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Pastoralism in Northern Peru during Pre-Hispanic Times: Insights from the Mochica Period (100–800 AD) Based on Stable Isotopic Analysis of Domestic Camelids

Elise Dufour[1]*, Nicolas Goepfert[2], Belkys Gutiérrez Léon[3], Claude Chauchat[2], Régulo Franco Jordán[4], Segundo Vásquez Sánchez[3]

1 Muséum national d'Histoire naturelle-CNRS, UMR 7209 Archéozoologie, Archéobotanique : sociétés, pratiques et environnements, Département Ecologie et Gestion de la Biodiversité, Paris, France, **2** CNRS-Paris 1, UMR 8096 Archéologie des Amériques, Nanterre, France, **3** Universidad Nacional de Trujillo, Trujillo, Peru, **4** Museo de Cao-Fundación Wiese, Lima, Peru

Abstract

Llama (*Lama glama*) and alpaca (*Vicugna pacos*) are the only large domesticated animals indigenous to the Americas. Pastoralism occupies a fundamental economic, social and religious role in Andean life. Today, camelid livestock are confined to the ecozone of the *puna* (above 3,500 masl), while their presence on the Pacific coast during pre-Hispanic times is attested by archaeological skeletal remains. This study aims to document herding practices on the northern Peruvian coast during the Early Intermediate Period (200 BC-600 AD) by gaining insights into diet, location of breeding and mobility of archaeological camelids from the funerary and ritual contexts of two Mochica sites, Uhle Platform in Huacas de Moche and El Brujo. The three first early years and the long-term life histories of the animals were documented by the combined bulk analysis of bone collagen ($\delta^{13}C_{col}$ and $\delta^{15}N_{col}$) and bone structural carbonate ($\delta^{13}C_{bone}$ and $\delta^{18}O_{bone}$) and the serial analysis of structural carbonate of molar tooth enamel ($\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$). Mochica camelids were bred in the low and/or middle valleys, unlike their modern counterparts, who are restricted to highland *puna* C_3 pastures. Archaeological camelids had diverse and complex life histories, usually with substantial maize foddering. An ontogenetic switch in diet and possible residential mobility during the course of life were identified for some specimens. Although the inference of geographic origin from $\delta^{18}O_{bone}$ and $\delta^{18}O_{enamel}$ values was limited because of the lack of understanding of the influence of environmental and biological factors, tooth enamel analysis has great potential for exploring camelid herding practices and Andean pastoralism. Our study suggested that Mochica herders adapted their practices to the difficult lowland environment and that herding practices were varied and not restricted to breeding at higher altitudes. The role of maize in different aspects of the economic life of the Mochicas is also underlined.

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* E-mail: edufour@mnhn.fr

Introduction

Andean pastoralism and the establishment of trade routes between different ecological zones, the so-called concept of Andean verticality, is one of the foundations for the emergence of complex societies in the pre-Hispanic world [1]. Alpacas (*Vicugna pacos*) and llamas (*Lama glama*) were domesticated 4,000–6,000 years ago, and experienced an intensification in livestock management from at least the end of the Early Horizon (900–400 BC) [2]. From then onwards, camelids have occupied a fundamental economic, social and religious role, both in pre-Hispanic and modern Andean cultures [3]. During the pre-Hispanic period, the llama was the only beast of burden and caravans providing goods to different ecological zones were crucial to the development of extensive trade networks [1,4–6]. Textiles were manufactured from camelid wool and traded throughout the Andes, their meat was consumed, leather and bones served as raw materials to make tools and various ornaments, and dung was used as fuel. Domestic camelids were sacrificed and deposited into graves to fulfil various symbolic functions [7] and their entrails could be used to read omens. Finally, they were a symbol of prestige and a marker of identity [8].

Today, camelid husbandry is essentially restricted to the highlands [9], in an ecozone called the *puna* that comprises plateaus above 3,500 masl, and more precisely between 3,900 and 4,500 masl [10]. *Puna* conditons are characterized by hypoxia, low intra-annual variation in temperature but daily variation as high as 20°C and a higher precipitation rate than that of the lower western slopes of the Andes (between 200 and 1,500 mm per year [11]). Water is supplied by rain, snow and hail during the rainy season. The vegetation comprises wetlands such as *bofedales* (peatlands of the central Andes where Juncaceae species dominate and serve as the primary peat-formers) which are naturally conducive to llama and alpaca breeding. The optimum life conditions for llamas and alpacas vary according to the function the animal serves [12].

Alpaca herds devoted to wool production are raised in rich *bofedales* pasturelands at higher altitudes than llama herds. The presence of domestic camelids in remote and dramatically different habitats, like the Pacific coast – characterized by a higher mean temperature and higher seasonal variations in temperature than the *puna* and almost no precipitation – is attested by skeletal remains, textiles and iconography from at least 200 BC onwards [2,8,13–17]. It was formerly assumed that lowland camelids were not raised locally but instead were brought by caravans from the Andes shortly before being butchered or sacrificed [18]. This classical view is challenged by new zooarchaeological studies [7,13,19]. The northern coast (0–500 masl) of Peru has witnessed – among others – the development of rich and powerful cultures, such as the Mochica culture (100–800 AD), famous for the construction of monumental ceremonial centers and cultural artefacts such as vessels and metal ornaments [20]. Camelid skeletal remains were found in different Mochica contexts: domestic, burials, sacrifices, funerary banquets and offering deposits. Because of the arid to hyper arid conditions that prevail today, the Peruvian coast does not seem to provide favorable conditions to camelid herding, compared to the rich productive grasslands and wet *bofedales* of the *puna*. Only a few habitats located in the lower part of the valleys, fog oases (*lomas*) developing in the foothills, or irrigated fields could have provided pastures rich enough to sustain large herds. Maize foddering, diet supplements comprising marine resources (algae) or seasonal transhumance to mid-altitude valleys could have been used to compensate low food availability. Therefore, the breeding of flocks in an environment radically different from their original environment during pre-Hispanic times raises questions about the nature and the location of the dietary resources necessary to maintain animals and the seasonal or year-round nature of their keep. Furthermore, the presence of camelid remains on the north coast is not in itself indicative of local herding. With the exception of juveniles (under two years old) that have not been documented to travel long distances [21], the skeletal remains found in the northern coast could have belonged to animals first bred in the *puna* and subsequently brought to the coast. In order to answer these questions and document the management systems developed by coastal breeders it is essential to reconstruct camelid diet and zone of growth.

Measurements of stable isotopes of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), oxygen ($\delta^{18}O$) and strontium ($^{87}Sr/^{86}Sr$) in human and animal remains found in archaeological contexts are a primary source of information on the life history of humans and animals. The scope of isotopic analyses is still limited in South America compared to other regions but it is growing rapidly. The western slopes of the Andes present a wide variety of ecological zones [22] from the coast to the highlands, characterized by differences in physical parameters such as temperature and precipitation, as well as availability of different food resource categories. This results in relatively predictable geographical variations in dietary and environmental isotopic signatures across the landmass [11,23], even though the baseline of environmental $\delta^{18}O$ water data remains to be established on a local scale [11,24,25]. A number of paleodietary studies have been completed using $\delta^{13}C$ and $\delta^{15}N$ values that enable, for instance, the identification of maize consumption [26–30]. $\delta^{13}C$ and $\delta^{15}N$ values, as well as $\delta^{18}O$ and $^{87}Sr/^{86}Sr$ values (that rely on climate and geology) can also be used to assess animal mobility between geographical areas that present distinct isotopic values [31–34].

Stable isotopic studies of past camelids in the Central Andes have mostly been conducted on bone collagen (reviewed by [34]) and more recently on bone structural carbonate [35,36] of remains from various archaeological contexts, located at different elevations (lowlands, intermediate lands, highlands). They revealed some diversity in diet, pasturelands and foddering practices among sites and within sites. As bone tissue is constantly renewed during life, it provides a record of diet and habitat averaged out over the lifetime of the animal. Only tissues with accretional growth that do not undergo remodeling after deposition can record the chronology of the animal's life history. Enamel of high-crowned teeth records events that occurred during the period of tooth formation and reconstructs this record through the isotopic profiles when an appropriate serial sampling protocol is applied.

The serial analysis of tooth enamel has been used successfully in different regions of the world to document herding practices [37,38]. Preliminary data presented in Goepfert et al. [36] showed that this technique appears to be very promising in the Central Andean region. Based on these first data, this study aims to document herding practices on the northern Peruvian coast during the Early Intermediate Period (200 BC-600 AD). In order to provide insights into diet, location of breeding of domestic camelids and mobility patterns between the coast and higher elevations, the age of archaeological specimens from two Mochica sites (Uhle Platform in Huacas de Moche and El Brujo, La Libertad region) in the Moche and Chicama Valleys was determined and their stable isotopic composition was analysed and compared to that of modern camelids. The serial analysis of $\delta^{13}C$ and $\delta^{18}O$ values of structural carbonate from molar enamel ($\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$) was used to retrospectively record the animals' early life histories. Enamel $\delta^{13}C$ and $\delta^{18}O$ values were compared to those of bone apatite ($\delta^{13}C_{bone}$ and $\delta^{18}O_{bone}$) and to $\delta^{13}C$ and $\delta^{15}N$ values for bone collagen ($\delta^{13}C_{col}$ and $\delta^{15}N_{col}$), to document diachronic changes in diet and growth location.

Materials and Methods

Geographical and Cultural Context

The Mochica territory ranged from the Piura Valley to the Huarmey Valley on the northern coast of Peru (Fig. 1). Mochica political power was not centralized, but was probably divided into independent centers located around the valleys [39] carved by rivers and streams between the coast and the Andean foothills along a northeast-southwest axis (Figs. 1–2). The Mochica people occupied the lower elevations of the Andes (0–500 masl), which presents contrasting environments. A relative chronology based on stylistic changes in the form and decoration of Mochica ceramic vessels (stirrup spout bottles) was defined by Larco Hoyle [40]. The sequence includes five successive phases: Moche I and II (100–200 AD), Moche III (200–450 AD), Moche IV (450–650 AD) and Moche V (650–800 AD).

At the latitude of the Moche region, the coast is a zone approximately 25 km wide, bordered to the west by a cool and rich ocean and to the east by the foothills of the Andes (Fig. 2). The coast is very arid and covered with sand and large dunes [41]. With less than 20 mm of rain per year, surface waters result mostly from the winter mists called *garúa*, which occur between May and December, and the resurgence of the underground water network [42]. *Lomas* develop on the foothills between 200 and 1,000 masl and present specific vegetation which is particularly attractive to wildlife and game. The northern boundary of the *lomas* is located on the foothills of the Cerro Campana, a few kilometers from the modern city of Trujillo. The rivers and the valleys are the most active and dynamic components of the coastal environment and have been classified as oases by Dollfus [43]. With the exception of *lomas*, river mouths and valleys, the arid desert environment of the coast is not conducive to agriculture and permanent domestic

Figure 1. Topographic map of Peru with valleys and provenance of Mochica and modern domestic camelids.
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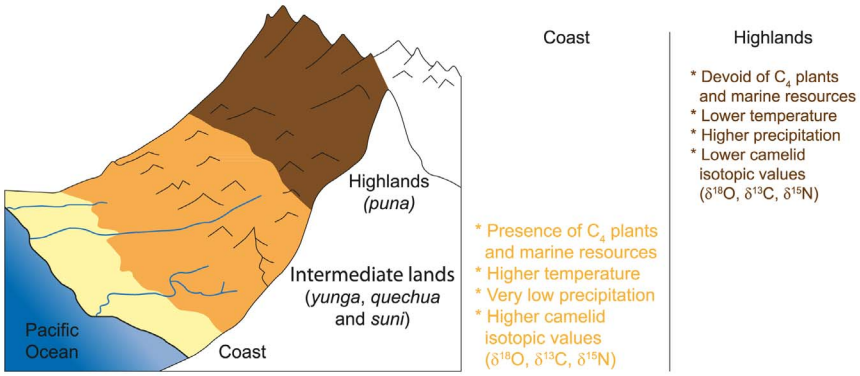

Figure 2. Central Andes ecozones and altitudinal environmental variations. Cross-section of the western slopes of the Central Andes with the main ecological zones considered in the study with expected trends in variations in environmental conditions and $\delta^{13}C$, $\delta^{15}N$ and $\delta^{18}O$ measured in domestic camelid tissues.
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animal herding. The sustainability of diversified agriculture was made possible by the development of a complex irrigation system formed of canals, which undoubtedly constituted one of the bases for the expansion of the Mochicas into each valley [44,45].

