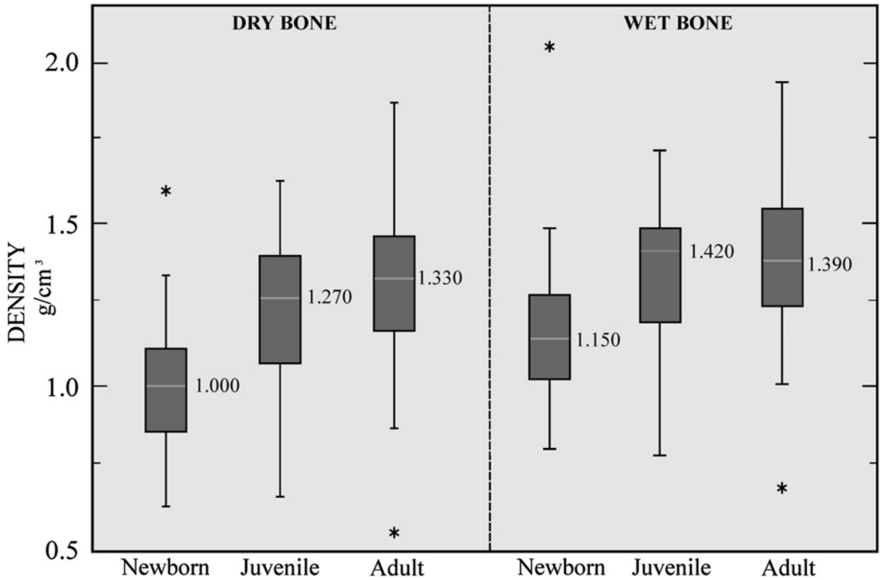

Fig. 3. Boxplot showing global density (dry and wet) values obtained for the newborn, juvenile and adult individuals. Asterisks represent outliers.

median is 1.33 g/cm^3. On the other hand, the wet density ranges from 0.81 g/cm^3 to 2.05 g/cm^3, being the median 1.15 g/cm^3 for the newborn individual; it ranges from 0.79 g/cm^3 to 1.73 g/cm^3, and the median is 1.42 g/cm^3 for the juvenile; and for the adult the range is between 0.69 g/cm^3 and 1.94 g/cm^3 while the median is 1.39 g/cm^3.

One-way ANOVA and pairwise comparisons showed that dry and wet density values for the newborn individual were significantly different from the juvenile and adult individual ones. However, dry and wet density values for the two latter individuals were not significantly different (Table 5). The differences in dry and wet density values between the newborn and the two other age classes allow us to propound that the greater bone transportability presented by the younger individual is related to its lower global density.

Table 5
Results of ANOVAs of the dry density, wet density and sphericity of different age classes.

	ANOVA		Tukey
	F	*P*	
Dry density	23.270	0.000	N-J*, N-A*
Wet density	14.437	0.000	N-J*, N-A*
Sphericity	0.741	0.479	

Tukey lists those comparisons between two groups (age classes) that are significant; N = newborn; J = juvenile; A = adult (d.f. = 2 for all ratios; *F*, the *F*-statistic for ANOVA; *P*, the *P*-value for each comparison; * significant at 0.01).

Moreover, the importance of global density in hydric displacement is also evidenced when comparing this property in the bones composing the different transport groups (Fig. 4). Table 6 shows that the comparison performed by the one-way ANOVA test and the pairwise analysis evidences that the established transport groups for each series showed in all cases significant differences in this global density; that is to say, elements in group 1 always presented lower densities than elements in group 2 and 3, and elements in group 2 always presented lower densities than in group 3 (Table 6). The exception, however, was the wet low flow velocity 15 cm/s series due to its scanty number and/or absence of elements in some transport group.

As mentioned before, another variable conditioning transport is bone shape. With the aim of determining whether this property influenced the differential bone transport of the different

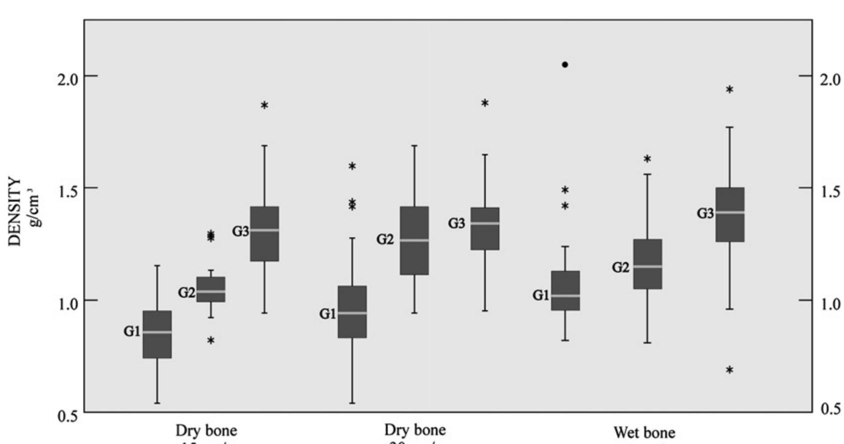

Fig. 4. Boxplot showing the wet and dry global density value range (taken from Kaufmann and Gutiérrez, 2004) of the elements composing each transport group in the different series. Wet bones-15 cm/s series was not included due to the small sample sizes in G1 and G2. Asterisks represent outliers and circles extreme outliers.

