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Isotopic investigation of pre-Hispanic macaw breeding in Northwest Mexico

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ABSTRACT

The pre-Hispanic settlement of Paquimé (ca. 1200–1450 AD) lay outside of urban Mesoamerica in arid northern Chihuahua, Mexico, yet the excavated remains of 322 scarlet macaws, tropical parrots whose northernmost habitat is 500 km to the south, suggest that Paquimé had relationships with distant communities. Here, carbon and oxygen stable isotope analysis of 30 macaw bones determines whether the Paquimeños actively bred these parrots or traded with Mesoamerican groups to obtain the birds. The $\delta^{13}\text{C}$ values indicate that the macaws ate a diet of C_4 plants, foods that were unavailable to wild macaws. In addition, $\delta^{18}\text{O}$ data suggest that the majority of the macaws spent their entire lives at Paquimé. We conclude that the ancient Paquimeños were in fact breeding scarlet macaws, although one bone with $\delta^{18}\text{O}$ values outside the local range suggests that the breeders also maintained exchange ties with the source areas of the birds. By confirming that Paquimeños implemented a system of local macaw reproduction outside the Mesoamerican region itself, this analysis provides new evidence about the economic and ideological interdependence of pre-Hispanic societies in the Americas. It is also suggestive of the pre-industrial capabilities of humans to extend the natural ranges of animal species.

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Introduction

To the pre-Hispanic peoples of Mesoamerica, feathers were highly prized items with significant economic, ritual, and political value. Especially important were the colorful, iridescent feathers of tropical birds, which prompted long-distance trade and sustained procurement strategies, such as breeding programs, in order to secure their steady supply. In the early 1500s AD, the Aztecs were receiving colorful feathers as tribute from subject polities (Durán, 1994) and colonial documents describe a large aviary at their capital city of Tenochtitlan where a variety of parrots were bred and annually harvested for their feathers (Diaz, 1963, pp. 228–229). Similarly, the Huastec of Mexico's Gulf Coast kept captive parrots in order to pluck their feathers for use in ceremonial and military dress (Stresser-Péan, 1971, p. 589). Of particular interest to many Mesoamerican groups were the red, blue, and yellow feathers of the scarlet macaw (*Ara macao*). Pictorial and glyphic representations of the scarlet macaw are evident as early as 300 BC where the species was associated with rule by shamans in the Itzapa and Epi-Olmec groups (Kappelman, 2001). The Classic Maya (250–900 AD) frequently depicted the macaw on carved stelae and sculptures (Freidel et al., 1993), and its feathers were one of

the most frequently used for featherworking by the Aztec elite. Across Mesoamerica, symbolic associations of the scarlet macaw and its feathers included the end of the dry season (Tedlock, 1985), the sun (Paddock, 1966), fire (Aguilera, 1985), light and lightning (Seler, 1993), and warriorhood (Seler, 1992). Ceremonial centers in arid northern Mexico lack the hieroglyphic texts and codices of the Maya and the Aztecs, but other evidence suggests the presence of macaws, their feathers, and possibly their local breeding.

The present study investigates scarlet macaw remains from Paquimé, a pre-Hispanic site in arid northern Chihuahua, Mexico. Unearthed over 500 km from the most northern extension of their natural habitat, these macaws raise questions concerning the relationship between the North American Southwest and Mesoamerica. Through stable isotope analysis of carbon and oxygen in macaw bone carbonate, we explore whether the large collection of scarlet macaws at Paquimé ($n = 322$) was a result of sustained trade relations with Mesoamerican groups to the south or the product of a large-scale breeding program designed to reproduce the valuable birds and their feathers for political, ritual, or economic needs. This study provides new information concerning exotic-goods production and elite legitimation at Paquimé by determining that the Paquimeños had in fact developed the breeding technology and cultural knowledge to sustain a reproducing population of scarlet macaws in the highlands of northern Chihuahua.