The site of Huacas de Moche is located on the left bank of the Moche Valley, 4 km from Trujillo (Fig. 1). It comprises two pyramids, the Huaca del Sol and Huaca de la Luna, which are now separated by a vast desert plain which covers an ancient city, the Urban Area, which included domestic sectors and craft workshops. The Uhle Platform, a 75 m long and 25 m wide structure, is located at the bottom of the west side of the Huaca de la Luna. Several excavations were conducted at the Uhle Platform by the Moche International Programme between 1999 and 2008 [46–51]. They led to the discovery of 57 Mochica graves, several human sacrifice areas and large ceremonial deposits. Camelids were found in 42 graves (Fig. 3) [13].

The site of El Brujo is located 60 km north of Trujillo, close to the village of Magdalena de Cao, in the lower part of the Chicama Valley (Fig. 1), along the ocean shore [52,53]. It comprises two Mochica pyramids, The Huaca Cao Viejo and the Huaca El Brujo. Like Huacas de Moche, El Brujo was one of the major religious centers on the northern coast of Peru. Excavations have been conducted at El Brujo since 1990 by the El Brujo Archaeological Project [52–54]. Tens of Mochica burials have been discovered [52–57], of which eleven contained camelid remains [13].

Material

Ethic statement. All necessary permits were obtained for the described study, which complied with all relevant regulations. Permissions were obtained from the Ministerio de Cultura of Peru to study archaeological remains.

Archaeological material. Species-specific determination of camelids based on the study of skeletal remains is theoretically possible but proved to be difficult. The phalange is usually the preferred anatomical element [58], but is of limited use here as the

Figure 3. Tomb 48 at Uhle Plateform (Huacas de Moche) with artefacts and domestic camelid offerings.
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presence of this bone in the archaeological site is restricted to adults and it cannot be used to separate hybrid specimens. We therefore used tooth shape [59] and the size of skeletal remains to discriminate between large (*Lama* sp.) camelids and small camelids (*Vicugna* sp.). Only *Lama* sp. were identified in our two archaeological sites and were probably llamas. However, this does not preclude the presence of alpacas on the coast during pre-Hispanic times. Eight archeological camelid specimens curated at the site Museum of the Huacas de Moche (Moche, La Libertad, Peru) were selected from five graves and from one ceremonial context of the Uhle Platform (Table 1) [46–49,51]. These contexts were dated from the Moche I to Moche IV phases. One piece of bone was selected from the mandible, the skull or a phalanx for six out of the eight individuals for bone collagen extraction (Table 2). All the permanent molars present in each hemi-mandible were extracted. Depending on the stage of tooth eruption, one (UH-4, UH-7), two (UH-3, UH-5, UH-9) or the three molars (UH-8, UH-10, UH-11) were present (Table3). $\delta^{18}O_{enamel}$ values for the M2 and M3 of three individuals were previously published in Goepfert et al. [36]. Four specimens (*Lama* sp.), curated at the site Museum of El Brujo (Magdalena de Cao, La Libertad, Peru), were selected from four graves at El Brujo (Table 1). Three graves were located in the Huaca Cao Viejo, the fourth was situated near the ceremonial place (Ceremonial Wells 2). These contexts were dated from the Moche III and IV phases. A piece of bone from the mandible or the pelvis was collected for each specimen for bone collagen extraction (Table 2). One (EBT2-1995, EBT6-1994) or three (EBT2-1998, EBE1-1995) permanent molars were present on each jaw (Table 3).

Modern material. Teeth and bone from modern butchered animals (Table 1; Fig. 1) were kindly obtained with the permission of herders, Cayetano Mamani (Tocra, Arequipa, Peru) and Santos Mantilla (Quiruvilca, La libertad, Peru). Two alpacas and one llama from the southern region (National reserve of Salinas y Aguada Blanca, Tocra, Arequipa region at 4,200 masl) and one modern alpaca from the northern region (Quiruvilca, La Libertad region at 4,100 masl) were selected. While Quiruvilca is located in the upper Moche Valley, an area which could have provided camelids for the Mochicas, Tocra is situated outside the potential area of interaction between the Mochicas and highland camelid breeders. However, the two *puna* regions present similar environmental characteristics and vegetation formed of *bofedales*. In both locations, modern livestock are raised for meat production and wool and spend their whole life feeding on natural pastures. They thus appear well suited to exploring variations in isotopic values of camelids originating from the *puna* ecological zone. $\delta^{18}O_{enamel}$ values for the M2 and M3 of Areq-1 have been described in Goepfert et al. [36]. Mandibles were defleshed and cleaned by boiling. A piece of mandibular bone was collected from the four individuals for bone collagen and bone apatite analyses (Table 2). Depending on the specimen, the three permanent molars (Areq-1, Quiru-1), or the Pd4 premolar (Areq-3) were extracted from the hemi-mandible (Table 3).

Individual age estimate and life history record. The age of studied specimens is rarely – if ever – mentioned in the literature, even though it appears essential for the interpretation of each specimen's life history from the isotopic analysis of its tissues. Age-at-death of modern and archaeological animals was estimated by the observation of tooth wear and eruption stages established by Wheeler [59]. Age varied between 1 year and 9 months and 13 years and between 3 months and 6 years 9 months, respectively for archaeological and modern camelids (Table 1).

Bone and enamel form at different stages of an individual's life and present different metabolic activities. Bone is constantly remodeled. Cogenetic bone collagen and structural carbonates remodel together and both provide a long-term isotopic signal. In humans, bone turnover varies between 10 to 30 years, depending on the age of the individual [60,61]. Our sample comprises both young and old specimens. Therefore, the bulk analysis of bone collagen and bone apatite represents on average a few years (for young individuals) and the entire lifespan (for old individuals). Tooth enamel is metabolically inert. It is not remodeled once formed and integrates an individual's life history over a fixed period of time. Camelids have hypsodont teeth characterized by a

Table 1. Origin, context and individual age of modern and archaeological and modern domestic camelids.

Specimen	Region	Origin/Site	Context		Species	Age
Areq-1	Arequipa	Tocra	Modern		*Vicugna pacos*	9–11 years
Areq-2	Arequipa	Tocra	Modern		*Vicugna pacos*	0–3 months
Areq-3	Arequipa	Tocra	Modern		*Lama glama*	3–6 months
Quiru-1	La Libertad	Quirivulca	Modern		*Vicugna pacos*	6 year 3 months-6 years 9 months
UH-3	La Libertad	Uhle Platform	Tomb 14	Moche IV	*Lama sp.*	2 years 3 months
UH-4	La Libertad	Uhle Platform	Tomb 22	Moche IV	*Lama sp.*	1 year 9 months-2 years
UH-5	La Libertad	Uhle Platform	Tomb 48	Moche III	*Lama sp.*	3 years 3 months
UH-7	La Libertad	Uhle Platform	Tomb 55	Moche I	*Lama sp.*	1 years 3 months-2 years
UH-8	La Libertad	Uhle Platform	Element 21	Moche I	*Lama sp.*	6 years
UH-9	La Libertad	Uhle Platform	Element 21	Moche I	*Lama sp.*	3 years-3 years 6 months
UH-10	La Libertad	Uhle Platform	Element 21	Moche I	*Lama sp.*	4 years 6 months- 4 years 9 months
UH-11	La Libertad	Uhle Platform	Tumb 16	Moche III	*Lama sp.*	11–13 years
EBT2-1995	La Libertad	El Brujo	Tomb 2/Well 2	n/d	*Lama sp.*	1 year 3 months-2 years
EBT6-1994	La Libertad	El Brujo	Tomb 6/Huaca Cao Viejo	Moche III–IV	*Lama sp.*	<3 years
EBT2-1998	La Libertad	El Brujo	Tomb 2/Huaca Cao Viejo	n/d	*Lama sp.*	7 years-7 years 6 months
EBE1-1995	La Libertad	El Brujo	Tomb 1/Huaca Cao Viejo	n/d	*Lama sp.*	9 years 6 months

n/d : not determinate.

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Table 2. $\delta^{13}C$ (‰ VPDB) and $\delta^{15}N$ (‰ AIR) values of bone collagen and $\delta^{13}C$ and $\delta^{18}O$ values (‰ VPDB) of bone structural carbonate of modern and archaeological domestic camelids.

Specimen	Bone collagen							Carbonate			
	$\delta^{13}C$ (‰VPDB)	$\delta^{15}N$ (‰ AIR)	%C	%N	C:N	wt %	%C4	$\delta^{13}C$ (‰VPDB)	$\delta^{18}O$ (‰VPDB)	% C_4	$\Delta\ \delta^{13}C$ (‰VPDB)
Areq-1	−20.8	3.1	43.3	15.7	3.2	21.7	–	−12.3	−7.7	–	8.5
Areq-2	−20.2	5.1	43.7	16.3	3.1	17.3	–	−14.2	−10.0	–	6.0
Areq-3	−20.3	4.6	44.1	16.4	3.1	19.8	–	−14.7	−8.3	–	5.6
Quiru-1	−20.6	3.8	41.6	14.9	3.3	21.4	–	−13.6	−4.2	–	7.0
UH-3	–	–	–	–	–	–	–	–	–	–	–
UH-4	–	–	–	–	–	–	–	–	–	–	–
UH-5	–	–	–	–	–	–	–	−7.7	−0.5	45	–
UH-7	–	–	–	–	–	–	–	−9.3	1.3	34	–
UH-8	–	–	–	–	–	–	–	−7.8	0.7	44	–
UH-9	–	–	–	–	–	–	–	−7.8	0.7	44	–
UH-10	–	–	–	–	–	–	–	−8.9	−0.7	36	–
UH-11	–	–	–	–	–	–	–	−7.9	−3.4	44	–
EBT2-1995		–	–	–	–	–	–	−5.8	−2.1	59	–
EBT6-1994	−14.8	8.5	43.2	16.1	3.1	6.5	43	−7.2	1.5	49	−7.2
EBT2-1998	−13.6	10.0	44.0	16.3	3.1	17.0	51	−5.7	−1.9	59	−7.9
EBE1-1995	−13.2	7.4	41.2	15.4	3.1	1.9	54	−5.6	−1.9	60	−7.6

$\delta^{13}C$ values of modern specimens were corrected by +1.5 ‰ for the Suess effect [108]. Proportion of C_4 (%) in the diet was reconstructed using mean estimated $\delta^{13}C$ values of pure-C_3 and pure-C_4 feeders.

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high crown with extended incremental growth [62]. The mineralization process is complex and composed of two different stages: growth and maturation. The duration of mineralization has been determined for domestic sheep (*Ovis aries*) and cattle (*Bos Taurus*) [63–65]. The schedule of crown growth completion, which is fixed for a given species, was estimated from the time of tooth eruption for domestic camelids. Camelid tooth eruption age is 6 to 9 months for the M1, 17 to 24 months for the M2 and 33 to 44 months for the M3 [59]. The beginning of crown formation is more difficult to assess. In comparison, in domestic sheep, the M1 crown starts to form in utero, the M2 during the second month after birth and the M3 when the lamb is 11 months old [65,66]. If camelid molar growth follows the same pattern, the analysis of molars M1 to M3 should theoretically allow us to reconstruct a continuous record of the first 3–3.5 years of life of these animals. However, the upper part of each tooth is often worn and therefore the first part of the record of each tooth is missing. In addition, the consumption of milk can influence the isotopic values of tissue in formation [67]. As the first permanent molar grows during the early childhood, breastfeeding can potentially confound its isotopic signal.

