

## Article

# Contextual, Taphonomic, and Paleoecological Insights from Anurans on Tiwanaku Sites in Southern Peru

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**Abstract:** We examine the processes that resulted in the deposition of bones of at least three anuran genera on four archaeological sites associated with the Tiwanaku culture occupied between 700–1100 CE in the Moquegua Valley of far southern Peru. We review archaeological data and ethnographic accounts of Andean peoples using frogs and toads for food and in rain-quest rituals. Anuran bones are common in prehispanic cemeteries, but far less common in habitational and ceremonial sites. The quantity of anuran remains in certain cemeteries is anomalous in comparison to other archaeological sites in the valley and to Tiwanaku sites in other geographic settings. We conclude that anurans are most common where abandoned below-ground rock-covered tombs are likely to have been reused by nesting owls, and propose that most anuran remains in archaeological contexts in Moquegua are the result of predation. We consider environmental, cultural and taphonomic explanations and posit that the abundance of anuran remains relates to the 14th-century Miraflores ENSO event. This event generated increased rainfall in the desert, creating conditions favorable for frogs and toads, and predation by owls. We also advocate for the use of fine-screening to recover small-sized animal remains, such as anurans, that can be used to understand taphonomic processes and paleoenvironmental conditions.

**Keywords:** Burrowing Owl (*Athena cunicularia*); ENSO; herpetofauna; Middle Horizon; Miraflores event; Moquegua



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## 1. Introduction

Archaeofaunal remains can provide a critical window into ancient human diet, behavior and practices. However, archaeological sites also often contain animal remains that are not the direct result of human behavior, but that nonetheless provide important insights into the past. Animals that people did not consume and that did not pass through a cultural selection process can serve as indicators of past habitats and palaeoecological conditions. In the south-central Andes, anurans (frogs and toads) are primarily a non-food animal whose presence in archaeological deposits has cultural implications or may be used as a paleoenvironmental proxy. Here, we examine deposits of anuran remains on sites in the hyper-arid, mid-elevation setting (900–1400 masl) of the Moquegua Valley of far southern Peru. We report on archaeological evidence of frogs and toads from four sites associated with the Tiwanaku culture occupation of the region (~700–1100 CE). The original goal of the zooarchaeological analysis was focused on the identification of economic and ritual uses of animals by the Tiwanaku. However, the unexpected recovery of large numbers of frog and toad remains in certain contexts of the faunal assemblages warranted investigation.

Some archaeologists working in the Central Andes have interpreted the scant remains of frogs and toads as food remains [1]. Other possible explanations for anuran remains are as non-food refuse or ritual animals depending on the archaeological context. In the recent past and among modern populations in the Lake Titicaca region and the city of La Paz in Bolivia, people are known to consume frogs, particularly the very large-sized Titicaca water frog, *Telmatobious culeus* [2,3]. It is possible that people in the past ate these large-sized frogs as well as smaller frogs that naturally inhabit the south-Central Andes. Ethnographic accounts of human–anuran interactions primarily focus on Andean Indigenous peoples collecting frogs for a variety of therapeutic purposes and using them in ceremonies to bring on the rainy season [3–6]. Frogs also appear in Andean ceramic iconography attesting to the animals’ cultural significance [7,8].

Today, numerous species of frogs and toads are common in the highlands, particularly near and in Lake Titicaca, the homeland of the Tiwanaku civilization, as well as in the eastern Andean tropical region [9]. Conversely, frogs and toads are uncommon in the western Andean valleys and Sierra due to the extreme aridity that characterizes this region. Therefore, the discovery and identification of abundant anuran remains in excavations at Tiwanaku sites in Moquegua warranted further analysis.

Here, we examine the possible explanations for the deposition of frog and toad bones on sites that had been occupied by Tiwanaku communities in the second half of the first millennium CE. Based on the contexts and patterns of deposition, and on comparisons with other archaeological deposits in the region and south-Central Andes, we consider natural death, human deposition as food or ritual deposits, animal predation, and other natural processes as explanations. Our analysis of archaeological contexts and different processes leads us to hypothesize that the anuran remains resulted primarily from animal predation. Our hypotheses regarding the taphonomic processes responsible for the accumulation of anuran remains are preliminary and await more detailed taphonomic analysis. In addition to our initial suggestions of the agents responsible for the deposition of anuran remains, we then use the frog and toad remains to hypothesize past paleoclimatic conditions in the Moquegua region during the first half of the second millennium CE. By combining the study of herpetofauna, site abandonment processes and paleoclimate in the central Andes, this paper contributes new data on anuran deposition at open-air archaeological sites and desert environments in line with a growing knowledge of anurans and taphonomy in the ancient Americas [10].

#### *Anurans and Taphonomy*

Taphonomic studies have proposed different agents responsible for accumulations of animal remains in archaeological sites. These studies tend to rely on the analysis of scats and pellets of birds of prey and carnivore mammals to identify taphonomic patterns caused by animal predation, such as the accumulation of small mammal remains in caves [11–16]. Regarding anuran remains, Pinto Llona and Andrews [17] and Stoetzel et al. [18] have compiled markers of animal predation for several predatory species and applied them to contexts with high anuran accumulations in Spanish and Moroccan archaeological sites, respectively. Besides physical marks of predations in specimens (gnawing, perforations), other markers encompass taxa-level digestion, breakage, and element representation patterns that, together, can indicate species-specific predation. Additional studies have expanded on these foundational studies while considering multiple lines of evidence, from archaeological and cultural contexts, to site taphonomy and paleoenvironmental conditions [19–23]. Biton et al. [22] and Bisbal-Chinesta et al. [23] hypothesized that the accumulation of anuran remains in an open-air site in Israel and a Spanish cave resulted from diverse processes such as natural death, human exploitation for consumption or ritual/symbolic use, accidental human encounter, and animal predation. Blain and Villa [19], Blain [20], and Martin et al. [21] also explored the taphonomic processes responsible for anuran accumulation in archaeological deposits, but complement their interpretations with discussions on paleoclimatic and paleoenvironmental conditions. This previous research

has improved our ability to more accurately distinguish between natural and anthropogenic accumulation patterns, and it guides our use here of anuran remains to reconstruct paleoenvironmental conditions.

## 2. Anurans in the Andes

### 2.1. Cultural Entanglements

Andean peoples have had diverse cultural associations with frogs and toads, in particular through ritual practice and artistic expression. Despite modern consumption of Lake Titicaca frogs, there is no definitive archaeological evidence for the use of frogs and toads as food. Warwick [5] (p. 51) summarizes previous anthropological work on the different uses of amphibians in Aymara and Quechua communities of the Lake Titicaca basin to treat maladies and diseases. For example, LaBarre [6] describes the use of claws for toothache and the whole animal for cataplasm. He also concludes that Aymara communities did not use frogs as a food resource. Tschopik [4] (pp. 277–278) describes the Rain Making Rite (or *haju luraña*) that was practiced by Aymara communities of Peru and Bolivia. This ceremony was performed only in periods of extreme drought. He describes one ceremony sponsored by the Chucuito Village in 1939. This community paid for a “magician” and an orchestra to go to Lake Titicaca to collect frogs (presumably, the large lake frog *Telmatobius culeus*) for the rite. While playing and singing the Frog Song, the orchestra and local Chucuito inhabitants accompanied the “magician” in collecting frogs that were then placed on a shrine in the village, where they all prayed for rain [4] (p. 278). Similar ceremonies have been reported elsewhere in the region, indicating a possible long history of the cultural significance of frogs.