Table 6
Results of ANOVAs of the dry density, wet density and sphericity of the transport groups obtained in the different experimental series.

	ANOVA		Tukey
	F	*P*	
Dry density Transport groups (dry bones-15 cm/s)	99.640	0.000	G1-G2**, G1-G3**, G2-G3**
Dry density Transport groups (dry bones-30 cm/s)	58.008	0.000	G1-G2**, G1-G3**, G2-G3**
Wet density Transport groups (wet bones-30 cm/s)	17.756	0.000	G1-G3**, G2-G3**
Sphericity Transport groups (dry bones-15 cm/s)	7.048	0.001	G1-G3*
Sphericity Transport groups (dry bones-30 cm/s)	30.590	0.000	G1-G3**, G2-G3*
Sphericity Transport groups (wet bones-30 cm/s)	5.155	0.007	G1-G3*, G2-G3*

Tukey lists those comparisons between two groups (transport groups) that are significant; G1 = Group 1; G2 = Group 2; G3 = Group 3 (d.f. = 2 for all ratios; *F*, the *F*-statistic for ANOVA; *P*, the *P*-value for each comparison; *Significant at 0.05; **Significant at 0.01). Comparison between groups in wet bones-15 cm/s series was not performed due to the small sample sizes in G1 and G2.

individuals, sphericity values were compared among each of the three individuals. The one-way ANOVA test and pairwise comparisons showed that sphericity index presented no significant differences among the three individuals (Table 5). Also, the sphericity values between each one of the transport groups for each of the series were compared (Fig. 5). The one-way ANOVA test indicates that the different transport group series present statistically significant differences with respect to this index, whereas the Tukey; *i.e.*, pairwise analysis, shows that the significant differences related to this index are between group 1 and group 3, and between group 2 and group 3, but not between group 1 and group 2 (Table 6). However, it should be noted that in some cases presenting significant differences; such as the dry bone 15 and 30 cm/s flow velocity series, these differences could be related to the fact that many specimens presenting high sphericity index have low density. Taking into account that the Pearson test indicates a significant correlation between both variables ($r = -0.205$, $p = 0.013$) and that dry bone displacement was, in most cases, by floting (Table 4), it is suggested that in such cases sphericity would not have had a significant role in bone displacement. Nevertheless, this property would have played a more important role in the wet bone 30 cm/s flow velocity series where a great percentage of bones moved by rolling and sliding on the channel bed (Table 4).

The results obtained in this study alert over the possibility of sub-representation of immature individuals in the mortality as well as skeletal part profiles of fossil assemblages biased by hydrodynamic sorting. At the moment of reconstructing mortality profiles from long bone fusions or estimating skeletal part representations, it is necessary to consider distal and proximal portions of diaphyses rather than of the corresponding epiphysis, which according to the results of our experiments would be more affected by hydrodynamic sorting. A pattern with similar bias on bone assemblage can be generated by other taphonomic agents such as carnivores. Actualistic and experimental studies have demonstrated that carnivores have a strong impact on inter-bone survival affecting the skeleton less dense bones, as well as causing selective destruction on the limb bone ends in preference to limb shafts. This impact is also more intense in immature individuals (Binford and Bertram, 1977; Behrensmeyer et al., 1979; Cleghorn and Marean, 2007; Klein and Cruz-Uribe, 1984, 1991; Marean, 1995, 1997; Munson, 2000; Munson and Garniewicz, 2003; Paine and Munson, 1985). However, the analysis of taphonomic effects on bones allows us to discriminate between carnivores and hydrodynamic sorting.

5. Application to fossil assemblages

We have gathered very detailed information in our experiments concerning potential transport from a great variety of bone elements corresponding to three individuals of diverse ages under different conditions (dry and saturated in water) and flow velocities

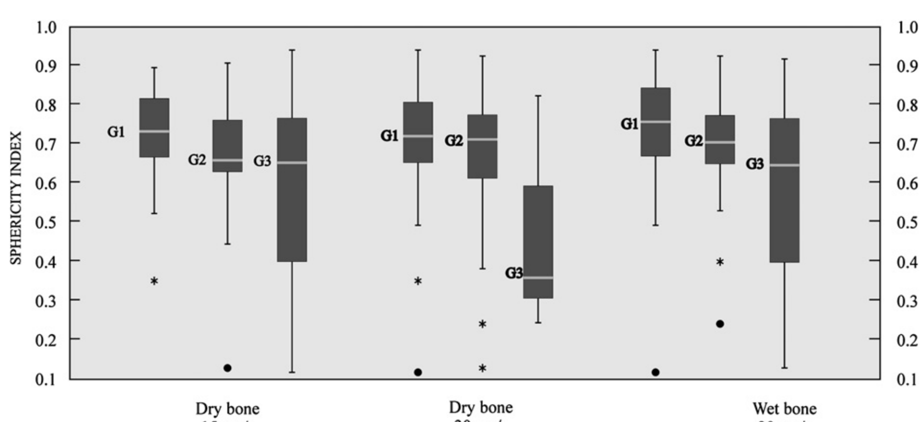

Fig. 5. Boxplot showing the sphericity value range (taken from Kaufmann and Gutiérrez, 2004) of the elements composing each transport group in the different series. Wet bones-15 cm/s series was not included due to the small sample sizes in G1 and G2.