Sampling and Analysis of Camelid Tissues

Enamel and bone surfaces were mechanically cleaned to remove soft tissue, adherent soil or other contaminants by abrasion with a tungsten drill bit. Mechanical cleaning also detached the adherent cement on teeth and the outmost layer of bone, which is most susceptible to diagenetic contaminants. Cleaned bone samples were hand ground using an agate mortar and pestle and passed through a series of sieves. The finer fraction ($<$300 μm) was selected for determining $\delta^{18}O_{bone}$ and $\delta^{13}C_{bone}$ values.

Crown height was measured for each tooth and the highest lobe was selected for sampling. Sequential sampling perpendicularly to the crown growth axis, from the apex to the enamel-dentine junction, was performed using a diamond drill bit. For El Brujo and modern camelid molars, each sample was a 1-mm-wide groove, taken from the buccal side through the whole thickness of the enamel layer (Fig. 4). Uhle Platform camelid molars were fragile and prone to breakage during this direct sampling. The enamel layer on the buccal face was thus first separated from the rest of the crown. Any adhering dentine was removed using a tungsten carbide drill bit and then the sequential sampling of the enamel was conducted as described previously to obtain an intra-tooth enamel sample series. Between 5 and 35 samples (5–11 mg) were obtained per tooth, depending on crown height.

Bone organic matter was eliminated using a NaOCl (2–3%) treatment. Then, both enamel and bone powder samples were purified with 0.1 M acetic acid (4 h, 0.1 ml mg^{-1}) and 1M acetic acid (1 h, 0.1 ml mg^{-1}), respectively, due to the higher susceptibility of bone to diagenetic contamination. The acetic acid treatment was used to remove exogenous carbonate and was carried out on both archaeological and modern specimens to ensure consistency when comparing results. All samples were then rinsed at least five times and oven-dried at 50°C. Bioapatite samples weighing 600 μg were reacted with 100% phosphoric acid at 70°C for 4 min in a Kiel IV device, interfaced with a Delta V Advantage isotope ratio mass spectrometer. Analytical precision was ±0.03 ‰ for $\delta^{13}C$ (1σ) and ±0.05 ‰ for $\delta^{18}O$ (1σ), based on the repeated analysis of an internal calcite standard (Marble LM), previously calibrated against NBS-19.

Collagen was extracted from the coarser grain size fraction (0.3–0.7 mm), following Longin's [68] protocol, modified by Bocherens et al. [69]. About 200 mg of powdered bone was demineralized in a 1 M HCl solution for 20 min at room temperature then filtered through a MF-Millipore 5 μm filter. Potential contamination of

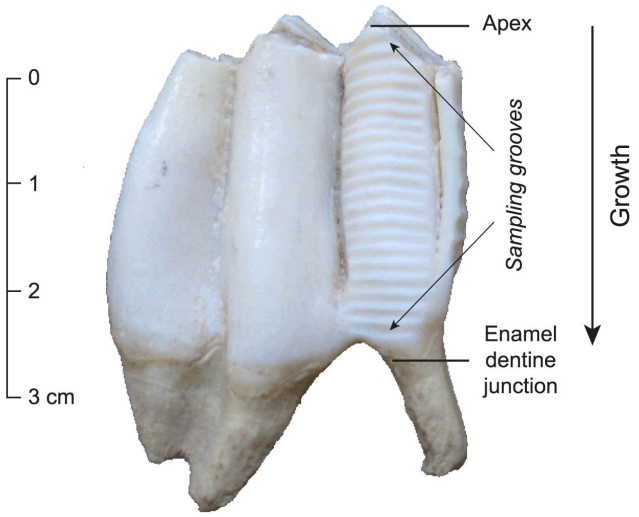

Figure 4. Sampling of molar enamel. Permanent M3 molar from specimen EBT2–1998 from El Brujo showing the series of enamel samples (grooves) that have been drilled along the highest lobe of the crown, from the apex to the enamel-root junction.
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fulvic and humic acids was removed by a 0.125 M NaOH (20 hours) treatment. After filtration, collagen was solubilized into a 0.02 M HCl (pH = 2) solution at 100°C for 17 hours, filtered again and freeze-dried.

Bone collagen samples (500 µg) were combusted using an Elemental Analyser Flash 2000, coupled with a Delta V Advantage (Thermo Scientific) isotope ratio mass spectrometer for $\delta^{13}C$ and $\delta^{15}N$ analysis. Analytical error was estimated to be 0.34 ‰ for $\delta^{13}C$ and 0.02 ‰ for $\delta^{15}N$, based on replicate analysis of the international standard IAEA 600.

The atomic C:N ratio, the carbon and nitrogen content, as well as the yield of collagen, are indicators that can be used to assess potential diagenetic alterations or contaminations of bone collagen. The atomic C:N ratio of unaltered bone collagen ranges from 2.9 to 3.6 [70]. Fresh bone contains approximately 20–22 wt % collagen, which consists of 34 to 43% of carbon and 11 to 16% of nitrogen [71]. The $\delta^{13}C_{col}$ and $\delta^{15}N_{col}$ values remain constant until bone collagen yields fall to less than 1% of the total bone mass [72]. The percentage of carbon and nitrogen in unaltered bone collagen should exceed 13% and 4.8%, respectively [73]. Structural carbonate of bone apatite is sensitive to diagenetic alteration [74]. Unlike for bone collagen, there is no well-established indicator to assess the preservation of structural carbonate in bone and enamel apatite [75]. In order to check the preservation of $\delta^{13}C$ and $\delta^{18}O$ for bone values, they can be compared with the bone collagen yields to assess the influence of collagen loss on structural carbonate. $\delta^{13}C$ values of bone structural carbonates can also be compared to those of bone collagen. In herbivores, the spacing ($\Delta\delta^{13}C_{bone\text{-}col}$) between the two tissues is 7.6±0.5 ‰ [76]. Enamel is considered to be highly resistant to diagenetic alterations and is generally thought to preserve its original $\delta^{18}O_{enamel}$ and $\delta^{13}C_{enamel}$ values [77,78].

Diet and Mobility through the Analysis of $\delta^{13}C$ and $\delta^{15}N$ Values

Measurements of $\delta^{13}C$ and $\delta^{15}N$ values are used for investigating past diet because 1) there is a direct relationship between the values of an animal's tissues and that of its food [79–82] and 2) certain food categories present distinctive isotopic values. The $\delta^{13}C$ values of bone collagen ($\delta^{13}C_{col}$) are generally 5‰ higher compared to those of consumed plants [81,83]. However, this fractionation value can vary as carbon collagen is mainly derived from dietary proteins (75% [83]). In contrast, $\delta^{13}C_{bone}$ or $\delta^{13}C_{enamel}$ values represent an average carbon input into the whole diet [82,84–85]. Therefore, the combined analysis of collagen and structural carbonate provides complementary dietary data [86]. Different fractionation values between structural carbonate and diet have been determined in the literature [84–87]. We used a value of ~+14 ‰, estimated for ruminant methanogenic herbivores [63,65,87–88]. The same fractionation value is often used for structural carbonate from both bone and enamel [86]. However, analysis of paired enamel and bone samples for pigs raised on controlled diets showed that enamel apatite was consistently enriched in ^{13}C (2–3 ‰) over bone apatite [86]. Because the two tissues formed concomitantly, without seasonal or ontogenetic variations in diet, the difference in tissue-diet spacing appears inherent to the two tissues. This difference was taken into account for camelid palaeodietary reconstructions.

Differences in the fixation of carbon during photosynthesis result in very different $\delta^{13}C$ values between plants using the C_3 (Calvin) and C_4 (Hatch-Slack) photosynthetic pathways [89] at the base of terrestrial food webs. CAM plants that use a third photosynthetic pathway (Crassulacean Acid Metabolism) have intermediate $\delta^{13}C$ values [90]. Marine plants mostly use the C_3 pathways but rely on dissolved inorganic instead of atmospheric CO_2 and also have intermediate $\delta^{13}C$ values. Many factors can affect the $\delta^{13}C$ value of terrestrial plants, such as the canopy effect, water availability and soil salinity (reviewed by Szpak et al. [23] for northern Peru). In the Andes, both C_3 and C_4 plants are present but C_3 plants are predominant. A few studies have documented the isotope composition of a variety of terrestrial and marine plants in the Central Andes [23,91,92]. Szpak et al.'s [21] comprehensive data provide the most relevant isotopic baseline for the present study, as it was conducted along an altitudinal transect of the Moche Valley. Mean $\delta^{13}C$ values are –27.6±1.9 ‰ and –13.5±1.0‰ for wild C_3 and C_4 plants, respectively. Maize is one of the key products in the diet of farming people and is the only major C_4 cultivar in the Central Andes. Consumable maize parts exhibited a mean $\delta^{13}C$ value of –11.8‰ ±0.4 ‰, while leaf mean value was –12.9±0.4 ‰ [23].

Among terrestrial plants only plants that fix atmospheric nitrogen, such as legumes, present clearly distinctive $\delta^{15}N$ values [93]. Variations in terrestrial plants can be linked to the application of fertilizers for agriculture [23,94], as well as consequences of local environmental factors, such as aridity and salinity [95,96]. *Lomas* vegetation in highly arid and saline soil conditions presents a wide range of $\delta^{15}N$ values and a tendency towards relatively high values [34,97]. It is usually generally assumed that marine plants have significantly higher $\delta^{15}N$ values than terrestrial plants but no difference was found between macroalgae and coastal terrestrial plants for northern Peru [23]. $\delta^{15}N$ analysis has proven fruitful for investigating the food chain level and degree of carnivory in past human diets because of the step-wise enrichment between the consumer's tissues and its diet [80,93,98] and the importance of marine protein because marine food chains are usually longer than terrestrial ones, resulting in higher values for secondary consumers [99,100]. $\delta^{15}N_{col}$ values can be affected by many factors, such as pregnancy [101], breastfeeding [102], growth [103], disease [104] or starvation [105].

The existence of geographic variations in isotopic values potentially enables us to distinguish whether camelids found in

coastal sites were raised locally or in the highlands. Natural variations in $\delta^{13}C$ and $\delta^{15}N$ among camelids bred at different altitudes are expected, with higher $\delta^{13}C$ and $\delta^{15}N$ values for lowland than highland camelids (Fig. 2). A positive relationship between the $\delta^{13}C_{col}$ values and elevation was observed for Argentinian llamas fed on natural pastures at different altitudes (3500–4000 masl) [106] but the reason for this relation – difference in vegetation assemblages or difference in $\delta^{13}C$ linked to altitude – is not clear. In contrast with this negative relationship between vegetation $\delta^{13}C$ values and elevation, a positive correlation was found in northern Peru [23] and northern Chile [91]. However, the frequency of C_4 plants increases with the decrease of altitude and the *puna* is nearly devoid of C_4 plants. Besides, the upper limit for maize cultivation ends at about 3,500 masl and *puna* crops are limited to C_3 plant species. The altitudinal distribution of C_4 plants is linked to temperature, sunlight and precipitation. Thus, the highlands can be characterized as an exclusively C_3 plant habitat type and camelids are expected to present a pure C_3 plant diet. Camelids grazing at low elevations have increased access to wild C_4 plants or could have been fed C_4 crops. C_4 plant and mixed C_3/C_4 plant diets thus indicate that camelids were raised in the lowlands or intermediate lands. Nevertheless, because the many C_3 plants that grow on the coast could have potentially provided fodder – various non-maize crops, pods or leaves –, a camelid with a pure C_3 diet did not necessarily originate from the highlands. Finally, potential access to marine resources in the lowlands could also influence camelid $\delta^{13}C$ values.