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Mesoamerica, the American Southwest, and macaw breeding at Paquimé

The degree of interaction between the pre-Hispanic North American Southwest and Mesoamerica has long been a subject of debate. Hypotheses have ranged from direct contact and domination of the Southwest communities by Mesoamerican traders (Di Peso et al., 1974, Kelley and Kelley, 1975; Weigand and Harbottle, 1992) to ideas of greater independence and local development of the Southwestern groups (Haurly, 1976; McGuire, 1980). Despite disagreements on the degree of interaction, archeological investigations have produced clear evidence for the exchange of some items and ideas between the two regions. Turquoise mined in New Mexico has been discovered at multiple Mesoamerican sites (Weigand, 1994, Weigand et al., 1977), ballcourts and evidence for the Mesoamerican-style ballgame appear as far north as northern Arizona (Wilcox, 1991), and most recently, chemical analysis of organic residues from ceramic sherds from Pueblo Bonito, Chaco Canyon indicates that the vessels held cacao drinks, a tropical Mesoamerican import (Crown and Hurst, 2009). Known for its iconographic, architectural, and artifactual similarities to Mesoamerica, Paquimé, while belonging to the Mogollon (American Southwest) cultural system, presents an ideal location to investigate the nature of interdependence between the two regions.

Located in high desert of northwestern Chihuahua, Paquimé, also known as Casas Grandes, lies about 110 km south of the modern border with the United States. During the Medio Period (ca. 1200–1450 AD), Paquimé was the center of one of the most influential and complex regional systems of Northwest Mexico and the North American Southwest (Whalen and Minnis, 2001). Due to the abundance of Mesoamerican-style objects and architecture, such as copper bells, ballcourts, and platform mounds, scholars have suggested that Paquimé was an intermediate trading site between the North American Southwest and Mesoamerica (Di Peso et al., 1974).

As in Mesoamerica, birds, and presumably their feathers, were important ritual and trade items to the Paquimeños, and the remains of 46 avian species, including white pelicans (*Pelecanus erythrorhynchos*), Canadian geese (*Branta canadensis*), Mexican ducks (*Anas diazi*), thick-billed parrots (*Rhynchopsitta pachyrhyncha*), and several species of eagles, owls, and ravens were uncovered at Paquimé, often in ritual contexts (McKusick, 1974). Moreover, several species of birds were kept captive and possibly bred for their feathers. Di Peso et al. (1974) uncovered the remains of over three hundred common turkeys (*Meleagris gallopavo*), which were associated with small adobe nesting pens. More surprisingly, excavations revealed 503 macaws, including 322 scarlet macaws (*A. macao*). The remainders were either military macaws (*Ara militaris*) or indeterminate macaw species (*Ara* sp.). While the military macaw is native to northern Mexico, the scarlet macaw's natural habitat lies over 500 km south in the humid Mesoamerican lowlands (Fig. 1; Howell and Webb, 1995).

Excavations at Paquimé revealed 56 adobe cages for the macaws; many contained macaw bones and feces, and a one contained a few fragments of eggshells (Di Peso et al., 1974). The macaw pens differed from the turkey pens in that they were associated with crafted stone doors, or cage stones, and pestle-like stone door plugs (Fig. 2), possibly owing to the tendency of macaws to chew and pick at their cages (Rizo, 1998). These pens, in addition to the presence of 125 “donut” cage-entrance stones give indication of the scale of macaw keeping at Paquimé; the extra cage-entrance stones probably belonged to pens from the collapsed upper stories of buildings where macaws were also being kept. Although the majority of evidence for macaw keeping was localized in several residential areas, macaw pens, remains, and

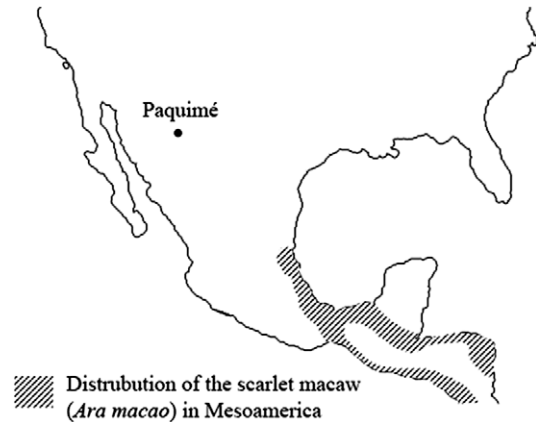


Fig. 1. Distribution of the scarlet macaw (*Ara macao*) in Mesoamerica. The most northern extent of the macaw's natural habitat is over 500 km south of Paquimé.

cage entrance-stones were found throughout the site (Di Peso et al., 1974). Whalen and Minnis (2001) suggest that this decentralized effort of macaw keeping implies an intermediate level of complexity for the Paquimé regional system where control of production was not concentrated in the hands of a single group; local elites and kin groups would have competed for followers and social power through the acquisition, production and manipulation of prestige goods.