(15 cm/s and 30 cm/s). These data synthesized in Tables 1–3, show that bone hydric behavior is sensitive to a great number of factors. Due to the impossibility to know the flow velocity of the current during the past, or the difficulties to assign the age class to every recovered anatomic element, the data obtained in our experiments cannot be used directly to evaluate the hydrodynamic sorting incidence in fossil assemblages. For this reasons, a simplified differential transport model of dry state bones is proposed involving a smaller number of bone elements within groups 1 and 3 (Table 7). Not considering the results of the wet bone series for this model is due to the fact that under the flow velocities used in our experiments, the number of mobilized elements (group 1) was extremely low. On the other hand, elements in group 2 were not taken into account because of the variable behavior in the different trials. The bone elements selection criteria included in the proposed model were: 1) the bone possibility of being discriminated in the fossil record in the corresponding age categories from their fusion state into either newborn, newborn-juvenile, or adult; and 2) to have been assigned to the same group (group 1 or 3) in both flow velocities (15 cm/s and 30 cm/s).

To evaluate the role of the hydric sorting archaeologically, we propose to compare the relative frequencies of anatomical parts (*i.e.*, NISP or MAU) integrating group 1 (*i.e.*, high transport potential bones) and group 3 (*i.e.*, low transport probability bones) (see Table 7). In order to avoid the influence of the mortality profile of the analyzed assemblage in the representation of the transport groups, the comparison should be completed for each of the newborn, newborn-juvenile, and adult age classes. In this way, the frequency corresponding to both transport groups for the three age categories proposed can be evaluated. The lack of resemblance between both groups frequency would indicate that the fossil assemblage could be biased by fluvial action. However, it is necessary to consider complementary criteria such as orientation of bone remains, presence of geological abrasion in the bone specimens, proportion of molars/vertebras, degree of association of bone elements, and geomorphologic characteristics of the sites that would provide comprehensive information to interpret adequately the bone assemblage taphonomic history (Badgley, 1986; Behrensmeyer, 1975; Fernández-Jalvo and Andrews, 2003; Gutiérrez and Kaufmann, 2007; Shipman, 1981; Toots, 1965; Voorhies, 1969).

Table 7
Groups with high (Group 1) and low (Group 3) hydric transport potential considering age categories commonly identified in the archaeological record.

	Group 1	Group 3
Newborn	Atlas dorsal arch	Ilium
Unfused bones	Axis odont. process	Radius diaph.
	Pubis	Ulna diaph.
	Scapula tubercle	
	Hum. ds epiph.	
	Radius ds epiph.	
	Ulna ds epiph.	
Newborn-Juvenile	Sacral vert.	Metacarp. diaph.
Unfused bones	Caudal vert.	Metatars. diaph.
	Sternum	Femur diaph.
	Hum. head	Tibia diaph.
	Hum. great. tub.	
	Ulna olecranon	
	Femur great. troch.	
	Femur ds epiph.	
Adult	Thoracic vert.	Skull
Fused bones	Lumbar vert.	Mandible
	Sacrum	Axis
	Caudal vert.	Cervical vert.
	Sternum	Rib
		Hum.
		Radius–ulna
		Metacarp.
		Tibia
		Calcaneus
		Metatars.
		1st phalanx

odont. = odontoid; Hum. = humerus; ds = distal; epiph. = epiphysis; diaph. = diaphysis; vert. = vertebra; great. = greater; tub. = tuberosity; troch. = trochanter; Metacarp. = metacarpal; Metatars. = metatarsal.

6. Conclusion

From the experiments performed, a reference frame was generated, complementary to the already existing ones (Behrensmeyer, 1975; Boaz and Behrensmeyer, 1976; Dodson, 1973; Hanson, 1980; Voorhies, 1969), that explains guanaco bone remains hydric transport considering the influence of varied factors; such as age, flow speed, dry or water-saturated bones, global density, and shape of the bones. The proposed methodology will allow for the evaluation of the role of the hydric sorting has had in the skeletal representation of a fossil assemblage located in the flooded plains of rivers or lacustrine borders where the hydric dynamics has been relatively low.

The results show that bone specimen global density would significantly influence the behavior of bones submitted to hydric current conditions of 15 and 30 cm/s. In this way, bones from newborn and juvenile individuals with unfused secondary growth centers and relatively low global densities would present high transportability condition with respect to fused bones from adult individuals, an aspect that had remained unexplored up to now.

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