Mean $\delta^{13}C_{col}$ values of –19.2±0.2 ‰ were measured for domestic camelids in southern Peru [34,93,107], while mean $\delta^{13}C_{bone}$ values of –12.0±0.4 ‰ were measured at La Raya (Peru) [93]. These values – as all following modern animal and plant $\delta^{13}C$ values –were corrected by 1.5 ‰ to adjust for the Suess effect [108]. There are no available data for modern camelids feeding on natural forage at coastal or very low elevations (<1000 masl), due to the scarcity of wild or domestic camelids in these habitats today. The $\delta^{13}C$ values of pure C_3 and pure C_4-feeders can be predicted from the $\delta^{13}C$ values of pre-industrial C_3 and C_4 plants and used to determine the proportions of C_3 and C_4 in the diet of archaeological specimens. The mean $\delta^{13}C$ for pre-industrial C_3 and C_4 plants is estimated to be ~–26 ‰ by correcting the average value of modern plants for fossil fuel effect (~1.5 ‰). Szpak et al. [23] suggested an average maize $\delta^{13}C$ value of –10.3 ‰ to be appropriate for human palaeodietary models in the Central Andes. However, kernels are consumed by humans whereas the leaf was more likely to be consumed by camelids. A mean leaf value of –11.4 ‰, which is similar to the average values of wild C_4 plants, thus appears more appropriate for camelid dietary studies. Using the +14 ‰ bioapatite-diet spacing and a collagen-diet spacing of 5 ‰, a C_3 plant-based diet therefore results in an average $\delta^{13}C_{enamel}$ of ~–12 ‰, $\delta^{13}C_{bone}$ of ~–14 ‰ and a $\delta^{13}C_{col}$ of ~–21‰. The mean $\delta^{13}C$ of pre-industrial C_4 plants is estimated to be ~–11.5 ‰ and a pure C_4-diet should result in an average $\delta^{13}C_{enamel}$ of~ +2.5 ‰, $\delta^{13}C_{bonel}$ of 0 ‰ and a $\delta^{13}C_{col}$ of –6.5 ‰. The estimated $\delta^{13}C$ values of pure C_3 and pure C_4-feeders were used as end-members in a simple mixing model for calculating the proportion of C_4 in the diet of archaeological camelids (Tables 1–2). However, absolute values for reconstructed C_4 proportion values of should be considered with caution because the range of variation in $\delta^{13}C$ values in natural C_3 plants is wide (~18 ‰).

Higher $\delta^{15}N$ values are expected for domestic camelids feeding extensively on coastal or low-altitude forage, due to the consumption of terrestrial plants with relatively high $\delta^{15}N$ values and the potential intake of marine resources [100,109] (Fig. 2). Szpak et al. [23] showed that the foliar $\delta^{15}N$ values were negatively correlated with altitude and mean annual precipitation along an altitudinal transect of the Moche Valley. The magnitude of difference between animals feeding on wild plants at lower (and drier) altitudes and animals feeding at higher (and wetter) altitudes has been estimated to be 4–6 ‰ [23]. However, the consumption of cultivated plants dependent on irrigation at lower altitudes could partly confound this difference [23]. As mentioned previously, there are no modern data for camelids feeding on natural forage at coastal or very low elevations. Camelids from the coastal site of La Paloma [109] are thought to be wild guanacos and therefore are likely to have consumed natural forage [34]. They present slightly to considerably elevated $\delta^{15}N_{col}$ values compared to modern *puna* camelids, suggesting that plants characterized by high $\delta^{15}N_{col}$ values can be naturally selected by wild camelids.

Origin and Mobility through the Analysis of Structural Carbonate $\delta^{18}O$ Values

The $\delta^{18}O$ values of structural carbonate in bone and tooth enamel reflect the $\delta^{18}O$ value of body water at body temperature. Body water oxygen comes mostly from drinking water and from food, and to a lesser extent from the atmosphere via inhalation, with a predictable fractionation [110–112]. Different equations that relate the $\delta^{18}O$ values of ingested water ($\delta^{18}O_{d\ w}$) to the $\delta^{18}O$ values of structural carbonate and phosphate phases of enamel have been developed in the literature. In this study, we used two equations (Eq. 1) [113] and (Eq. 2) [114] developed for all mammals:

$$\delta^{18}O_{dwVSMOW} = 1.113 \times \delta^{18}O_{phosphateVSMOW} - 26.411 \quad (1)$$

$$\delta^{18}O_{phosphateVSMOW} = (\delta^{18}O_{structuralcarbonateVSMOW} - 8.33)/1.035 \quad (2)$$

Basic Andean environmental trends do not seem to have changed over the past 2,000 years (see [11]). $\delta^{18}O_{bone}$ and $\delta^{18}O_{enamel}$ values measured in pre-Hispanic remains can be compared to those of modern $\delta^{18}O$ values for environmental water ($\delta^{18}O_{e\ w}$) for assessing an animal's movement to different geographical areas and estimating the place of residence [115,116]. Because variations in $\delta^{18}O$ values of meteoric water ($\delta^{18}O_{m\ w}$) are theoretically transferred and retained in the body of living organisms, studies of modern precipitation provide some of the necessary baseline data for residential mobility studies [36]. $\delta^{18}O_{m\ w}$ values are governed by the amount of rainfall, altitude, latitude, distance from the coast and temperature [117–119], through the preferential loss of ^{16}O during evaporation and the progressive loss of ^{18}O during precipitation as air masses move inland and upwards [118,120,121]. The wide amplitude of temperature, altitude, rate of precipitation and hydrological systems between the different ecological zones of the Andes leads to high natural variations in $\delta^{18}O_{m\ w}$ values, which tend to vary predictably across a landmass such as the Andean region in relation to local topography [11] (Fig. 2). The availability of measured $\delta^{18}O_{m\ w}$ is limited in the Central Andean region. Preliminary data obtained on an altitudinal transect along the Moche Valley indicate a difference as high as 14 ‰ between the coast and the highlands (4,100 masl) (*Elise Dufour, unpublished data*).

$\delta^{18}O_{m\ w}$ values for a specific geographical location can be estimated using the Online Isotopes in Precipitation Calculator (OPIC Version 2.2: http://www.waterisotopes.org/). This calculator takes into account the geographic location (latitude, longitude, distance to the sea and altitude) to model the annual and monthly variations in $\delta^{18}O_{m\ w}$ for the entire globe [119,122]. These average values do not take into account the inter-annual variations, the accuracy of which in a given geographical area is linked to the availability of actually measured $\delta^{18}O_{m\ w}$ values, which are limited in the case of the Andes. OPIC predicted mean annual $\delta^{18}O_{m\ w}$ values are –11.8 ‰ (annual range: –17.3 to –7.0 ‰ SMOW) and –12.8 ‰ (annual range: –17.4 to –8.3 ‰ SMOW) for the *puna* of Tocra and Quiruvilca, respectively, and –4.8 ‰ (annual range: –8.6 to –2.7 ‰ SMOW) for the coastal region of the modern city of Trujillo (−7°99′S).

However, domestic animals (and humans) do not ingest meteoric water but surface waters, or groundwater from wells. Environmental water comprises surface waters (rivers, lakes, reservoirs, irrigation channels) and groundwater. The $\delta^{18}O$ values of environmental water ($\delta^{18}O_{e\ w}$) are not solely tied to rainfall values, which complicates their use [11]. Different processes may result in magnitudes of variation in $\delta^{18}O_{e\ w}$ values within regions that may in fact exceed differences between regions [11]. Surface water values are influenced by evaporation, movements between ecozones, mixing with groundwater, El Niño Southern Oscillation events and local topographic relief [24,123]. Overall, $\delta^{18}O_{e\ w}$ values in the Central Andes have been reported to range from –6 to –3 ‰ on the coast, from –9 to –5 ‰ in the *yunga* (intermediate lands) and from –18 to –11 ‰ in the *puna* (data from IAEA/WMO [124] and [11]). In addition, consumption patterns, such as the intake of water collected in cisterns and water exposed to evaporative processes, may also influence $\delta^{18}O_{bone}$ and $\delta^{18}O_{enamel}$ values. Finally, weaning has been shown to cause a trophic enrichment of ^{18}O in human tissues formed during infancy, due to the equilibration with maternal body water during breastfeeding [125,126]. Breastfeeding usually lasts for six months in camelids and can influence teeth (such as the first permanent molar) and tissues that form during the first months of life. However, this influence might not be very significant for adult individuals because in most cases the upper part of the M1 is missing due to tooth wear.

Because of topographic variations in $\delta^{18}O_{e\ w}$ and $\delta^{18}O_{m\ w}$ values, higher aridity and evaporation of surface water, camelids raised on the coast or at low altitudes should present higher $\delta^{18}O_{bone}$ and $\delta^{18}O_{enamel}$ values than camelids raised in the highlands. Based on Eq. 1 and Eq. 2 and OPIC intra-annual variation in $\delta^{18}O_{m\ w}$ and IAEA/WMO $\delta^{18}O_{e\ w}$ values, $\delta^{18}O_{enamel}$ of animals living in the lowlands, *yunga* and *puna* can be predicted to vary from –5.8 to +0.5 ‰, –6.2 to –2.3 ‰ and –15 to –5.5 ‰, respectively. The enrichment of structural carbonate in enamel compared to that of bone structural carbonate has been estimated to be 1.7 ‰ in oxygen in pigs [86]. A correction of –1.5 ‰ was then applied to previous estimated values of $\delta^{18}O_{enamel}$ to estimate $\delta^{18}O_{bone}$ values for animals living along the coast and in the *yunga* (Figs. 5–6).

Results

All $\delta^{13}C$ values of modern specimens presented in Tables 1 and 2 have been corrected by +1.5 ‰ to account for the atmospheric enrichment in ^{12}C, caused by the burning of fossil fuel [108], and for comparison with $\delta^{13}C$ values of archaeological specimens.

Bone Collagen

Only three on the ten archaeological specimens, all from El Brujo, provided collagen (Table 1, Fig. 5). The bone collagen yields varied from 1.9 to 21.7% for both modern and archaeological specimens. C:N ratio varied from 3.1 to 3.3 for all specimens while the carbon and nitrogen concentrations in bone collagen ranged from 41.2 to 44.1% and from 14.9 to 16.4%, respectively. These criteria were used to check the quality of bone collagen preservation for the El Brujo specimens and showed that $\delta^{13}C_{col}$ and $\delta^{15}N_{col}$ values can be used for dietary reconstruction. $\delta^{13}C_{col}$ and $\delta^{15}N_{col}$ values for modern specimens varied from –20.8 to –20.2 ‰ and from 3.1 to 5.1‰, respectively (Table 1, Fig. 5). For archaeological specimens, $\delta^{13}C_{col}$ and $\delta^{15}N_{col}$ values were higher than those of modern specimens and varied from –14.8 and –13.2 ‰ and from 7.4 to 10.0 ‰, respectively.

Bone Structural Carbonate

$\delta^{13}C_{bone}$ and $\delta^{18}O_{bone}$ values of modern specimens varied from –14.7 and –12.3 ‰ and from –10.0 to –4.2‰, respectively (Table 1, Fig. 6). Both $\delta^{13}C_{bone}$ and $\delta^{18}O_{bone}$ values for archaeological specimens were higher than those of modern specimens. $\delta^{13}C_{bone}$ values varied from –9.3 to –7.4 ‰ and from –7.2 to –5.6 ‰ for Uhle Platform camelids and for El Brujo, respectively. $\delta^{18}O_{bone}$ values varied from –3.4 to 1.3 ‰ and from –2.1 to 1.5 ‰ for Uhle Platform and El Brujo, respectively (Table 2, Fig. 6). $\Delta\delta^{13}C_{bone\text{-}col}$ values varied from 7.6 to 7.9 ‰ and were typical of herbivores (Table 2). There was no relationship between variation in $\delta^{13}C_{bone}$ and $\delta^{18}O_{bone}$ values and extraction yield indicative of marked diagenetic alteration of bone.