Frogs and toads also feature in prehispanic Central Andean iconography. In particular, the Formative period Chiripa culture (600–100 BCE) of the southern Lake Titicaca basin depicted frogs, tadpoles, and/or toads along with other natural and supernatural animals in stone sculpture and other media as part of the Yaya-Mama Religious Tradition [7]. At the Tiwanaku (500–1100 CE) site of Pariti on the Lake Titicaca island, archaeologists excavated fragments of at least 435 intentionally “killed” ceramic vessels, several of which have painted polychrome images of frogs or toads and possible anuran eggs [8] (pp. 109–111; Plates 37 and 38). In the contemporaneous highland Huari culture further north, frogs or toads are painted on ceramics [24]. Additionally, both the coastal Moche and Chimú cultures of northern Peru produced zoomorphic effigy vessels in the form of frogs or toads [25].

### 2.2. Anurans Species and Ecology in the Western Andes

Peru today has a rich anuran diversity with at least 550 identified species [26]. A large number of the country’s endemic anuran species are found in the Andean cordillera at or above 1000 meters above sea level [27]. This is expected because the Tropical Andes are considered a hotspot of biodiversity [28] resulting from the altitudinal gradient, topographic complexity and the long climatic and geologic history that have helped shaped the biota of the Central Andes. In addition, the thermal gradient and dispersal limitation likely have contributed to the high number of endemism [29,30].

The greatest diversity of anurans in Peru is concentrated in the northern Andes and on the eastern slopes of the cordillera. These areas feature many ecoregions with environmental characteristics—such as greater humidity and vegetation coverage found in cloud and montane humid forest—that offer suitable microhabitats along the altitudinal gradient to sustain a variety of anuran species [27,31].

The western or Pacific slopes of central and southern Peru are characterized by drier and open environments with environmental conditions less favorable for the establishment of anuran populations; therefore, anuran diversity is significantly reduced along the western Andes and the Pacific coast [31] (pp. 15,41, Anexo 1). There are four anuran species—*Rhinella spinulosa* (Bufonidae); *Pleurodema marmoratum* (Leptodactylidae); *Telmatobius arequipensis* and *Telmatobius peruvianus* (Telmatobiidae)—for the departments of

Arequipa, Moquegua and Tacna, all with altitudinal ranges from 1000 to 4000 m above sea level [27]. None of these species are burrowing frogs [26,27]. All of these species are listed with some degree of threat in the IUCN Red List.

### 3. Moquegua Valley

#### 3.1. The Environmental Setting

The Moquegua Valley forms part of the Osmore drainage, one of the southernmost river valleys of Peru. Between the highlands and the coastal plain, the mid-section of the valley located 40 to 70 km inland from the Pacific coast ranges in elevation from 900–1400 masl. In contrast to the steeply incised highland valleys upriver, the mid-valley is a broad, flat expanse consisting of a fertile strip of floodplain roughly 28 km north–south by 75 km east–west along the banks of the Moquegua River. Along the margins of the valley are barren bluffs, dry river gorges, and mountains. At the lower portion of the middle valley at ~900 masl, the river channel descends into a deep gorge and emerges in a more open main channel 17 km from the coast.

The coastal plain and the mid-valley of the Moquegua drainage form the northern reaches of the Atacama Desert, one of the driest places on earth. Prior to a late 1990s large-scale hydrological engineering project that altered seasonal water pattern to generate river flow throughout the year, the river and its upper-valley tributaries primarily carried seasonal runoff from the western cordillera during the austral rainy season (December to April) when precipitation falls in the highlands above ~4000 masl [32]. Because mid-valley precipitation is less than <100 mm/year [33] and seasonal water was scarce, agriculture and food production during the archaeological past were dependent on the construction of canals and channels to irrigate the arid landscape [34].

In this desert region, the pattern of predictably minimal seasonal rainfall is occasionally disturbed by El Niño Southern Oscillation (ENSO) climatic events. During ENSO events warm waters originating from the tropical Pacific Ocean travel west along the equator and then south along the Pacific coast of South America resulting in the suppression of the cold upwelling currents that naturally dominate the region. The climatic consequences of ENSO often reverse the normal highland and coastal patterns of precipitation. Highland regions that generally have seasonal rainfall experience extreme drought while hyper-arid coastal and low elevation areas experience above-average to heavy precipitation [35].

In southern Peru and elsewhere, ENSO rainfall on the desert coast and the western foothills can trigger catastrophic flooding and debris flows that commonly travel down dry ravines or quebradas [33,36]. In mid-elevation settings, rainfall can result in floods that overwhelm the main channels of rivers as well as their tributaries. Overbanking and flood waters can destroy settlements as well as agricultural and irrigation systems [37]. Although ENSO events resulted in catastrophic disasters, ancient peoples also employed cultural mechanisms to mitigate ancient ENSO occurrences; in some instances, they even took advantage of ENSO-recharged aquifers to increase agricultural production [38,39].

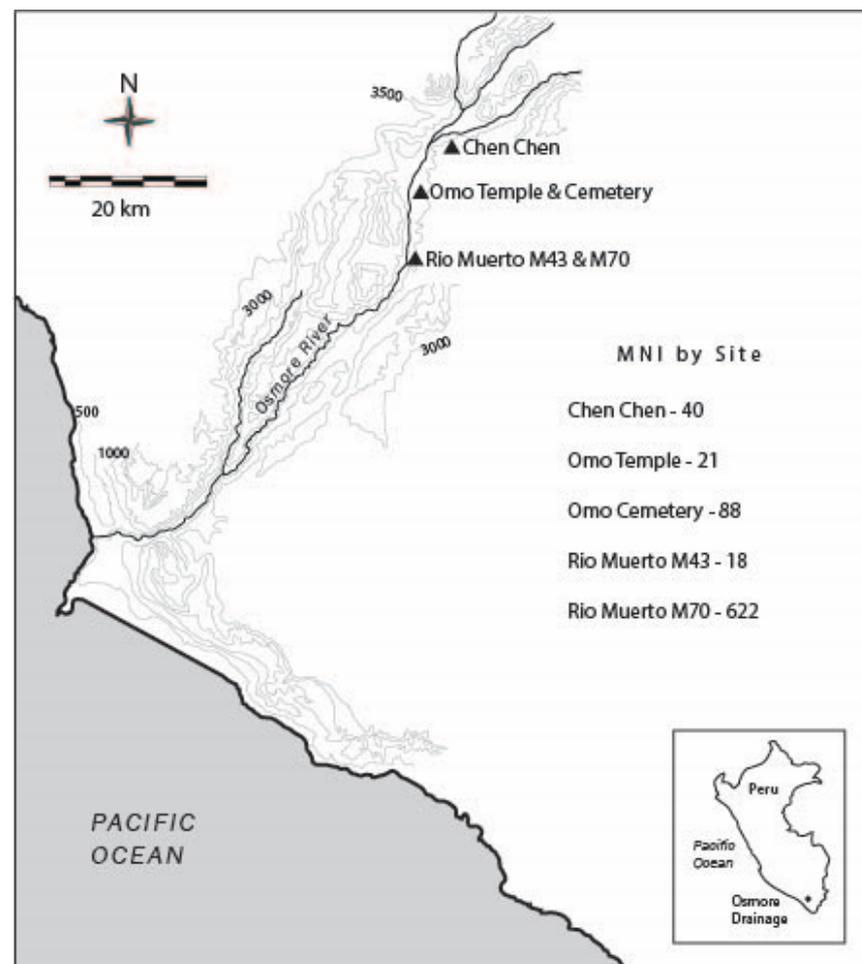
In far southern Peru, and the Moquegua Valley in particular, researchers have documented the history of ENSO events [36], as well as their impact on archaeological sites and irrigation systems [33,34,40]. One well-studied ENSO episode, known as the Miraflores event, occurred during the first half of the 14th century [38,41]. This ENSO generated catastrophic flooding along the southern coast that destroyed villages and agricultural systems [42–44]. We will explore the potential of studying anuran remain accumulations in providing insights into past ENSO events.