Scarlet macaws and their feathers would have been significant markers of status and power at Paquimé. Their symbolic importance is evidenced by the many bird burials where scarlet macaws were often arranged in patterns with a smaller number of green military macaws. Potters painted stylized parrots on ceramics and formed vessels into macaw-shaped effigies throughout the Medio Period and polychrome ceramic vessels occasionally display the macaw head motif linked with the body of a plumed serpent, similar to the Mesoamerican feathered serpent god Quetzalcoatl (VanPool and VanPool, 2007). In the monumental context of four-story buildings, ball courts, platform mounds, colonnades, and extensive waterworks, all implying coordinated leadership, the presence of the scarlet macaw remains are suggestive of the use of the tropical macaw feathers in the Mesoamerican way, to connote connection with the supernatural as a way of obtaining and legitimizing social power.

Although pre-Hispanic macaw specimens have been found at many sites in the American Southwest, including Pueblo Bonito, Wupatki, Point of Pines, and Galaz (Creel and McKusick, 1994; Di Peso et al., 1974, Hargrave, 1970; McKusick, 1974; Minnis et al., 1993), Paquimé is the only site in the region to contain such extensive evidence of macaws (Di Peso et al., 1974, vol. 2, pp. 599–600; Di Peso et al., 1974, vol. 8, pp. 67–268), suggesting that it might have been the source of the birds found at many other sites. Given the presence of eggshell fragments and breeding age birds at Paquimé, Paquimeños may have acquired scarlet macaws through trade and bred this initial stock for ritual consumption and for export into the American Southwest (Di Peso et al., 1974). Yet, several lines of evidence suggest that Paquimé itself might have continuously imported the tropical birds. Older female macaws frequently lay unfertilized eggs, negating the few shell fragments as sufficient evidence for breeding. Furthermore, 88.8% of the scarlet macaws discovered at Paquimé were under the breeding age (<4 years), with 79.8% of the total falling into the immature age range (4–11 months) (McKusick, 1974). Thus, for a species that can live up to 60 years, the actual number of birds allowed to live to an age suitable for breeding was quite small. Osteological studies demonstrate the majority of the scarlet macaws were sacrificed at or

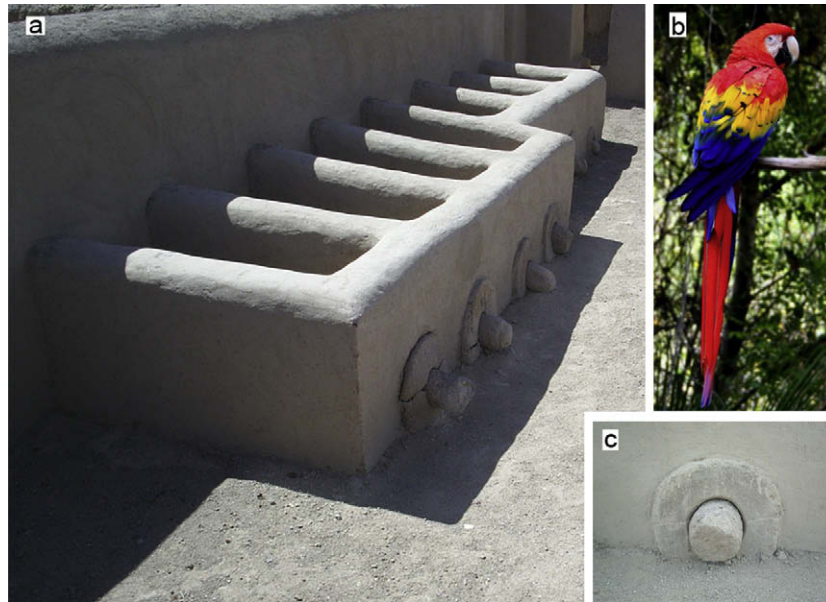


Fig. 2. Pens from Paquimé and the scarlet macaw: (a) Group of adobe pens from plaza 3–12 where most of the macaw burials were recovered. (b) Scarlet macaw (*Ara macao*). (c) Detail of cage-entrance stone from plaza 3–12. Photos by Mary C. Somerville and Andrew D. Somerville.