Enamel Structural Carbonate

For modern camelids, $\delta^{13}C_{enamel}$ values ranged from –13.6 ‰ (Areq-3) to –8.9 ‰ (Areq-1), with mean tooth values ranging from –12.1±0.8 to –9.6±0.2 ‰ (Table 3, Figs. 7–8). Intra-tooth variation ranged from 0.6 (M2 of Quiru-1) to 2.3‰ (M1 of Areq-1), while intra-individual variations (for specimens with three sampled teeth) were 2.0 ‰ for Quiru-1 and 2.3 ‰ for Areq-1. Archaeological specimens usually present higher $\delta^{13}C_{enamel}$ values than modern specimens (Table 3, Figs. 7–9–10). For Uhle Platform, $\delta^{13}C_{enamel}$ values varied from –10.5 to –1.5 ‰, with mean tooth values ranging from –10.0±0.4 to –2.4±0.5 ‰. Intra-tooth variation ranged from 0.3 (M1 of UH-8) to 2.8 (M3 of UH-11). Maximum intra-individual variation is 3.3 ‰ for the three molars of UH-8. At El Brujo, $\delta^{13}C_{en}$ values varied from –9.9 to –0.1 ‰ with mean tooth values varying from –8.1±0.2 to –1.4±0.4 ‰ (EBE1-1995). Intra-tooth variation ranged from 0.6 to 5.4 ‰ (EBT2-1995) while intra-individual variation was 4.7 ‰ for EBT2-1998 and 6.9 ‰ for EBE1-1995.

Modern camelid $\delta^{18}O_{enamel}$ values ranged from –10.1 (Areq-1) to –1.3 ‰ (Quiru-1), with mean tooth values ranging from –8.8±0.2 to –2.0±0.6 ‰ (Table 3, Fig. 7–8). Intra-tooth variation ranged from 1.4 to 4.7 ‰. Archaeological specimens usually presented higher $\delta^{18}O_{enamel}$ values than the modern ones but values overlapped (Table 3, Figs. 7–9–10). Uhle Platform values varied from –3.6 ‰ (UH-3) to 1.8‰ (UH-8). Intra-tooth maximum variation ranged from 0.2 to 2.6 ‰. At El Brujo, $\delta^{18}O_{enamel}$ values ranged from –2.9 ‰ (EBT2-1995) to 3.1 ‰ (EBT6-1994). Intra-tooth variation ranged from 0.3 to 2.8 ‰.

The M3 from modern specimens presented cyclic variations in $\delta^{18}O_{enamel}$ values (Fig. 8) whereas no cyclic variation was observed for the M3 of archaeological specimens (Figs. 9–10). Only the youngest individuals (M1 of UH-4, UH-7, EBT2-1995, EBT6-1994) exhibited cyclicity in $\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$ (Figs. 9–10).

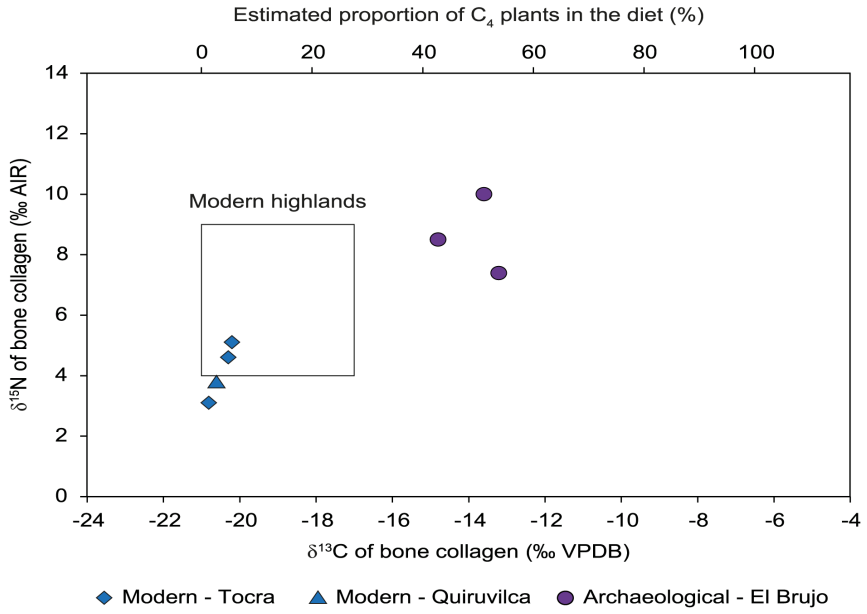

Figure 5. Isotopic composition of bone collagen. Plot of bone collagen $\delta^{13}C$ and $\delta^{15}N$ values of archaeological (El Brujo) and modern highland domestic camelids from Tocra and Quiruvilca, compared to the range of variations (represented by dashed lines) of modern specimens, compiled by Thornton et al [34]. The proportion of C_4 in the diet was reconstructed using mean estimated pre-industrial $\delta^{13}C$ values of pure-C_3 and pure-C_4 feeders.
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Discussion

In the present study, the life history of Mochica archaeological camelids was reconstructed through the analysis of the stable isotope composition of bone and enamel and comparisons with modern highland (*puna*) specimens. Archaeological camelids are discriminated from modern specimens by $\delta^{13}C$ values measured in

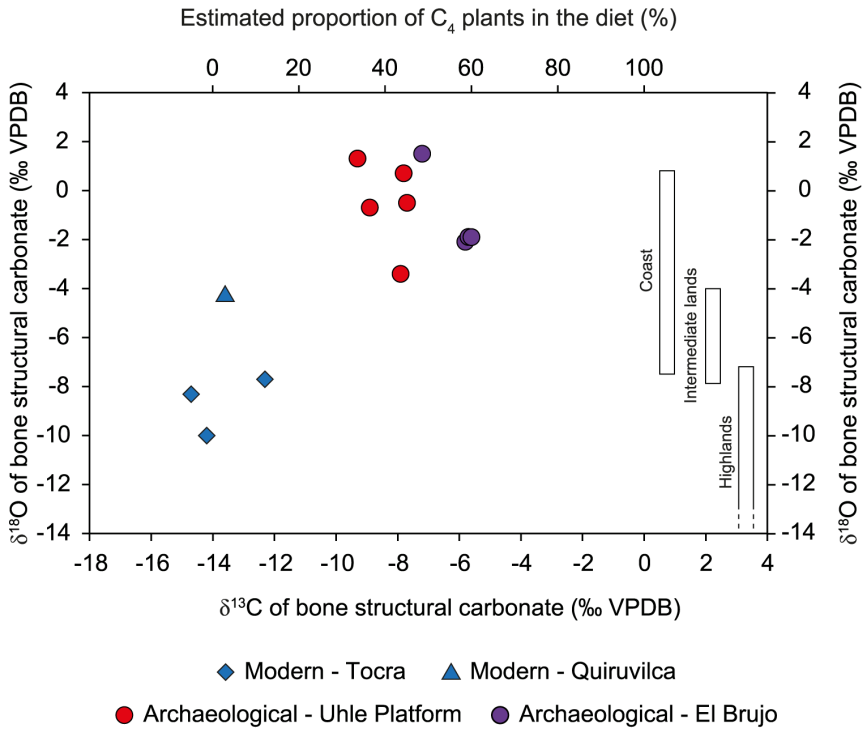

Figure 6. Isotopic composition of bone structural carbonate. Plot of $\delta^{13}C$ and $\delta^{18}O$ values (‰ VPDB) of bone structural carbonate of archaeological and modern highland domestic camelids. The proportion of C_4 in the diet was reconstructed using estimated mean pre-industrial $\delta^{13}C$ values of pure-C_3 and pure-C_4 feeders. Estimated ranges of $\delta^{18}O$ values for animals raised in the three ecozones are represented by rectangles.
doi:10.1371/journal.pone.0087559.g006

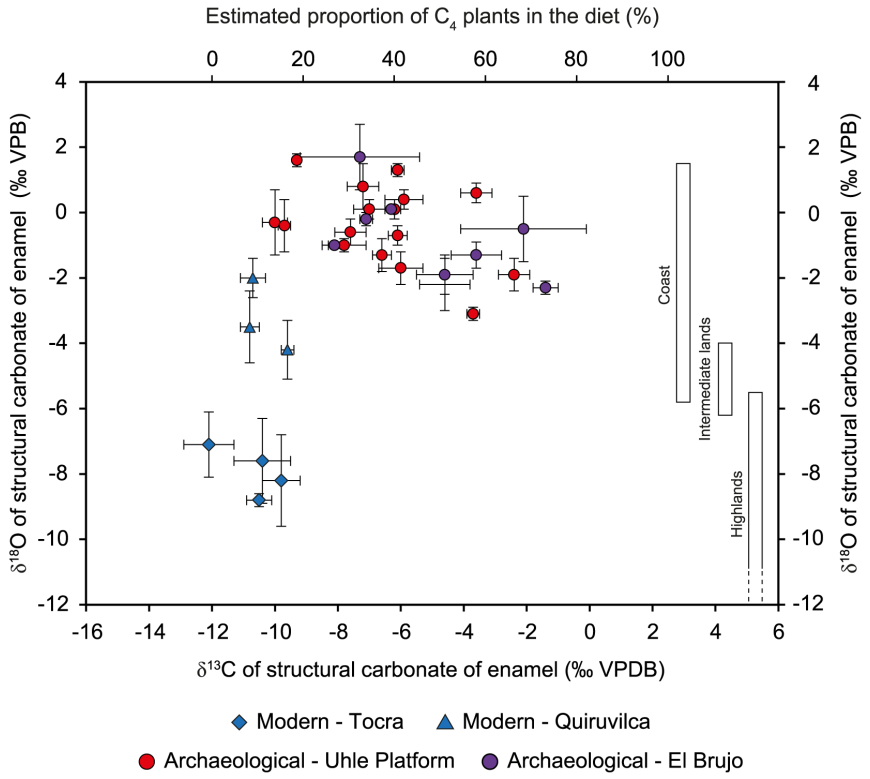

Figure 7. Mean isotopic composition of enamel structural carbonate. Plot of mean $\delta^{13}C$ and $\delta^{18}O$ values (‰ VPDB) of enamel structural carbonate for all teeth (molars) of archaeological and modern highland domestic camelids. The proportion of C_4 in the diet was reconstructed using estimated mean pre-industrial $\delta^{13}C$ values of pure-C_3 and pure-C_4 feeders. Estimated ranges of $\delta^{18}O$ values for animals raised in the three ecozones are represented by rectangles.
doi:10.1371/journal.pone.0087559.g007

both organic and inorganic bone fractions. $\delta^{13}C_{col}$ and $\delta^{13}C_{bone}$ values of modern specimens from the *puna* of Tocra (Areq-1, Areq-2, Areq-3) and Quiruvilca (Quiru-1) were consistent with predicted and previously measured values from the literature and all indicate the sole consumption of C_3 plants (Figs. 5–6). Considering that archaeological camelid diets consisted exclusively of C_3 and C_4 plants, the reconstructed proportion of C_4 plants is consistent among specimens, varying from 43 to 54% and from 34 to 60%, based on bone collagen and bone structural carbonate analysis respectively (Table 2, Figs. 5–6). $\delta^{18}O_{bone}$ values for archaeological specimens fall within the predicted range for animals raised in the lowlands and are distinct from those from modern specimens (Fig. 6). However, while the three specimens from Tocra fall within the predicted range of variation for animals raised in the *puna*, $\delta^{18}O_{bone}$ values of the Quiruvilca alpaca (Quiru-1) were higher.

$\delta^{13}C_{col}$ or $\delta^{13}C_{bone}$ and $\delta^{15}N_{col}$ values point to a mixed C_3/C_4 diet and relatively high $\delta^{18}O_{bone}$ values indicate an arid habitat, suggesting long-term herding of Mochica camelids outside the *puna* C_3 pastures. This lowland presence of Mochica domestic camelids is in contradiction with the modern distribution of camelids and the classical view that considers it impossible to maintain herds outside the *puna* grasslands. However, it does not necessarily challenge the model of verticality and exchange between the ecological zones of Andean pastoralism. Adult camelids analysed in the present paper could have spent their youth in the highlands and then been brought to the coast as part of a caravan. Their long-term, mixed C_3-C_4 diet signal, associated with an aridity signal, would thus have resulted from a diachronic switch in diet associated with the change in geographic location. Because of bone remodeling, the isotopic signal resulting from this diachronic switch cannot be distinguished from that of an entire life spent on the coast feeding on a mixed C_3-C_4 diet.