#### 3.2. The Cultural Setting

The Moquegua Valley has a long history of settlement dating to the end of the Pleistocene. Following several millennia of hunter-gatherer-forager lifestyles, populations increased in size and settled into villages where they practiced agriculture along with the rearing of domesticated animals (camelids and guinea pigs) in a local Formative cultural phase known as Huaracane (ca cal 385 BCE–CE 700) [45]. The fertile valley and agropastoral

productivity of local cultures were attractive to expansive empires who sought to extend their political economies. In the second half of the first millennium CE, two empires, the Huari and the Tiwanaku, colonized the Moquegua Valley.

Originating from a homeland in the Bolivian altiplano at over 3800 masl near Lake Titicaca, Tiwanaku colonists traveled over 250 km and settled in the mid-valley desert oasis of the Osmore drainage beginning in the 7th century AD. In contrast to the Huari, who settled the high sierra of the valley, the Tiwanaku occupied the highly productive middle Moquegua valley where their occupation was concentrated in four large cosmopolitan townsites at Omo, Chen Chen/Los Cerrillos, Rio Muerto, and Cerro Echenique (Figure 1). The Tiwanaku colonies thrived for over four centuries as evidenced by their construction of large towns, a sunken court temple, massive field and canal systems, geoglyphs, and extensive cemeteries [45,46]. At the height of settlement, the colony supported populations between 8000 and 20,000 people. Residents practiced intensive agriculture and produced crops amenable to the mid-valley setting, such as maize and legumes [45]. People transported locally produced foodstuffs to their highland homeland via llama caravans [47]. The demise of the Tiwanaku colony began around 1000 CE. At that time, the population dispersed into smaller settlements and none of the subsequent cultural groups reoccupied the original Tiwanaku townsites in the valley.



**Figure 1.** Map of analyzed Tiwanaku sites with anuran MNI by site.

## 4. Materials and Methods

### 4.1. Archaeological Sites

This study presents the analysis of anuran remains and associated taxa from 803 contexts excavated from habitational, ceremonial, and cemetery sectors at three of the four Tiwanaku site groups in the Moquegua valley. The sites are:

#### 4.1.1. Chen Chen (M1)

The Chen Chen M1 site is located northeast of the city of Moquegua at 1490 masl, representing the largest known Tiwanaku settlement and mortuary complex in the valley. Contexts analyzed for anurans include excavations in three large habitational sectors (8.6 ha), and a smaller habitational and ceremonial sector (2.5 ha) located near irrigation canals and a 90 hectare agricultural field system [45] (pp. 136,148). Analyzed tomb contexts from Chen Chen are from a large-scale rescue excavation conducted prior to the construction of a modern irrigation system and urban expansion [48]. As in all but one of the other Tiwanaku cemeteries from which fauna was examined, tombs at Chen Chen consisted of stone-lined cylindrical cists or unlined pits in which a single individual was interred.

#### 4.1.2. Omo Temple and Cemeteries (M10), and Domestic Sectors (M10, M12)

The Omo M10 site is located at 1200 masl on a desert bluff 20 m above the agricultural canal line, and adjacent to the most productive natural spring of this hyper-arid region. The M10 temple and cemeteries make up 1.5 ha of the M10 townsite (9.5 ha within the 35.5 ha Omo site group). The contexts that we analyzed for anurans are from the cemeteries and temple, which is the only sunken temple in the valley and the only Tiwanaku sunken temple outside of the highland capital in Bolivia, probably serving as ritual and administrative center [45] (p. 160). According to excavation field notes field crews recovered the anuran remains from below or around M10 cemetery capstones, high above the intentionally deposited burial contents. The anuran remains from the M10 temple are also from deposits closer to the surface, not from deeply buried contexts that would suggest they were offerings or ritual deposits.

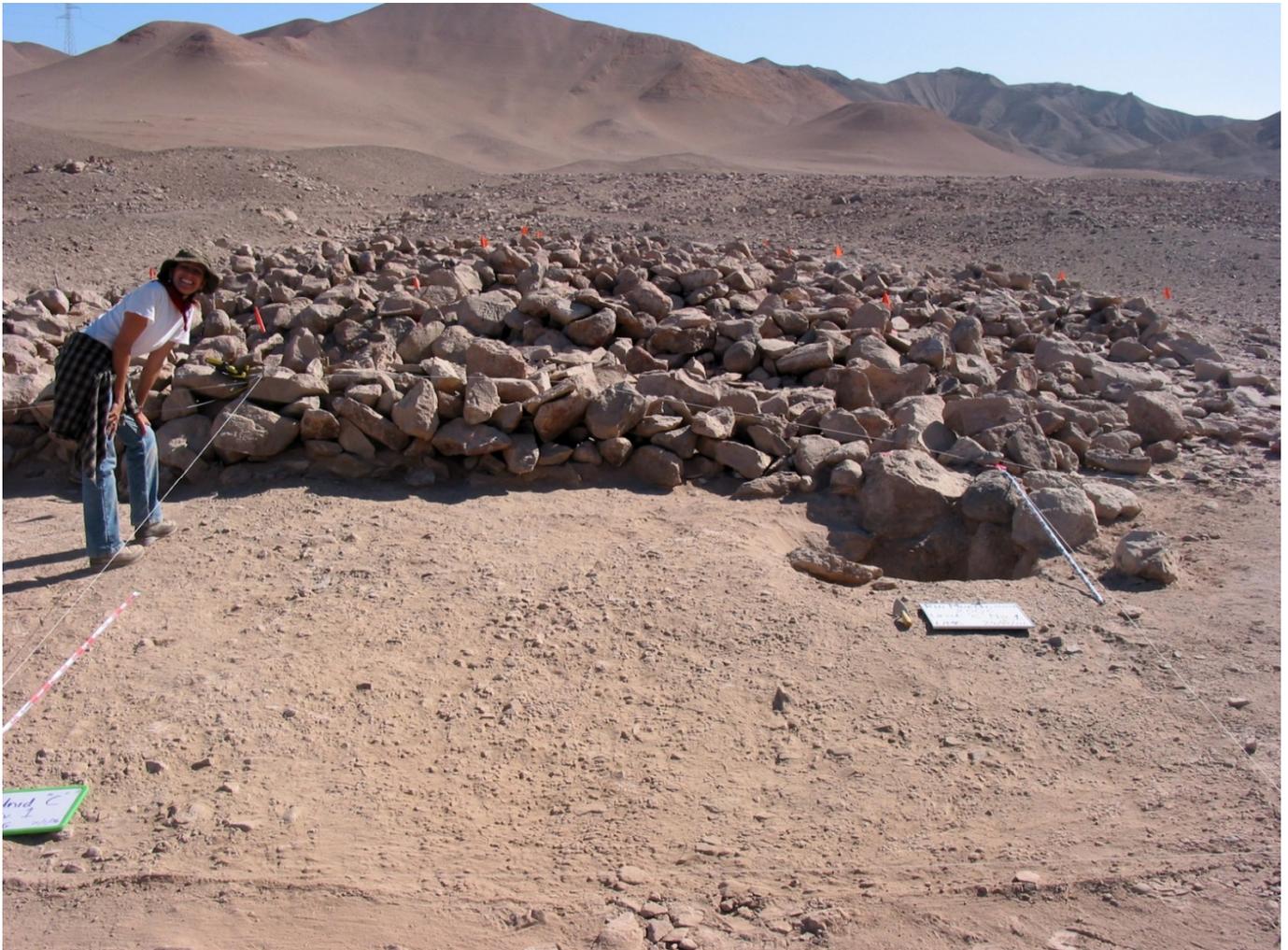
#### 4.1.3. Rio Muerto (M43 and M70)