around the vernal equinox, plucked of their feathers, and interred in formal burials before they could reproduce (Hargrave, 1970; McKusick, 1974). A final bit of evidence that raises questions about Paquimé-bred birds is that macaw remains appear to have been imported to the North American Southwest long before Paquimé was at its height. Chaco Canyon and the Mimbres region of New Mexico saw the first large groups of macaws imported during the period of 1000–1150 AD (Creel and McKusick, 1994). Macaws appear in the Hohokam region as early as 100 AD (Hargrave, 1970), nearly 1200 years before Paquimé's Medio Period. These early cases of macaw keeping imply alternative routes of acquisition. Until this study, it has not been possible to know if scarlet macaws at Paquimé were imported or whether they were locally bred. Before Paquimé is assumed to be the primary parrot supplier for the sites of the North American Southwest, this distinction needs to be made.

The past few decades witnessed the spread of stable isotope analysis as a popular method of reconstructing the diet and movements of animal species across a landscape (e.g. Bowen et al., 2005; Hobson, 1999). For example, researchers have successfully employed stable isotopes to locate natal origins of monarch butterflies (Wassenaar and Hobson, 1998), to reconstruct California gray whale migrations (Killingley, 1980), and to determine subsistence strategies of chimpanzee populations (Schoeninger et al., 1999). Unlike other traded goods, scarlet macaws, as living organisms, contain dietary and environmental information within the isotopic ratios of their bones. If the birds were relocated during life, these isotopic values will reflect the environmental conditions and dietary practices from the original location and contrast with the expected local isotopic signatures. The present study, using carbon and oxygen stable isotope analysis of macaw bone carbonate, examines the macaw keeping practices of Paquimé.

Principles of carbon and oxygen stable isotope analysis

Isotopic analysis of carbonate (CO_3) in biogenic hydroxyapatite [$\text{Ca}_{10}(\text{PO}_4)_6(\text{OH})_2$] is a useful tool in archeology for reconstructing past dietary practices and migrations (e.g. Ambrose and Krigbaum, 2003; Katzenberg and Harrison, 1997; Pate, 1994). Carbonate sub-

stitutes for the phosphate ($-\text{PO}_4$) and hydroxyl ($-\text{OH}$) groups in hydroxyapatite and an isotopic analysis of carbonate provides simultaneous carbon and oxygen isotope data. The carbon isotope ratio of carbon-13 to carbon-12, expressed as $\delta^{13}\text{C}$,¹ is useful in measuring the amount of C_3 , C_4 , and, to a lesser extent, crassulacean acid metabolism (CAM) plant contribution to an organism's diet. Incorporated in the bone mineral during growth and new bone deposition, the $\delta^{13}\text{C}$ apatite ($\delta^{13}\text{C}_{\text{ap}}$) values reflect the average proportions of these plant categories consumed by the organism in life. Plants that utilize the C_3 photosynthetic pathway have relatively negative $\delta^{13}\text{C}$ values, with an average centering around -26‰ (O'Leary, 1988; Smith and Epstein, 1971). Examples of plants included in this category are fruits, nuts, vegetables, shrubs, and grasses from shaded or temperate environments. Plants that utilize the C_4 photosynthetic pathway characteristically have higher $\delta^{13}\text{C}$ values that center around -12‰ (O'Leary, 1988; Smith and Epstein, 1971). New World plants included in this group are dry-adapted grasses, such as maize (*Zea mays*), and several chenopodium and amaranth species (*Amaranthus* sp.). CAM plants have $\delta^{13}\text{C}$ values similar to C_4 plants and include cacti, agave, and arid environment succulents (O'Leary, 1988).