The analysis of tooth enamel reveals more diverse and complex life histories for Mochica camelids than bone analysis. Whereas all the modern specimens had a pure C_3 diet during their youth, most of the archaeological camelids consumed C_4 plants. The mean C_4 contribution to the juveniles' diet was much more variable than the long-term C_4 contribution recorded in bone, ranging from 14 to 73% (Table 3; Fig. 7). Although the use of the mixing model leads to the reconstruction of a small proportion of C_4 for the M1 from the two youngest camelids from the Uhle Platform (UH-4 and UH-7) and from an adult (UH-8), their $\delta^{13}C_{enamel}$ values were very similar to those of modern *puna* camelids (Table 3, Fig. 6). Keeping in mind the high variability in $\delta^{13}C$ values for C_3 plants, these three animals may have had a pure C_3 diet throughout their first year of life. Considering the other specimens, diet change during youth was usually moderate (10–25%), except for one adult from El Brujo (EBE1-1995), for which the C_4 contribution increased by 50% between the second and third years of life (Table 3, Fig. 11). The $\delta^{18}O_{enamel}$ values for modern animals from Tocra fitted into the estimated range for *puna* camelids, while the alpaca (Quiru-1) from Quiruvilca exhibited higher $\delta^{18}O_{enamel}$ values than predicted values (Table 2, Fig. 7). In the absence of a comprehensive survey of $\delta^{18}O$ values of surface water ingested by camelids, the reason for this discrepancy remains unknown. $\delta^{18}O_{enamel}$ values of archaeological specimens partially overlap those of modern camelids. However, they all fitted into the estimated range of variation for the lowlands or intermediate lands (Fig. 7), suggesting a youth spent in environments characterized by

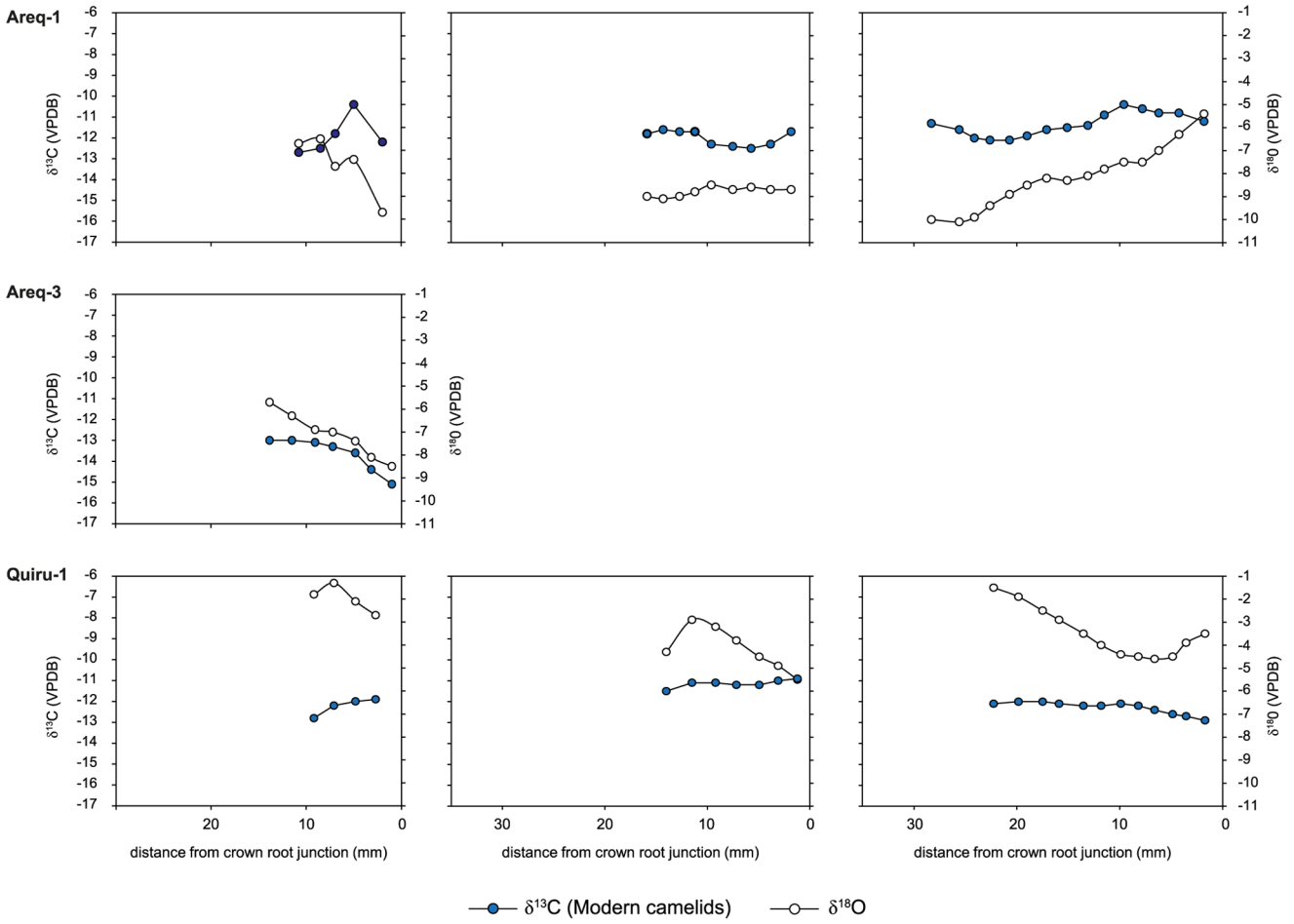

Figure 8. Intra-tooth isotopic composition of enamel structural carbonate of modern camelids. Intra-tooth variations in $\delta^{13}C$ and $\delta^{18}O$ values (‰ VPDB) measured along the molar crowns of modern highland domestic camelids and estimation of the contribution of C_3 and C_4 plants during crown growth. For each specimen, the left graph is for the M1 molar (except for Areq-3), the middle graph for the M2 molar and the right graph for the M3 molar. On each graph, the left axis refers to $\delta^{13}C_{enamel}$ values and the right to $\delta^{18}O_{enamel}$ values.
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high $\delta^{18}O_{e\ w}$ values or surface water affected by a high evaporation rate. Most individuals exhibited moderate variations in $\delta^{18}O_{enamel}$ values during youth, suggesting no major change in habitat, except for one adult from the Uhle Platform (UH-11) that might have moved to a habitat characterized by lower $\delta^{18}O_{e\ w}$ values or less arid conditions, probably at a higher altitude.

The comparison of the enamel isotopic signal with that of bone indicated that most adults were kept outside the *puna* all their life, as shown by the incorporation of C_4 plants. However, the comparison between these two tissues also identified an ontogenetic switch in diet and possible residential mobility throughout life for three animals from the Uhle Platform (UH-4, UH-7 and UH-8). This ontogenetic switch indicates a pure (or almost pure) C_3 diet during the first year of life, followed by a mixed C_3-C_4 plant diet afterwards. A pure C_3 diet alone is not indicative of the animal's geographic origin because C_3 plants dominate in all habitats. Many C_3 species that thrive on the coast could have potentially provided fodder – various non-maize crops, shrub leaves or pods – for camelids. *Prosopis* sp. remains have been reported from camelid coprolites dated of the Chimú Period [127]. Due to relatively low M1 $\delta^{18}O_{enamel}$ values for the two youngest camelids (UH-4 and UH-7; Figs. 7,9) – and the wide variation in $\delta^{18}O_{enamel}$ values for modern *puna* camelids – it is not possible to identify their whereabouts during their first year of growth. Theoretically, they could have been born in the *puna* but could have fed in the lowlands during at least several months of the year, and again before death (because of the mixed C_3/C_4 diet recorded by bone collagen). Regarding the adult specimen (UH-8), the arid signal exhibited in the M1 $\delta^{18}O_{enamel}$ values (the highest values recorded for all Uhle Platform individuals) suggests that this animal was bred in the lowlands where it switched diet during the second year of life (Table 3; Fig. 9).

Despite the importance of domestic camelids in the Mochica culture, management strategies and pastoralism remain poorly documented. In the present study, adults and juveniles of more than 1 year were analysed. Combined isotopic measurements of bone and tooth enamel clearly showed that all the adults and most juveniles spent their all life outside the *puna*, in the lowlands (and/or intermediate lands for UH-11). Furthermore, all juveniles were present locally at least several months before slaughtering. The probable pure C_3 diet during early life for two young individuals from Uhle Platform (UH-4 and UH-7) raises questions concerning their geographic origin. These individuals could have either been raised locally or in the highlands. If so, they would have subsequently reached the coast during trips for product exchanges (fish, cotton, *aji*, corn, gold, silver, etc.) between ecological zones.

Table 3. Summary of $\delta^{13}C$ and $\delta^{18}O$ values (‰ VPDB) of enamel structural carbonate of molars of archaeological and modern camelids.

Specimen	Teeth	n	$\delta^{13}C$ (‰VPDB)					% C_4	$\delta^{18}O$ (‰VPDB)				
			mean	SD	min.	Max.	range		mean	SD	min.	max.	range
Areq-1	M1	5	−10.4	0.9	−11.2	−8.9	2.3	−	−7.6	1.3	−9.7	−6.5	3.2
	M2	9	−10.5	0.4	−11,0	−10.1	0.9	−	−8.8	0.2	−9.1	−8.5	0.6
	M3	15	−9.8	0.6	−10.6	−8.9	1.7	−	−8.2	1.4	−10.1	−5.4	4.7
Areq-3	Pd4	7	−12.1	0.8	−13.6	−11.5	2.1	−	−7.1	1,0	−8.5	−5.7	2.8
Quiri−1	M1	4	−10.7	0.4	−11.3	−10.4	0.9	−	−2.0	0.6	−2.7	−1.3	1.4
	M2	7	−9.6	0.2	−10,0	−9.4	0.6	−	−4.2	0.9	−5.5	−2.9	2.6
	M3	12	−10.8	0.3	−11.4	−10.5	0.9	−	−3.5	1.1	−4.6	−1.5	3.1
UH-3	M1	14	−3.7	0.2	−4.1	−3.4	0.7	57	−3.1	0.2	−3.6	−2.9	0.7
	M2	27	−2.4	0.5	−3.4	−1.5	1.9	66	−1.9	0.5	−2.8	−1.2	1.6
UH-4	M1	14	−9.7	0.2	−10.0	−9.2	0.8	16	−0.4	0.8	−1.4	1.0	2.4
UH-5	M1	20	−7.8	0.7	−8.7	−6.6	2.1	29	−1.0	0.2	−1.4	−0.6	0.8
	M2	34	−5.9	0.6	−6.7	−4.9	1.8	42	0.4	0.3	−0.4	0.9	1.3
UH-7	M1	16	−10.0	0.4	−10.5	−9.2	1.3	14	−0.3	1.0	−2.2	1.0	3.2
UH-8	M1	5	−9.3	0.1	−9.5	−9.2	0.3	19	1.6	0.2	1.3	1.8	0.5
	M2	25	−7.0	0.5	−7.8	−6.2	1.6	34	0.1	0.3	−0.8	0.4	1.2
	M3	17	−6.1	0.3	−6.5	−5.3	1.2	41	−0.7	0.3	−1.6	−0.4	1.2
UH-9	M1	12	−7.2	0.5	−8.3	−6.7	1.6	33	0.8	0.7	−0.4	1.6	2.0
	M2	25	−6.2	0.2	−6.6	−5.9	0.7	40	0.1	0.3	−0.4	0.9	1.3
UH-10	M1	10	−7.6	0.5	−8.2	−7.0	1.2	30	−0.6	0.4	−0.9	0.4	1.3
	M2	22	−6.6	0.3	−7.3	−6.1	1.2	37	−1.3	0.5	−2.0	−0.3	1.7
	M3	19	−6.0	0.7	−7.1	−4.9	2.2	41	−1.7	0.5	−2.3	−0.9	1.4
UH-11	M1	6	−6.1	0.2	−6.4	−5.9	0.5	41	1.3	0.2	1.0	1.5	0.5
	M2	22	−3.6	0.5	−4.4	−3.1	1.3	58	0.6	0.3	0.1	1.2	1.1
	M3	35	−4.6	0.8	−5.9	−3.1	2.8	51	−2.2	0.8	−3.4	−0.8	2.6
EBT2-1995	M1	15	−2.1	2.0	−5.5	−0.1	5.4	68	−0.5	0.9	−2.2	0.6	2.8
EBT6-1994	M1	16	−7.3	1.9	−9.9	−5.0	4.9	32	1.7	1.0	0.6	3.1	2.5
EBT2-1998	M1	7	−6.3	0.2	−6.6	−6.0	0.6	39	0.1	0.1	0.0	0.3	0.3
	M2	15	−4.6	0.9	−6.7	−3.4	3.3	51	−1.9	0.6	−2.9	−1.2	1.7
	M3	21	−3.6	0.8	−4.6	−2.0	2.6	58	−1.3	0.4	−2.0	−0.8	1.2
EBE1-1995	M1	8	−7.1	0.2	−7.6	−6.8	0.8	34	−0.2	0.2	−0.4	0.1	0.5
	M2	13	−8.1	0.2	−8.3	−7.6	0.7	27	−1.0	0.1	−1.2	−0.9	0.3
	M3	18	−1.4	0.4	−1.9	−0.7	1.2	73	−2.3	0.2	−2.6	−2.1	0.5

$\delta^{13}C$ values of modern specimens were corrected by +1.5 ‰ for the Suess effect [108]. Proportion of C_4 (%) in the diet is reconstructed using mean estimated $\delta^{13}C$ values of pure-C_3 and pure-C_4 feeders.