The Rio Muerto complex located at 1025 masl, is the third-largest Tiwanaku settlement in Moquegua [45] (p. 149). Unlike Omo, Rio Muerto is not on a blufftop, but is located in a dry gulch tributary just outside of, but only slightly higher than, the canal-irrigated valley. Rio Muerto includes two sites, M43 (6.7 ha), which is closest to the modern canal, and M70 (2.8 ha), which is further removed from the valley bottom. At M70, the small cemetery M70B, located northwest of the domestic sector M70A, is of greatest interest to this study. The M70B cemetery is unique for our sample and unusual for the Moquegua Tiwanaku culture because the approximately 90 tombs are located under or within a massive rockpile up to 1m in height of loosely stacked stones (Figure 2) [45]. Excavators recovered anuran remains in deposits above the intact tombs. Anuran remains were not in direct association with the burials themselves, indicating that they are not offerings.

### 4.2. Methods

The zooarchaeological assemblage analyzed in this study was collected from excavations and surface materials from the four archaeological sites described above during field projects directed by various excavators (Berta Vargas at Chen Chen in 1987, Goldstein at Omo and Rio Muerto since 1986 and Baitzel in 2010 at Omo). Sediment from (near) surface levels was screened through 1/4" (6.35 mm) screens; all tomb fill and domestic and temple floors and features were screened through 1/16" (1.8 mm) mesh. We recognize that some differences in anuran remain abundance across the contexts we examine may be attributed to different excavation and recovery methods over multiple projects, notably in salvage work at Chen Chen; however, other recovery techniques were largely consistent. In all

cases, faunal material was bagged separately and analyzed in the archaeological laboratory of the Contisuyo Museum in Moquegua.

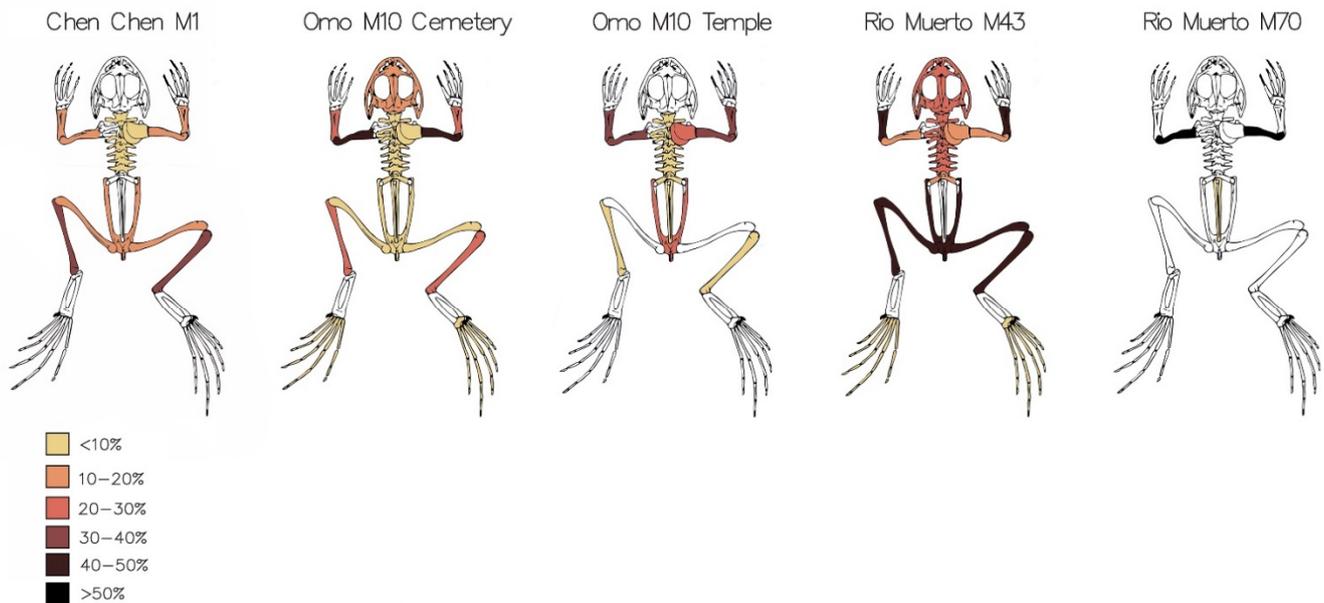


**Figure 2.** Rockpile cemetery feature at Rio Muerto, M70B prior to excavation (photo by Paul S. Goldstein).

Using the laboratory facilities at the Contisuyo Museum (Moquegua, Peru), deFrance completed identification of the anuran specimens. At the time of taxonomic identifications in Peru, deFrance identified the majority of elements only to the order Anura. Additionally, deFrance photographed selected specimens from Rio Muerto sites, mainly elements from the large assemblage of anuran humeri (and a single urostyle) from M70B. Although the ilium is highly diagnostic for anuran identification [49] and ilia are present in a modern owl pellet (see discussion below), this element was not well-preserved in the studied archaeological materials (Figure 3). Therefore, we used the humerus, which is the most abundant element in our assemblages, for quantification and more precise taxonomic identification of genera.

Using the photographs of humeri, Vallejo-Pareja used dry specimens and X-ray computed microtomography (CT-scans) of alcohol-preserved specimens from the comparative collection at the Herpetology Division of the Florida Museum of Natural History to identify a subsample of anuran bones to make more specific taxonomic identifications (SI Table S1). The CT scans were used to digitally segment and create three-dimensional (3D) models of the humerus of specimens used for comparisons using VG StudioMax v. 3.4 (Volume Graphics, Heidelberg, Germany). The 3D models of the humerus are available through

Morphosource.org. Taxonomic identification was hindered by not having access to the assemblage, which is currently curated in Peru, and therefore, relied on the photographs of selected specimens from sites M43 and M70.



**Figure 3.** Diagram of anuran element relative abundance by site.

Sexual dimorphism in some groups of South American anurans may present as marked differences in size with females being larger than males [50] or as morphological differences in humeri—with additional crests or spines in males that help during the amplexus or during combats for female section [51,52]. However, because the photographic material examined in this research does not display these dimorphic traits, we did not attempt to sex the specimens.

For the preliminary taphonomic analysis, deFrance recorded evidence of human consumption, such as burning and butchering traces. Digestion and other evidence of non-anthropogenic factors were not considered for the present study. Bone breakage was most commonly classified using whole vs shaft/fragment categories (though some were classified through whole, 3/4, 1/2, 1/4 or shaft/fragment). We tabulated the Number of Identified Specimens (NISP) and calculated the Minimum Number of Individuals (MNI) by context for both anurans and other associated taxa according to Reitz and Wing's recommendations [53]. The relative abundance of anuran elements was also calculated by site according to Andrews [11] (p. 145).