In contrast to $\delta^{13}\text{C}$ values, which can be used to determine paleodiet, the stable isotope ratio of oxygen-18 to oxygen-16, expressed as $\delta^{18}\text{O}$, can aid in determining the past environmental conditions in which an organism lived (Ayliffe and Chivas, 1990; Kolodny et al., 1983; Longinelli, 1984; Luz et al., 1984). In the bone hydroxyapatite of homeothermic organisms the $\delta^{18}\text{O}_{\text{ap}}$ values are correlated with the $\delta^{18}\text{O}$ values of ingested water, which can be either imbibed or consumed with plant material (Longinelli, 1984; Luz et al., 1984). Since captive macaws are known to drink excessive amounts of water, the $\delta^{18}\text{O}_{\text{ap}}$ values will reflect local water sources. Imbibed water is primarily taken from meteoric water sources, which vary with altitude, humidity, temperature, distance from the sea, and latitude (Ayliffe and Chivas, 1990; Poage and Chamberlain, 2001; Yurtsever and Gat, 1981). Generally, the oxygen isotope values in meteoric water ($\delta^{18}\text{O}_{\text{mw}}$) tend to be more positive the closer they are to the ocean, the lower in altitude the source is, the lower the relative humidity in the source location,

¹ $\delta = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1000$ where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{18}\text{O}/{}^{16}\text{O}$.

and the higher the local temperature (Ayliffe and Chivas, 1990; Yurtsever and Gat, 1981). Since these factors differ from region to region and the isotopic ratios are reflected in biological tissue, oxygen isotope studies have been useful in tracking past migrations of fauna and humans (e.g. Hobson, 1999; Killingley, 1980; Knudson and Price, 2007; White et al., 2002).

Expected isotopic signatures in macaws

The natural habitat of the scarlet macaw stretches from the humid lowlands of southern Tamaulipas, Mexico, to Brazil and Bolivia in South America (Blake, 1953; Forshaw, 1973). Across this range, scarlet macaws feed on fruits, nuts, seeds, flowers and tree bark (Abramson et al., 1995; Vaughan et al., 2006), a diet composed entirely of C_3 plants. If the macaws from Paquimé had been born outside of captivity, their $\delta^{13}C$ values would reflect a C_3 diet. If raised in captivity, maize, the staple crop of the Paquimeños and most Mesoamerican groups, would likely have been included in the diet of the macaws. Indeed, veterinarians and macaw breeders today commonly include maize in the diets of their parrots as it is nearly universally accepted by psittacine birds, it is suitable for weaning nestlings, and it provides a sustainable source of nutrition (Abramson et al., 1995; Clubb, 1989). Dried maize can also be stored for long periods of time, providing a steady supply throughout the year. As an analog, recent studies demonstrate that the diet of captive turkeys from Pecos Pueblo, New Mexico contained a large proportion of maize (Kellner et al., in press), illustrating nearby methods of raising captive birds. Palynological investigations of several macaw pens at Paquimé found evidence that squash (C_3), maize (C_4), agave (CAM), and amaranth (C_3/C_4) were potential food items for the scarlet macaws (Di Peso et al., 1974). A similar diet for captive macaws was found during excavations at Pueblo Bonito in northern New Mexico, where remains of piñon nuts (C_3), squash seeds (C_3), and roasted corn-on-the-cob (C_4) were found in association with several macaw remains (Judd, 1954, p. 264). These foods are all unavailable to wild macaws.