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Although young individuals are not considered robust enough to carry large burdens during such trips [7,13], they might have accompanied their mothers. This latter hypothesis cannot be totally excluded, even though ethnographic data indicate that young llamas do not integrate caravans before adulthood, when they are around two years old [21]. We can thus assume that UH-4 and UH-7were born in the lowlands like the other juveniles and the adults.

At both El Brujo and Uhle Platform, animals used for funerary and ritual purposes were kept in the lower part of the valleys. Local herds were maintained both for slaughtering purposes and reproduction, as indicated by demographic data based on the study of archaeozoological remains and domestic camelid ethology [7,13]. Local breeding not only implies the presence of young age classes outside the *puna* during the Mochica period but also that of gregarious adult females. The latter do not travel during the gestation period, which lasts from eleven to twelve months [9]. Moreover, this suggests that camelid breeding was an important activity. Young camelids were sacrificed before reaching their maximum meat yield by weight and consequently herds had to be large enough to absorb the loss of young immature animals. Herds might have been large or alternatively small but numerous, at the scale of a site or a valley. While large herding has also been suggested by the increased number of camelid remains [16], there is currently no available estimate of herd size during Mochica times.

Camelid management outside the modern geographical range has been documented for middle valley areas in Andean regions

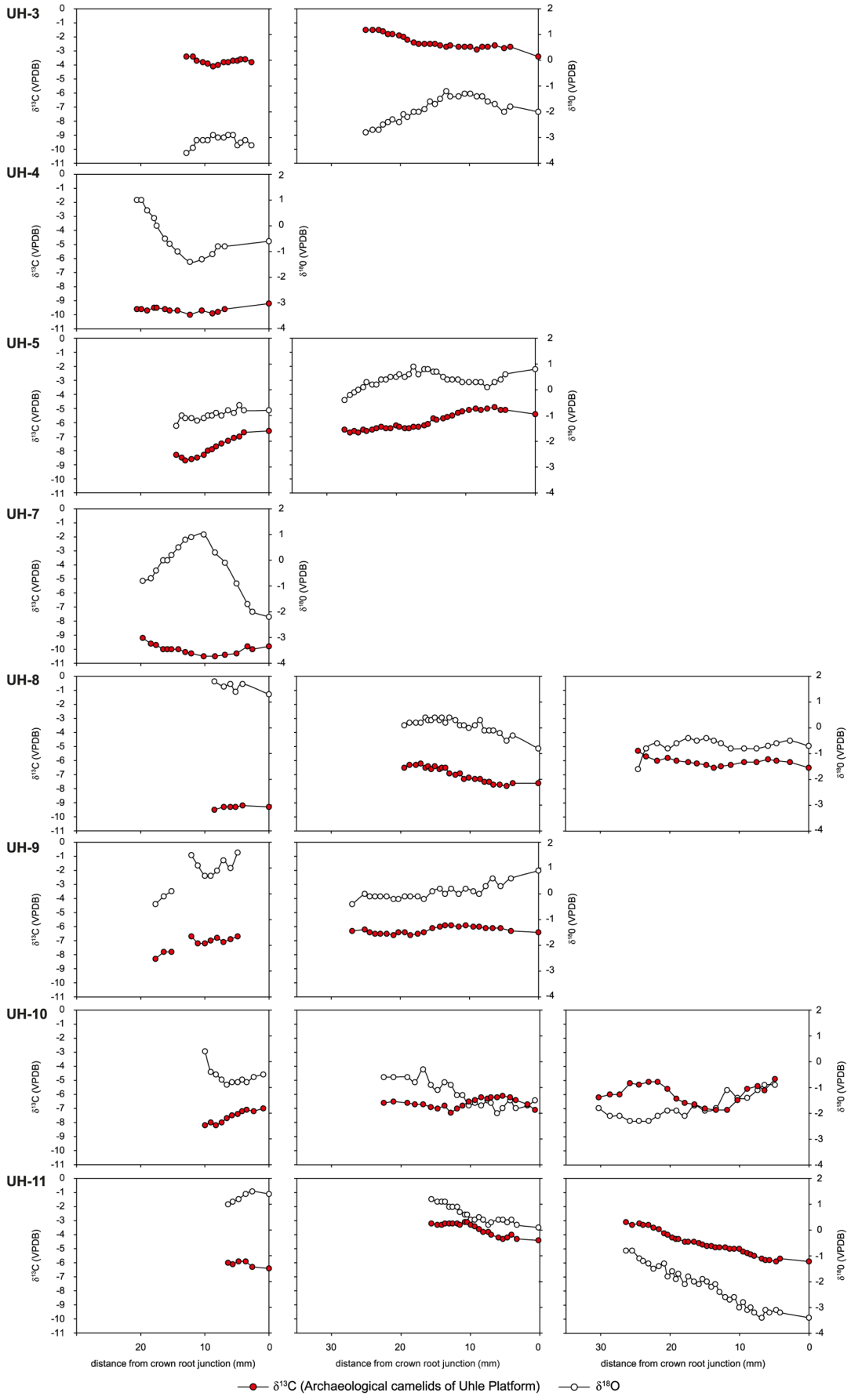
UH-3
UH-4
UH-5
UH-7
UH-8
UH-9
UH-10
UH-11
δ13C (VPDB)
δ18O (VPDB)
distance from crown root junction (mm)
δ13C (Archaeological camelids of Uhle Platform)
δ18O

Figure 9. Intra-tooth isotopic composition of enamel structural carbonate of Uhle Platform camelids. Intra-tooth variations in $\delta^{13}C$ and $\delta^{18}O$ values (‰ VPDB) measured along the molar crowns of archaeological and modern highland domestic camelids and estimation of the contribution of C_3 and C_4 plants during crown growth. For each specimen, the left graph is for the M1 molar, the middle graph for the M2 molar and the right graph for the M3 molar. On each graph, the left axis refers to $\delta^{13}C_{enamel}$ values and the right to $\delta^{18}O_{enamel}$ values.
doi:10.1371/journal.pone.0087559.g009

where richer pasturelands are available and foddering might have been practiced during pre-Hispanic times [34,35,128,129]. As for the Peruvian coast where arid conditions prevail, questions subsist concerning the availability and precise location of food resources to maintain herds. *Lomas* are present close to Cerro Campana, between the Moche and Chicama valleys, and can be considered as a potential herding location, at least during the austral winter, as suggested for other sites in Peru [34]. In intermediate lands, C_4 plants are relatively rare and high $\delta^{13}C_{col}$ (or $\delta^{13}C_{bone}$) values, such as those recorded at the Middle Horizon Wari-affiliated site of Conchopata [128], can be confidently interpreted as the result of the consumption of maize. On the coast, wild C_4 species, such as the saltgrass *grama salada* (*Distichlis spicata*), can locally form relatively large patches and pastures where herders could have taken their animals. C_3 plants nevertheless dominate the Peruvian flora and it could be difficult for herders to find wild C_4 pastures capable of contributing as much as 50–70% of the diet of some camelids. Maize but also marine algae can supplement the diet of wild or domestic herds [130,131], at least seasonally when the terrestrial pastures are restricted. Records of this practice during ancient times are hard to come by as seaweed is rarely preserved in archaeological sites. High $\delta^{13}C_{col}$ and $\delta^{15}N_{col}$ values measured at the coastal sites of central and south Peru of La Paloma and Chilca were interpreted as lowland breeding, on the arid coast itself [109]. These high values were attributed to the consumption of non-terrestrial resources, such as marine plants or aquatic vegetation growing along lagoons, riverbanks or the shores of saltwater lakes because of assumed distinctive (higher) $\delta^{15}N$ values for marine plants compared to terrestrial plants [109,132]. In fact, no distinction between the two types of plants was found along the northern coast of Peru [23] that could also explain the high $\delta^{15}N_{col}$ values of archaeological camelids. Marine algae have a mean $\delta^{13}C$ value of –15.0 ‰ [23]. Their contribution to the diet of Mochica camelids should have been as high as 75% to explain the highest measured $\delta^{13}C_{col}$ and $\delta^{13}C_{bone}$ values. Although this high proportion of marine algae seems unlikely, they may still have contributed to the camelid diet, along with C_4 plants. This hypothesis cannot be ruled out by the isotopic tracers used in the present study.

The geographical origin of camelids appears difficult to assess from $\delta^{18}O_{enamel}$ and $\delta^{18}O_{bone}$ values, but they might nevertheless provide insights into herding practices. A negative trend in the relationship between $\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$ values is observed when all archaeological teeth are considered, suggesting that there is no connection between aridity and dietary signals (Fig. 6). A positive relation was expected because the lower the elevation, the higher the aridity, the $\delta^{18}O_{e\ w}$ values and the frequency of wild C_4 in the vegetation assemblage. The disconnection between aridity and dietary signals could result from the consumption of water and maize (and other cultivated crops) grown at various altitudes from the arid coast to intermediate lands. Cultivation on the coast is rendered possible by the presence of irrigation networks supplied by rivers from the Andes, which have different $\delta^{18}O_{e\ w}$ values from those predicted at local altitudes, as well as different precipitation rates and temperatures. The control of drinking by the herders is not only suggested by the absolute $\delta^{18}O_{enamel}$ values, but also by the difference in the shape of isotopic intra-tooth profiles between archaeological and modern specimens. The two modern adult alpacas (Areq-1 and Quiru-1) were raised on natural *puna* pastures all year around, without fodder, and widescale geographic movement over throughout life. The intra-tooth cyclic variation in $\delta^{18}O_{enamel}$ recorded in their M3 is linked to seasonal variation in temperature and $\delta^{18}O_{e\ w}$ values [36]. In contrast – except for the M1 from the youngest specimens (UH-4, UH-7, EBT6-1994, EBT2-1995) – most archaeological Mochica camelids do not display cyclicity in $\delta^{18}O_{enamel}$ intra- tooth cyclic variations, independently of the proportion of C_4 plants in their diet (Fig. 9–10). The flat profiles for the $\delta^{18}O_{enamel}$ values of Mochica camelids not only suggest that no important change in geographic location occurred (except UH-11), but also that drinking water was not affected by seasonal variations, such as natural surface water and precipitation, but came from controlled sources such as wells or canals.