## 5. Results

The sites in this study yield a combined total of 5647 anuran specimens (NISP) and a minimum of 789 individuals (MNI) (Table 1; for data, consult SI Table S2). Anuran remains are most abundant at Río Muerto cemetery M70B, totaling 4808 specimens, followed by the Omo M10 Cemeteries with 541, Río Muerto M43 with 158, Omo M10 Temple with 80, and Chen Chen with at least 60 specimens (NISP was not calculated from the rescue project tombs, which were not screened). The order of sites changes slightly when considering MNI. Anurans are still most abundant at M70, with a minimum of 622 individuals, followed by Omo cemeteries with 88, Chen Chen with 40, Omo Temple with 21, and M43 with 18.

**Table 1.** Anura NISP and MNI by site and context type.

Site	NISP	Total MNI	MNI from Tombs	Percentage MNI from Tombs	MNI from Domestic Contexts	Percentage MNI from Domestic Contexts	MNI from Ceremonial Contexts	Percentage MNI from Ceremonial Contexts	MNI from Midden	Percentage MNI from Midden
Chen Chen M1	60	40	30	75.0	8	20.0	2	5.0	n/a	n/a
Omo Cemetery	541	88	85	96.6	n/a	n/a	n/a	n/a	3	3.4
Omo Temple	80	21	n/a	n/a	n/a	n/a	21	100.0	n/a	n/a
Rio Muerto M43	158	18	11	61.1	7	38.9	0	0.0	n/a	n/a
Rio Muerto M70	4808	622	352	56.6	1	0.2	n/a	n/a	269	43.2
TOTAL	5647	789	478	60.6	16	2	23	2.9	272	34.5

### 5.1. Taxonomic Identifications of Anurans and Non-Anuran Fauna

Vallejo-Pareja identified at least three *Anura* genera based on the photographs of 149 humeri, representing a minimum of 87 individuals (MNI), from tomb M70B-66 at the Rio Muerto M70B cemetery (M70-2961; Table 2). *Rhinella* sp. is the most common taxon, represented by 58 humeri (38.9% of the total humeri in this context). The humerus of *Rhinella* can be identified and differentiated from other taxa found in the region by having a distal condyle (humeral head) that is wider than long, and more oval than rounded. The ulnar and radial epicondyle are reduced and there are no lateral or medial crests along the shaft. The ventral crest is well developed (Figure 4). *Telmatobius* sp. is represented by 17 humeri (11.4%). This genus can be diagnosed and differentiated because of its well-developed medial crest that is wide and extends proximally past the middle of the humerus shaft. The lateral crest is well developed, wide and short. The radial epicondyle is not developed, the ulnar epicondyle is well developed, and the humeral head is rounded (Figure 4). The third taxon identified from the sample is *Pleurodema* sp. with 10 humeri (6.7%). It can be diagnosed and differentiated by its robust humerus with a rounded humeral head, a poorly developed radial epicondyle, and a well-developed ulnar epicondyle. There are no lateral or medial crests but the humeral shaft is laterally expanded towards the humeral head (Figure 4). The remaining 42 humeri (28.2%) could not be identified to genus, and 22 (14.9%) are classified as possibly belonging to one of these three genera. Although not all humeri from the cemetery context could be identified to genus, the three identified taxa account for 73% of the humeri present. Additionally, a preserved owl pellet from Rio Muerto, M70-4075 (22 NISP, MNI = 2) contains remains of at least one *Rhinella* sp. individual as well as a smaller anuran, probably another juvenile *Rhinella* sp. (see discussion below). We do not know if other mortuary and non-mortuary contexts have similar ratios of anuran taxa or if they contain other unidentified anuran species.

**Table 2.** Number of *Anura* humeri from M70-2961 identified to the genus level by NISP and MNI (photos reproduced with permission: *Rhinella* sp. [54], *Telmatobius* sp. [55], and *Pleurodema* sp. [56]).

Image	Taxon	Probable species	NISP	% of NISP	MNI	% of MNI
	<i>Rhinella</i> sp.	<i>Rhinella limensis</i> or <i>spinulosa</i> <a href="https://calphotos.berkeley.edu/cgi/img_query?seq_num=904525&amp;one=T">https://calphotos.berkeley.edu/cgi/img_query?seq_num=904525&amp;one=T</a>	58	38.9	32	36.8
	<i>Rhinella</i> sp. (possible)		10	6.7	9	10.3
	<i>Telmatobius</i> sp.	<i>Telmatobius arequipensis</i> , <i>marmoratus</i> or <i>peruvianus</i> <a href="https://calphotos.berkeley.edu/cgi/img_query?enlarge=0000+0000+0810+0233">https://calphotos.berkeley.edu/cgi/img_query?enlarge=0000+0000+0810+0233</a>	17	11.4	11	12.6
	<i>Telmatobius</i> sp. (possible)		8	5.4	8	9.2
	<i>Pleurodema</i> sp.	<i>Pleurodema cinereum</i> or <i>marmoratum</i> <a href="https://calphotos.berkeley.edu/cgi/img_query?seq_num=364994&amp;one=T">https://calphotos.berkeley.edu/cgi/img_query?seq_num=364994&amp;one=T</a>	10	6.7	5	5.7
	<i>Pleurodema</i> sp. (possible)		4	2.7	2	2.3
	unidentified		42	28.2	20	23
	All		149	100	87	100



**Figure 4.** Humeri of anuran species used for comparison with fossil material. (a) *Telmatobius carrillae*; (b) *Rhinella marina*; (c) *Pleurodema nebulosa*; (d) *Hyla boans*; (e) *Gastrotheca nebulanastes*; (f) *Psychrophrynella bagrecito*. (a–e) Right humerus, scale bar = 5 mm; (f) left humerus, scale bar = 2 mm. [51] (Anatomical nomenclature). Composite image by Vallejo-Pareja from photographs of digitally segmented specimens (ct-scans) at the Herpetology Division of the Florida Museum of Natural History.

During excavations field crews collected the remains of a variety of other taxa from contexts with anuran bones, including camelids, rodents, carnivores, bats, cervids, fish, crustacean, mollusca, and coral (Table 3). Notably, small-sized rodents exhibit the strongest co-occurrence with anurans, perhaps either because they occupy similar site environments or because both have the same origin of accumulation. Rodent, bat, and squamate remains were found in 69 out of the 106 contexts with anurans (65.1%) and represent a minimum of 225 individuals across all sites (in contrast to the anuran MNI of 789) (Table 4; SI Table S3).

### 5.2. Abundance and Ubiquity of Anuran Remains

The relative abundance of elements is highest for limb bones across all sites (Figure 3). Regarding breakage, the vast majority of remains are classified as shaft/fragment (89.2%). Few specimens are whole (4.5%) or mostly whole (3/4, 3.7%). No specimen from any sites exhibits butchering, burning, or other human modifications. The only exceptions to the fragmentary remains are two complete mummified frogs (species unidentified) wrapped in wool recovered from M10A-1, an apparent offering context in the Omo temple (Figure 5).