Based on differences in elevation, humidity, temperature, and annual precipitation, we assume that the high desert of northern Chihuahua exhibits significantly different $\delta^{18}O_{mw}$ values than the humid lowland forests of the macaw's natural habitat. The Paquimé region is much higher above sea-level (1470 m.a.s.l.), farther from the ocean, and less humid than Mesoamerican sites in contact with scarlet macaws. Consequently, the $\delta^{18}O_{mw}$ from the Paquimé region is significantly more depleted than the humid, lowland Mesoamerican sites that may have supplied the tropical birds. In turn, macaws that drank water from Paquimé are expected to have significantly lower $\delta^{18}O_{ap}$ values than macaws originating in Mesoamerica. The isotopic difference between the highlands and lowlands is indicated by results from the International Atomic Energy Agency's Global Network for Isotopes in Precipitation (GNIP) where a weighted mean $\delta^{18}O_{mw(V-SMOW)}^2 = -4\text{‰}$ in Veracruz and $\delta^{18}O_{mw(V-SMOW)} = -7\text{‰}$ in Chihuahua (IAEA, 2006). Relying on the GNIP data, Bowen and Wilkinson (2002) and Bowen and Revenaugh (2003) use a spatial estimation method of detrended interpolation to predict the geographic variability of $\delta^{18}O$ in precipitation.³ As expected, their calculations indicated that the arid highlands of Chihuahua are significantly more depleted in ^{18}O than the natural range of the scarlet macaw (Fig. 3). Based on their data, an average difference of $\delta^{18}O_{mw(V-SMOW)} = 4\text{‰}$ is expected between the Mesoamerican lowlands and the Chihuahuan highlands. This trend is supported by recent analysis of oxygen isotopes from groundwater

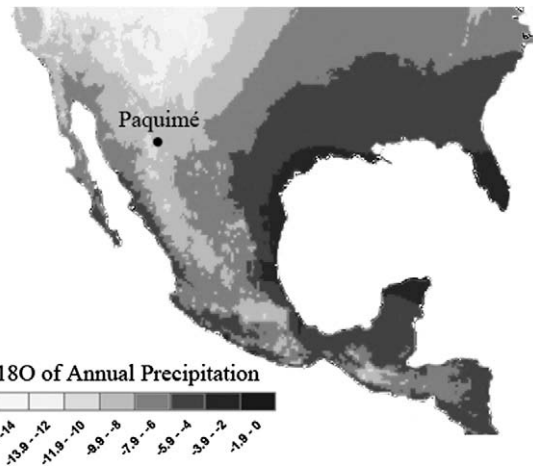


Fig. 3. Map of $\delta^{18}O$ variation in annual precipitation across North America. Precipitation from the humid Mesoamerican lowlands is more enriched in ^{18}O than the arid highlands of Chihuahua. Adapted from Bowen and Revenaugh, 2003 and www.waterisotopes.org.

samples collected from across Mexico (Wassenaar et al., 2009). Wassenaar and colleagues (2009) observe a $\delta^{18}O_{mw(V-SMOW)}$ difference of about 2–4‰ between Paquimé and the natural habitat of the scarlet macaw. Moreover, data produced from our own analysis of water samples collected from North and Central America demonstrate clear isotopic differences between the highlands and lowlands of Mexico. In the Paquimé region, we find a mean $\delta^{18}O_{(V-SMOW)} = -6.3\text{‰} \pm 0.53$ ($n = 9$, 1σ) in river and spring water, while lowland water from Lake Peten Itzá, Guatemala exhibits $\delta^{18}O_{(V-SMOW)} = 2.15\text{‰} \pm 0.02$ ($n = 4$, 1σ). Additionally, Hodell et al. (1995) report an average $\delta^{18}O_{(SMOW)} = 3.24\text{‰}$ from Lake Chicancanab in Yucatan, Mexico. These examples all demonstrate the trend of less negative $\delta^{18}O_{mw}$ values in the southern lowlands and more negative values in the semi-arid highlands.

Although $\delta^{18}O_{ap}$ data are correlated with the meteoric water of the environment in which an organism develops, no attempt was made in this study to correlate the $\delta^{18}O_{ap}$ macaw values with any specific geographic region or archeological site. Macaw physiology is not understood well enough to accurately derive a $\delta^{18}O_{mw}$ value from a $\delta^{18}O_{ap}$ value. Instead, we evaluate the internal patterning of the Paquimé data on the assumption that more negative values will suggest an origin in the Chihuahua highlands and more positive values suggest an origin in a more tropical environment.

Materials and methods

Macaw remains

Scarlet macaws have seven general stages of development (Hargrave, 1970, pp. 3–10; McKusick, 1974, p. 276; Rizo, 1998, pp. 48–52, Table 1). Macaws younger than seven weeks are considered

Table 1
Developmental stages of the scarlet macaw.

Developmental stage	Age range
Nestling	Hatching – 7 weeks
Juvenile	7 weeks – 4 months
Immature	4–11 months
Newfledged	11–12 months
Adolescent (adult I)	1–3 years
Breeding (adult II)	4+ years
Aged (adult III)	Decades old

² Vienna Standard Mean Ocean Water.