Combined isotopic measurements of bone and tooth enamel indicate that most Mochica camelids relied upon substantial maize foddering on coastal irrigated (and/or fertilized) fields or at different elevations in the valleys. Maize played a key role in the political economy and has constituted a primary component of the diet of diverse Andean polities and cultures from at least the late Archaic [127,133–134]. In the Moche Valley, the intensification of maize production appeared during the Gallinazo phase [135] and maize was a crucial crop during the development of the Mochica state [127,136–138]. Herders could have let the animals graze on the stalks in maize fields, forage in cultivated plots or fields, or brought stalks to the herds in corrals and pens. Further archaeological research is needed to determine if maize culture and herds were spatially segregated or in close relation with each other. No corrals or pens used for keeping the herds have been found in the proximity of Huacas de Moche and El Brujo. Thus, if the camelids lived on the coast, their settlement was not in the direct vicinity of the sites. Our study showed that the animals were bred in the low and/or middle valleys and that none of the domestic camelids originated from the *puna*. As the Mochica polities exerted their political and social power at the scale of the valleys, the provisioning of domestic camelids might also have been organized at this level. All animals were bred in the lowlands but had different life histories, with the exception of the three specimens (UH-8, UH-9 and UH-10) recovered from the same ceremonial context (Element 21) at the Uhle Platform. They shared similar trends in life histories despite differences in age and may represent a single ritual event (Fig. 9). Part of the inter-individual variability could be linked to the fact that remains were recovered from different chronological phases of occupation. It also suggests that camelids came from various herds presenting difference in herding management strategies. The presence of camelids from different geographic origins (classified as local and non-local) at the same site has previously been related to the different functions of camelids: sacrifice *versus* meat or wool production [34–35,128]. The site of Tiwanaku is situated in a zone of rich *puna* pastures and the provisioning of non-local – but still originating from the highlands – camelids [35] illustrates the complexity of ritual contexts. The present work concerns camelids from funerary and ritual contexts. The lack of analysis of remains from domestic contexts does not enable us to discuss the specialization of Mochica herds for meat procurement or animal sacrifice, as was described for Inka times.

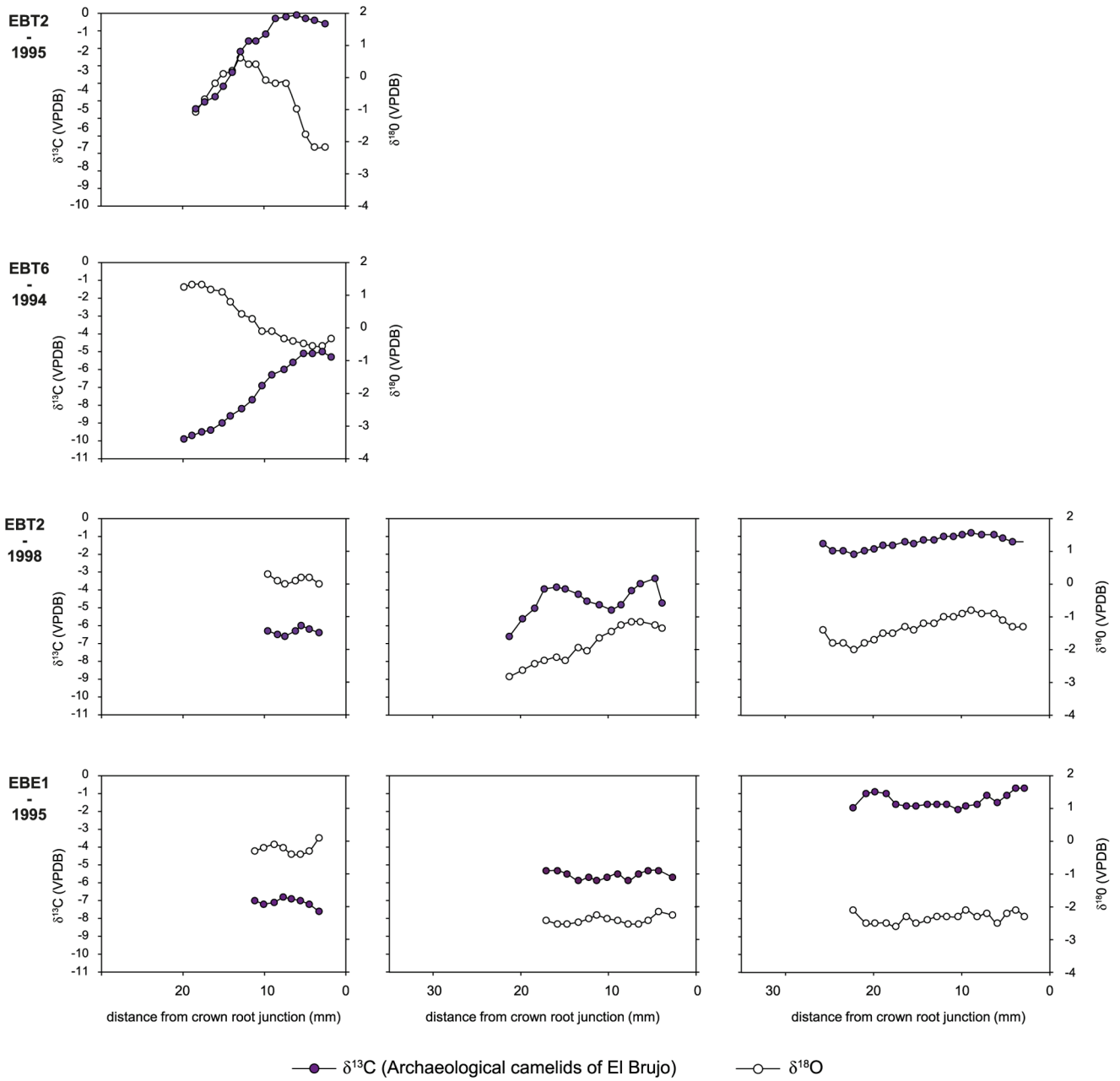

Figure 10. Intra-tooth isotopic composition of enamel structural carbonate of El Brujo camelids. Intra-tooth variations in $\delta^{13}C$ and $\delta^{18}O$ values (‰ VPDB) measured along the molar crowns of archaeological and modern highland domestic camelids and estimation of the contribution of C_3 and C_4 plants during crown growth. For each specimen, the left graph is for the M1 molar, the middle graph for the M2 molar and the right graph for the M3 molar. On each graph, the left axis refers to $\delta^{13}C_{enamel}$ values and the right to $\delta^{18}O_{enamel}$ values.
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Conclusion

The present study underlines the adaptive capacities of the Mochica people to their environment. Irrigation allowed for the development of extensive agriculture in a very arid environment. Herders also adapted their practices to this difficult environment. This study also emphasizes the role of maize in different aspects of Mochica economic life. Further work will be conducted on Mochica camelids from different valleys to confirm these first results and to compare herding practices on a regional scale. Strong relationships might have been established between two major religious centers, such as the Huacas de Moche and El Brujo, and their hinterlands. A better understanding of these relationships is required in order to describe how herd management was spatially organized. Camelids from domestic contexts should also be analysed to compare them with camelids from ritual contexts, to determine whether or not they have the same origin and to gain insights into meat exchange in the different Andean ecozones. Our study also indicates that diversity in herding practices existed in the lowlands, as already described for higher altitudes, even though only animals with similar functions (funerary and ritual) were analysed. Species-specific identification of llamas and alpacas was not possible from the osteological study

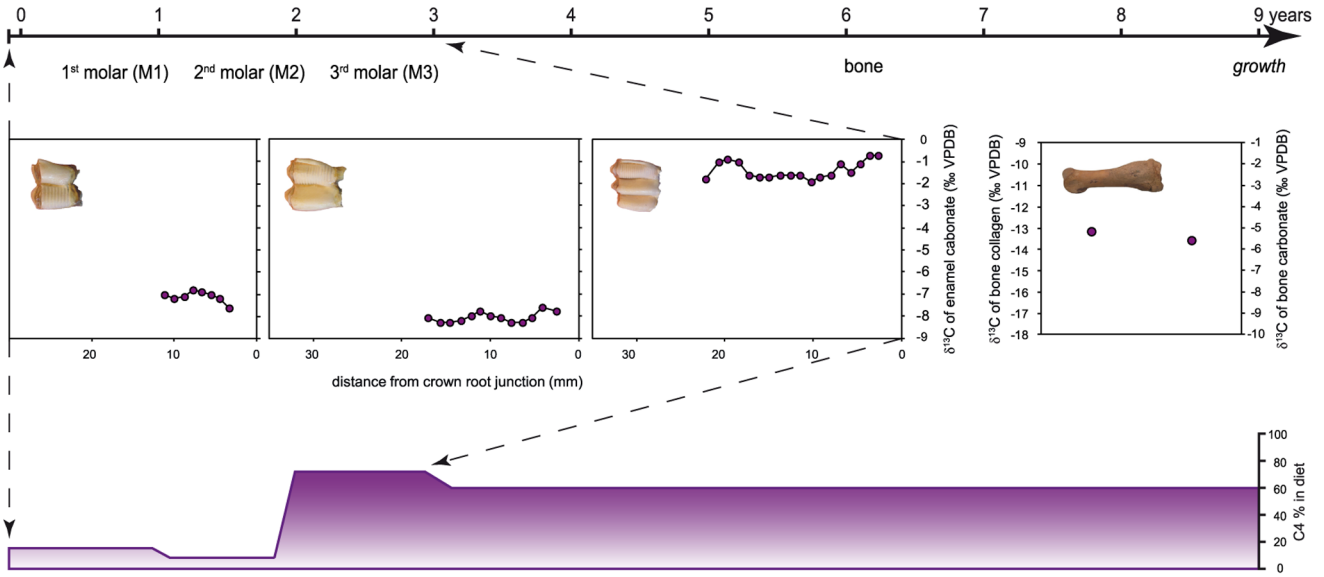

Figure 11. Reconstruction of diachronic changes in the contribution of C_4 plants to camelid diet. Dietary contribution of C_4 plants over the first years of life of specimen EBE1-1995 and in the long term is estimated by the combined analysis of enamel ($\delta^{13}C_{enamel}$) from the three molars and the bulk analysis of collagen ($\delta^{13}C_{col}$) and structural carbonate ($\delta^{13}C_{bone}$) from bone.
doi:10.1371/journal.pone.0087559.g011

of archaeological remains. This would, however, provide a better understanding of the relation between camelid functions and herding practices.

An increasing number of studies have used stable isotopic analyses to document camelid diet and herding practices in Peru, Chile and Argentina, during the pre-Hispanic period [34,128–129,139–141]. Together with the data presented in this study, these analyses have identified variations in the geographic locations of camelid breeding and pastureland and/or foddering practices outside the modern geographic range. Our work underscores regional and temporal variations in Andean pastoralism and disparity with the classical model of vertical exchange. Most previously published studies were performed on bone tissue and make no reference to the age of the sampled individuals. Because of the remodeling of bone tissue, age is essential for reconstructing the individual life history of each specimen and for identifying the place of birth. The serial analysis of tooth enamel brings new information on camelid pastoralism and complements bone collagen analysis. The combined analysis of different tissues, which form at different times, enables us to detect potential diachronic change in diet and geographical location throughout an animal's life. Besides, tooth enamel is better preserved over time than bone collagen. The poor quality of preservation of bone collagen in the Moche Valley was also observed for human remains at Cerro Oreja [135]. Moreover, enamel analysis offers the opportunity to independently assess the geographic habitat of organisms through climate records. $\delta^{18}O_{enamel}$ values provide some information but inferences are limited so far because the environmental and biological factors that might influence $\delta^{18}O_{enamel}$ values need to be better understood. The influence of the circulation of surface water that might mask the difference in $\delta^{18}O_{e\ w}$ values between ecological zones, breastfeeding and milk consumption are some of the factors that have to be documented. The duration of tooth mineralization in domestic camelids would also need to be determined. Finally, a more precise reconstruction of the geographic location of pastureland and mobility is expected from the combination of the measurement of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{18}O_{enamel}$ values with $^{87}Sr/^{86}Sr$ values.

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Author Contributions

Conceived and designed the experiments: ED NG BGL CC RFJ SVS. Performed the experiments: ED NG. Analyzed the data: ED NG. Contributed reagents/materials/analysis tools: ED NG BGL CC RFJ SVS. Wrote the paper: ED NG BGL CC RFJ SVS.

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