**Figure 5.** Mummified frogs wrapped in camelid fiber from Omo M10 Temple (photo by Susan D. deFrance).

**Table 3.** Non-anuran taxa present in analyzed site contexts.

Site\Taxa	Vertebrata	Mammalia	Camelidae	Rodentia	Carnivora	Chiroptera	Artiodactyla and Cervidae	Aves	Squamata	Osteichthyes	Crustacean	Mollusca	Coral
Chen Chen M1	X	X	X	X	X						X	X	
Omo Cemetery	X	X	X	X	X	X	X	X		X		X	X
Omo Temple	X	X	X	X		X			X	X	X	X	
Rio Muerto M43	X	X	X	X	X		X	X	X	X	X	X	X
Rio Muerto M70	X	X		X		X		X	X	X	X		

**Table 4.** Anurans and other possible owl prey taxa MNI by site.

Site	Anura MNI	Rodentia MNI	Chiroptera MNI	Squamata MNI
Chen Chen	40	15	0	0
Omo Cemetery	88	43	2	0
Omo Temple	19	13	1	1
RM M43	17	10	0	1
RM M70	622	144	11	1
<b>TOTAL</b>	<b>786</b>	<b>225</b>	<b>14</b>	<b>3</b>

The ubiquity index of anuran remains by site and by context type is given in Table 5. At Chen Chen, frog and toad remains are present in eight habitation, two ceremonial, and 12 tomb contexts (15.3% of the 144 contexts analyzed for this site). At the Omo Temple (specifically M10A), anurans are present in only 13 contexts (4.3% of 304 analyzed contexts from this sector). Among the 142 contexts analyzed from Omo Cemeteries, anurans occur in 26 tombs and three non-tomb contexts from the cemeteries (20.4% of analyzed tombs). Interestingly, tomb M10H-24 contained 133 anuran remains representing 21 individuals. This deposit alone accounts for 23.8% of the Omo M10 site NISP. The excavators noted an abundance of small bones under the capstones prior to opening this undisturbed burial. The Rio Muerto site M43 samples are from eight tombs and six domestic contexts (9.2% of the 153 analyzed contexts from this site). At Rio Muerto site M70, the anuran bones are from 23 tombs and four non-tomb contexts from the M70B rockpile cemetery, and from only one domestic context from M70C. Thus, 43.8% of the 64 analyzed contexts from M70 contain anurans.

Frog and toad remains are most common in cemeteries and tombs. At the Rio Muerto M70B cemetery, 23 of the 27 analyzed tomb contexts yielded 352 anuran individuals (see Tables 1 and 5) resulting in an anuran ubiquity index of 85.2%. At Omo M10, 26 of the 65 studied tomb contexts produced an MNI of 85 anuran individuals (40.0% ubiquity index). The assemblage from Rio Muerto M43 included eight individuals collected from eight tombs, while the other 34 tombs excavated did not yield any anuran bones indicating a ubiquity index of 23.5%. Similarly, the assemblage from Chen Chen cemeteries yields 30 individuals from 12 tombs out of a total of 36 analyzed tombs (ubiquity index of 33.3%). The contrast between M43 and M70B is notable, considering that both cemeteries are located at a similar elevation but M43 is slightly closer to water sources where frogs would naturally occur.

Anuran remains were considerably more commonly associated with Tiwanaku cist tombs than in other contexts, and anurans were remarkably ubiquitous in the unique M70B “rockpile” cemetery. The quantity of frog/toad individuals in and around tombs contrasts with the small number of anuran individuals in habitational and ceremonial areas of Chen Chen (MNI = 10), in the ceremonial site of the Omo Temple (MNI = 21), in the habitation areas of Rio Muerto M43 (MNI = 7), and in habitation areas of Omo M10 (178 contexts) and M12 (123 contexts) where no anurans were found. Even though anurans are present in some Moquegua Tiwanaku monumental and domestic contexts, they are rare in comparison to tombs and cemeteries.

Further contextual evidence is found from specific anuran contexts in cemeteries. All anuran bones in the Omo cemeteries were recovered from pit or cist tombs whose capstones were found in various states of intactness, collapse, or anthropogenic disturbance, allowing for at least gradual infilling of sediment and accumulation of intrusive fauna (Figure 6).

**Table 5.** Contexts and Ubiquity Index by site and context type.

Site	Total Contexts Analyzed	Total Contexts with Anurans	Ubiquity Index (%)	Total Tombs Analyzed	Total Tombs with Anurans	Tomb Ubiquity Index (%)	Total Domestic Contexts Analyzed	Total Domestic with Anurans	Domestic Ubiquity Index (%)	Total Ceremonial Contexts Analyzed	Total Ceremonial with Anurans	Ceremonial Ubiquity Index (%)	Total Midden Contexts Analyzed	Total Midden with Anurans	Ceremonial Ubiquity Index (%)
Chen Chen	144	22	15.3	36	12	33.3	90	8	8.9	18	2	11.1	n/a	n/a	n/a
Omo Cem.	142	29	20.4	65	26	40.0	n/a	n/a	n/a	n/a	n/a	n/a	80	3	n/a
Omo Tem.	304	13	4.3	n/a	n/a	n/a	n/a	n/a	n/a	304	13	4.3	n/a	n/a	n/a
Rio M43	153	14	9.2	34	8	23.5	100	6	6.0	4	0	0	n/a	n/a	n/a
Rio M70	64	28	43.8	27	23	85.2	31	1	3.2	n/a	n/a	n/a	6	4	n/a
TOTAL	807	106	13.1	162	69	42.6	221	15	6.8	326	15	4.6	86	7	8.1



**Figure 6.** **Top left**, diagram of cist tomb view from above and cross section; modified from [45]; **top right**, Omo cemetery tomb with intact capstone; **bottom left**, collapsed rock capstone of an Omo cist tomb; **bottom right**, Omo cemetery collared tomb on the left (U10) and radiocarbon dated pit (U8) next to tomb. Arrow is pointing to volcanic tephra from the February 1600 eruption of the Huaynaputina volcano. Note the openings allowing infill sediment and creating a burrow for animals. (photos by Sarah I. Baitzel).

## 6. Discussion

### 6.1. Anurans and Agents of Accumulation

We consider the multiple possibilities for the accumulation and distribution of anuran remains. One possibility is that the anuran assemblages resulted from natural death. As mentioned previously, frog and toad species common to the Moquegua Valley are not burrowing anurans [26,27]; therefore, they would not have naturally sought shelter in the archaeological deposits described here. Today farmers occasionally capture anurans in fields, but anurans are not found in the hyper-arid settings outside of irrigated fields. Given the low frequencies of frogs or toads today around these sites and the low frequencies of their remains at highland Tiwanaku sites, where frogs are naturally abundant, the quantity of anuran remains at the hyper-arid Moquegua Tiwanaku sites is anomalous [57–59]. Thus, we do not think that natural death is a sufficient explanation to account for the high number of anurans accumulated.

Secondly, we consider the possibility of frog or toad consumption as a cultural practice among Tiwanaku colonists in Moquegua. Because anuran remains are mostly absent in other (highland) Tiwanaku sites, we argue that Tiwanaku peoples did not consider anurans as regular food resource. Thus far, archaeological evidence indicates that the use of toads and frogs in Tiwanaku culture was primarily ritual. Specimens identified as Lake Titicaca frogs (*Telmatobius culeus*) and unidentified anurans are included along with other animals in a Lake Titicaca underwater ritual site, Khoa Reef near the Island of the Sun [60]. This site is interpreted as a ritual locale where religious specialists made repeated state offerings in the lake. Although the authors suggest that the frog remains from this site could be natural inclusions, it is also possible that people intentionally included frogs as offerings along with camelids and birds. The only unequivocally ritual use of anurans at Tiwanaku sites in Moquegua is the deposition of the two wool-wrapped complete anurans in an offering context at the Omo M10A temple. An X-ray revealed both frogs were mummified, possibly desiccated, and fully articulated. There are no other known examples of mummified frogs wrapped in wool from Tiwanaku sites; therefore, we hypothesize that these objects may have been ritual talismans used as a dedication or other offering.