³ Bowen and colleagues produced high-resolution global maps of annual $\delta^{18}O$ values, which can be viewed and downloaded at <http://www.waterisotopes.org>.

nestlings. At this young age, the birds are very reliant on adult birds or handlers as their eyes do not open until the 2nd week and their down does not fully develop until the 6th week, leaving them vulnerable to the cold. The second stage of development is the *juvenile* stage, which ranges from 7 weeks to 4 months. According to McKusick (1974), p. 276, in captivity macaws are typically removed from the nest during this stage and hand raised in order to tame the birds. After approximately two months the macaws develop enough feather covering to maintain their body temperature and are thus ready for transportation. The next stage is the *immature* stage (4–11 months). At this time the macaws are as big as their parents, are able to fly, and are capable of feeding themselves (McKusick, 1974; Rizo, 1998, p. 50). Significantly, the long, red tail feathers begin to develop towards the end of the phase. Most of the macaws from Paquimé died during immature stage and McKusick (1974), p. 276 suggests that they were sacrificed at or around the vernal equinox. The macaws receive their full adult plumage during a short interval between the 11th and 12th months of life, a period known as the *newfledged* stage. By the *adolescent* stage, which lasts from the 13th month to the third year, the birds are considered adults but do not yet breed. The *breeding* stage begins by about the 4th year and can last for many decades. Finally, the *aged* stage begins at an unspecified time period when the macaws are old and exhibit osteological manifestations of age, such as “saw-toothed” edges on the parts of the cranium and pelvis (Hargrave, 1970, p. 9). The aged stage lasts until the time of death and scarlet macaws have been known to live for 50–75 years (see Table 1).

For the present study, all macaw bone samples were selected from the archeological collection housed at the Museo de las Culturas del Norte in Casas Grandes, Chihuahua. Although an attempt was made to sample individuals from all stages of development, no juvenile or aged birds are included in the present analysis. A single well-preserved long bone from each macaw (femur $n = 10$; humerus $n = 18$; tibiotarsus $n = 2$) was chosen as the relatively dense cortical bone is expected to better preserve a biogenic signal and to have a slower turnover rate than less dense bones. Turkey vultures, birds of similar size to the scarlet macaw, exhibit a bone turnover half life of >600 days (Fry, 2004) and since the majority of bones selected for this project were from immature macaws (ca. 4–11 months of age), the measured isotope values are expected to represent near lifetime averages.

Analysis

A subset of samples, including the outliers, was tested for diagenetic alteration. Fourier transform infrared spectroscopy (FTIR) was performed at the University of California, San Diego Department of Chemistry and Biochemistry Laboratory to determine the degree of apatite recrystallization by calculating the crystallinity index (CI). The FTIR spectra demonstrated that all measured samples had a CI of less than 3.8, indicating a well-preserved biogenic signal (Shemesh, 1990; Wright and Schwarcz, 1996).

The preparation for carbonate analysis was conducted in the Archeological Chemistry Laboratory at Arizona State University following procedures similar to those of Koch et al. (1997). The bone cortex was cleaned with a mechanical drill and all trabecular bone was removed. Bone from each specimen was finely powdered in an agate mortar and pestle. Fifteen milligrams of powder from each specimen were then reacted in 2% bleach (NaOCl) for 24 h, in 0.1 M acetic acid (CH₃COOH) for 24 h, dried for 24 h at 50 °C, and then analyzed at the W.M. Keck Foundation Laboratory for Environmental Biogeochemistry at Arizona State University using a Thermo MAT 253 mass spectrometer. The samples were reacted with pure phosphoric acid at 70 °C for 6 h, then sampled with a Gas Bench and normalized with NBS-18 and NBS-19. Sample

ACL-0837 was analyzed in triplicate and resulted in a reproducibility of ± 0.04 (1σ) and ± 0.02 (1σ) for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, respectively. Data are expressed using the standard formula $\delta = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1000$ where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{18}\text{O}/{}^{16}\text{O}$ (Coplen, 1994) relative to the V-PDB (Vienna PeeDee Belemnite) and V-SMOW (Vienna Standard Mean Ocean Water) standards (Coplen et al., 1983).