In contrast, the quantity, uneven distributions, and contexts of disarticulated frog and toad bones at the Moquegua sites suggests that the majority of anuran remains accumulated as the result of non-cultural processes rather than anthropogenic factors (e.g., food discard, which consists primarily of butchered and fragmentary camelid remains in domestic contexts, or other intentional human action). Although we cannot discount the possibility that cultural practices (i.e., ceremonial or ritual behavior, or human consumption) resulted in the deposition of some of the anuran bones, the most parsimonious explanation is that frogs and toads are non-cultural deposits.

As taphonomic studies of anuran remains the world over show, one of the principal taphonomic agent for introducing these bones into archaeological assemblages are the natural predators of frogs/toads [17–23,61,62]. In Moquegua, identifying one of the probable taphonomic agents that produced the accumulations of frog and toad skeletons described here was largely serendipitous. During a field visit to the post-Tiwanaku site of Estuquiña (~1250–1470 CE), located north of the city of Moquegua, one of us (deFrance) observed several pairs of adult Burrowing Owls and owlets of the species *Athene cunicularia* near ancient below-ground tombs that had been disturbed and partially opened, probably by recent and past looting activity (Figure 7). In subsequent years, deFrance and others observed Burrowing Owls also nesting in tombs at this site. Significantly, no one observed predatory birds other than Burrowing Owls occupying the cemeteries.

The Burrowing Owl (*Athene cunicularia*) is a common species across western and southern Peru (Figure 8). These owls favor dry, open habitats, feeding on insects, small mammals, reptiles, and amphibians (Figure 9) [63–65]. They are known to nest in abandoned burrows excavated by small mammals. The owl parents at Estuquiña became highly agitated when researchers approached them, suggesting nests were nearby. The abandoned Estuquiña tombs with their cavities protected by surface rocks resemble the burrows typically used by Burrowing Owls and serve as a suitable space for nidification. Inspection of the open tombs revealed that roughly 20 cm below the ground surface several tombs contained abundant remains of owl pellets and nesting material (e.g., feathers, animal fur, small-sized twigs and dry vegetation). The pellets consisted of the remains of small rodents, scorpions, and frogs and toads among other owl food refuse. These observations align with studies of the Burrowing Owl pellets across South America [66–68].



**Figure 7.** Burrowing Owl (*Athene cunicularia*) surrounded by seven (7) tombs at the site of Estuquiña (photo by Susan D. deFrance).



**Figure 8.** Map of Burrowing Owl distribution in Peru [69], and study region location in southern Peru.



**Figure 9.** Burrowing Owl eating a frog at Fort Lauderdale, FL [70].

Similar to the modern Burrowing Owls using Estuquiña tombs for their nests and deposits of prey, we hypothesize the abundance of anuran remains at Tiwanaku sites is the result of Burrowing Owl predation (see Figures 7–9). The shelter offered by the intact and collapsed capstones of Tiwanaku tombs at Chen Chen, Omo M10 and Rio Muerto M43 mimic the spaces Burrowing Owls tend to inhabit. In particular, the crags and crannies of the M70B rockpile tombs seems to have made this cemetery highly suitable to owl needs (see Figures 2 and 6). The abandoned tombs in the Moquegua valley would have provided a favorable habitat for the Burrowing Owls by offering nesting spaces where they would bring back prey to their offspring. Modern owl pellets collected from Estuquiña corroborate our hypothesis that some tomb fill resulted from owl predation because the pellets contain large numbers of frog elements together with remains of other taxa; the faunal composition of modern pellets analyzed resembles that found around capstones and in infill sediment of tombs from several Tiwanaku sites (Figure 10). The higher relative abundance of limb bones, and the relative scarcity of cranial fragments and extremities may be in keeping with patterns observed for owl predation in the literature [17–23,61,62]. The remains of Chiroptera (bat), *Phyllotis* sp. (leaf-eared mouse) and Squamata (lizards) might also have been introduced as owl prey, or they could have taken shelter in the tombs.

Non-Anura taxa such as bats, mice, and lizards seem unlikely to have been included as grave goods or offerings. Only fauna with known value as food or offerings in Tiwanaku culture (e.g., camelids, guinea pigs, fish, river crayfish, mollusks) are interpreted as possibly intentional inclusions in the tombs or cemetery surface as offerings.

Several other birds of prey inhabit the Moquegua valley, such as hawks (*Geranoaetus* sp. and *Parabuteo unicinctus*), other owls (*Tyto alba*, *Glaucidium peruanum* and *Bubo virginianus*), falcons (*Falco* sp. and *Phalcoboenus megalopterus*), and vultures (*Vultur gryphus* and *Cathartes aura*) [71]. However, these birds are either rare in the region or have vastly different nesting habits (high terrain or near cliffs) than the Burrowing Owl, and their hunting behavior would be an unlikely explanation for anuran accumulation in the tombs [72,73].

However, we caution that a full taphonomic study would be warranted and would like to consider the limitations of our analysis. As previously discussed, the anuran remains are currently curated in Peru and additional analysis of digestion, fragmentation, and other modifications (such as beak marks and gnawing) is not possible at this time. The lack of access to materials also hindered a more careful quantified analysis of the contents of modern owl pellets. Future deductive studies of these aspects, together with broader anuran taxonomic identification, will allow for a more comprehensive examination of the hypotheses considered here. That would include comparisons with results to many studies on Burrowing Owl pellets in similar settings across South America, some of which include the identification of markers as the ones described in the section on anurans and taphonomic studies [61,62,66–68,74–76].



**Figure 10.** Owl pellet with *Rhinella* sp. remains from Rio Muerto tomb (M70B-4075) (photo by Susan D. deFrance).

The quantity and context of frog/toad remains suggest that paleoenvironmental conditions in the mid-valley were highly favorable for anurans and owl predators, particularly after the abandonment of Tiwanaku settlements. None of the sites were reoccupied during subsequent periods and there was little subsequent human presence to discourage animals from using the remnants of these townsites and cemeteries. This suggests that sometime after the abandonment of the Tiwanaku settlements around 1100 CE, there was greater moisture and accumulated water in the valley leading to an increase in the frog/toad population. In the desert setting of Moquegua, changes in the normal seasonal pattern of rainfall signal a larger-scale climatic anomaly.

#### 6.2. Anurans and Palaeoecology

The proliferation of anurans that resulted in their deposition in the hyper-arid setting of the Moquegua Valley requires consideration of past climatic conditions, especially given that the archaeological sites examined here are located away from/above the canal/fields. The anuran genera identified from these sites, *Telmatobius*, *Pleurodema* and *Rhinella*, are

Andean taxa found at altitudes between 1000 to 4000 masl, in open areas, grasslands, dry forest or arid environments [27,77]. The *Telmatobius* and *Pleurodema* species of the Peruvian Andes are found near or in permanent water bodies and their dispersion and distribution is limited by the presence and connectivity of these water bodies such as rivers and ponds [78]; few species of *Telmatobius* inhabit humid *paramos* and forest [79]. At least three species of *Telmatobius* are found in the rivers and ponds of the central Peruvian coastal valleys but none have overlapping distribution since their dispersal is limited by the hyper-arid environmental conditions [77]. *Pleuroderma* species are well adapted for environments with strong seasonality and are explosive breeders, an adaptation for living in dry environments, in which the presence of water bodies is crucial for reproduction, which is characterized by laid foam-nests during rainy seasons [78,80,81]. Because southwestern Peru is a hyper-arid region, we hypothesize that the region would not have provided an adequate environment for the survival of the large number of anurans identified from these sites under predictable minimal seasonal rainfall. However, observations from other Andean location have shown a close relationship between these anuran genera and changes in environmental conditions and water availability. This is the case for *Telmatobius marmoratus*, *Rhinella spinulosa* and *Pleurodema marmoratum* in the Cordillera Vilcanota, southeast Peru, where new ponds created after ice recession expanded the altitudinal range of this species [82]. This evidence suggests that periods of intense rainfall and water accumulation in ponds or other settings created a more favorable habitat for anuran populations to thrive. Significantly, increased rainfall in the Moquegua Valley is historically associated with the onset of ENSO [33,40].

In the mid-valley of Moquegua, researchers documented an early 14th-century flood event occurring in the lower valley tributary that passes within 30m of Rio Muerto (M43 and M70) [33]. This flood deposit almost certainly represents the Miraflores event. Here, rainfall triggered a high-velocity flood deposit adjacent to the abandoned Rio Muerto Tiwanaku site. Because major ENSO events may correspond to extended periods of anomalous increased rainfall, the mid-valley probably experienced significant precipitation prior to and after the flooding [83]. Over the longer term, additional effects likely included recharging of subterranean aquifers, replenishing and enhancing local springs, and creating wetter local microenvironments.

We hypothesize that the onset of this 14th-century Miraflores ENSO altered the local habitat making the otherwise arid environment suitable for anurans. Under non-ENSO conditions, local frogs and toads would be restricted to active watercourses, irrigated fields and local springs/wetlands. Under ENSO, small-scale episodes of rainfall or residual pools from quebrada floods generated habitats of standing water suitable for the reproduction of anuran populations. Larger frog/toad populations in turn would have inhabited the area, potentially dying if stuck in flooded stone-lined tombs at Chen Chen, Omo, and Rio Muerto, a process more closely resembling cases of catastrophic death. The infill stratigraphy of some Tiwanaku tombs provides further evidence for tombs as places of localized water accumulation that might have attracted or trapped anurans. Tombs at Rio Muerto and Omo M10 had silty infill sediments that were sometimes laminated and compacted from periods of heavy rain. If anuran populations occupied these habitats, they would have attracted predation by Burrowing Owls that also nested in the abandoned tombs. However, these sites and the analyzed contexts are above (higher elevation) than nearby field systems, streams, and probable water habitats that would have attracted anurans. Because of the location of the cemeteries and analyzed contexts these areas would not have been habitats suitable for anurans in the past.

Pools of standing rainwater, springs, and canals could also fill and regenerate vegetation growth in relic and abandoned canals and field systems; such seasonal habitats increased insects and other anuran prey that attract frogs and other animals to the areas near sites. In north-central Chile, increased plant productivity during ENSO supported periods of abundance of small mammals, including *Phyllotis* sp. (leaf-eared mouse), a small rodent present in our assemblage [84]. On the one hand, increased rainfall in other environments, including arid ones, has been linked to higher anuran egg masses and

call production [85–87]. At Rio Muerto and Omo, even a small amount of rainfall could have potentially resulted in standing pools suitable for frogs to colonize and to deposit eggs. On the other hand, even after ENSOs and with lower availability of anurans, the established populations of Burrowing Owls could rely more heavily on insects, *Phyllotis* sp., and Squamata (lizards) as food sources, and continue to occupy the tombs [66,74,76]. We therefore suggest that ENSO in Moquegua may have created conditions favorable for frog and toad growth, in turn sustaining predator populations.

The 14th-century Miraflores ENSO was among the first such climate alterations that made the otherwise arid environment suitable for anurans. That the Miraflores ENSO event created favorable conditions for anurans is supported by the recovery of frog/toad remains from a radiocarbon-dated non-mortuary context at Omo M10 that corresponds to the Miraflores ENSO time frame. In 2010, Baitzel uncovered a small carbon-filled pit (Feature M10U-8) next to an intact tomb rock collar (Burial Feature M10U-10) that was initially interpreted as an offering or burning event associated with the tomb (see Figure 6). However, a radiocarbon date obtained from charcoal recovered in the pit produced a calibrated (SHCal20) date of 1328–1455 cal CE (2-sigma) ( $^{14}\text{C}$  age BP:  $547 \pm 38$ ; AA101909) indicating the deposit postdates the Tiwanaku occupation but overlaps with the Miraflores ENSO event. This pit may have been used by nesting owls feeding on anurans. Future direct radiocarbon dating of anuran specimens could help identify the period of accumulation and examine if it corresponds to the Miraflores ENSO, or possibly to a yet unidentified ENSO event. Other future work would consist in monitoring anuran populations in the region during the next ENSO to determine if these events would be linked to anuran population explosions.

Although ENSO may create conditions that are highly favorable for frog and toad proliferation in arid regions such as Moquegua, other research on the impact of El Niño events on anuran populations shows that increased rainfall can lead to higher embryonic mortality, proliferation of infectious diseases, and decreased species diversity and range [85,88]. These studies, however, have been conducted in areas where frogs and toads tend to be naturally abundant; in those settings, higher-than-normal rainfall might exceed the range to which local anurans are adapted. Our study indicates that the effects of ENSO on herpetofauna need to consider the role of geographic variability on population outcomes.

Today, the impact of climate change is altering the rainfall patterns associated with ENSO. Therefore, it is probable that more frequent and irregular El Niño events, together with increasing temperatures and habitat fragmentation, could lead to permanent declines in frog and toad populations [85,89–91]. Our work points to the potential of zooarchaeological research in supplementing contemporary studies of anuran populations, refining our understanding of the impacts of climate change in amphibians and their related ecosystems, and improving the development of conservation strategies.

## 7. Conclusions

Zooarchaeological assemblages from four Tiwanaku-culture sites in the Moquegua Valley of far southern Peru contain abundant skeletal remains of frogs and/or toads. Anuran remains are most common in tombs, with far lesser quantities in habitation and ceremonial sites. Our analysis indicates that at least three genera of anurans are present on these sites. Andean people have a long history of ritual interaction with frogs, particularly to bring about rainfall during drought conditions, but other than two complete mummified frogs from a temple context at Omo, we have no evidence that the inhabitants of these sites intentionally deposited anurans. On the basis of modern Burrowing Owl behavior and their preferential use of abandoned archaeological tombs for nests, we interpret the frog and toad remains on these sites as accumulations primarily from the hunting activities of nesting Burrowing Owls, and secondarily from natural death more likely post-ENSO event. At one of the sites in particular, Rio Muerto's M70B "rockpile cemetery," the large quantity of anuran remains may be related to a 14th-century El Niño event that generated rainfall and created conditions favorable for frog populations near an unusual Tiwanaku

cemetery that was uniquely suited to owl nidification. Future research on the assemblages of frog and toad remains studied here can contribute to a more comprehensive examination of the hypotheses we have considered. Future research on similar assemblages in other areas of the Central Andes may serve as a proxy for past El Niño events and complement existing biological data for the study of species distribution and environmental change. Our results also point out considerations on best practices to reduce collection bias with the consistent use of 1/16" screens to improve chances of recovering important small animal remains; many researchers have highlighted the importance of smaller screens for zooarchaeological and paleoenvironmental research [53,92–94]. Furthermore, we caution against automatically interpreting the remains of non-food animals as possible ritual inclusions, particularly in burial contexts, and advocate for archaeologists to explore taphonomic explanations.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/quat5010016/s1>, Table S1: Comparative specimens used in this analysis. Table S2: Data from anuran specimens included in this analysis. Table S3: Context and MNI of Rodentia, Chiroptera, and Squamata compared to Anuran MNI.

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**Data Availability Statement:** Data are contained in the article and the Supplementary Materials. CT-scans and 3D reconstruction of the humeri of comparative species are open access and available on Morphosource.org.

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