Results and discussion

The macaw bone samples exhibit a range of $\delta^{13}\text{C}_{\text{ap(V-PDB)}} = -7.8\text{‰}$ to -1.1‰ with mean $\delta^{13}\text{C}_{\text{ap(V-PDB)}} = -0.3 \pm 2.0\text{‰}$ ($n = 30$, 1σ). However, when the two negative outliers (ACL-0823 and ACL-0835) are removed, the range becomes $\delta^{13}\text{C}_{\text{ap(V-PDB)}} = -0.6$ – 1.1‰ with mean $\delta^{13}\text{C}_{\text{ap(V-PDB)}} = 0.2 \pm 0.47\text{‰}$ ($n = 28$, 1σ) (Fig. 4; Table 2). Previous studies demonstrated that pre-Hispanic maize has an average value of about $\delta^{13}\text{C}_{\text{PDB}} = -9\text{‰}$ (Hard et al., 1996, p. 268; Schwarcz et al., 1985). In a compilation of multiple feeding studies on laboratory animals, Kellner and Schoeninger (2007) demonstrated that an organism's bone carbonate is enriched in ${}^{13}\text{C}$ by about 9.7‰ relative to its diet (c.f. Ambrose and Norr, 1993; Howland et al., 2003; Jim et al., 2004; Tieszen and Fagre, 1993). This offset is somewhat stable across different species and appears to differ significantly only with ruminants, although more experimental data are needed in this area. Scarlet macaws do not ferment their food and thus should exhibit a similar diet-carbonate offset to previously published mammal values. Consequently, birds that consumed a pure maize diet would be expected to display a measured value of about $\delta^{13}\text{C}_{\text{ap(V-PDB)}} = 0.7\text{‰}$. The macaw carbon values presented here are consistent with a diet composed almost entirely of C₄ foods. Following Schwarcz (1991), the percentage of C₄ in the macaw's diet was calculated using the formula:

$$\%C_4 = ((\delta_3 - (\delta_b - \Delta)) / (\delta_4 - \delta_3)) \times 100,$$

where δ_3 is the assumed end-member $\delta^{13}\text{C}$ value for Paquimé C₃ foods and is here expected to be -25‰ ; δ_4 is the assumed end-member $\delta^{13}\text{C}$ value for Paquimé C₄ foods and is here expected to be -9‰ , which is the average value for archeological maize; δ_b is the measured $\delta^{13}\text{C}_{\text{ap}}$ value from macaw bone; and Δ is the 9.7‰ diet-apatite spacing. The average macaw in our sample subsisted on a diet of 94% C₄ foods. Once the two outliers (ACL-0823 and ACL-0835) are removed, the average percentage of C₄ foods in the macaw diet becomes 97%. This is, however, to be considered a rough estimate due to the uncertainties in the diet-apatite offset for macaws, the unknown exact values for archeological C₃ and C₄ foods at Paquimé, and analytical uncertainty. Nevertheless, the calculation demonstrates the high percentage of C₄ foods, presumably maize, in the diet of the macaws, which contrasts sharply with their naturally available C₃ diet. The stable carbon isotope ratios indicate that the majority of the scarlet macaws from Paquimé had been captive since birth and fed on a diet of readily available maize. However, the two outliers ACL-0823 and ACL-0835 exhibit values of $\delta^{13}\text{C}_{\text{ap(V-PDB)}} = -7.2\text{‰}$ and -7.8‰ , which corresponds to diets composed of about 51% and 47% C₄ plants, respectively – still far from the expected values for wild macaws. These two individuals will be discussed in more detail below.

A second interesting trend is observed in the carbon data. A sorting of the sampled macaws by bone element reveals a significant difference between the $\delta^{13}\text{C}_{\text{ap}}$ values of the humeri and those of the femora (Fig. 5). An independent samples *t*-test demonstrates that the humeri are significantly ($p = 0.017$) more enriched in ${}^{13}\text{C}$ than the femora. The lower limbs of macaws, represented here by the tibiotarsi and femora, are the first bones to ossify as the ability to move and remain upright to feed are critical in the nestling

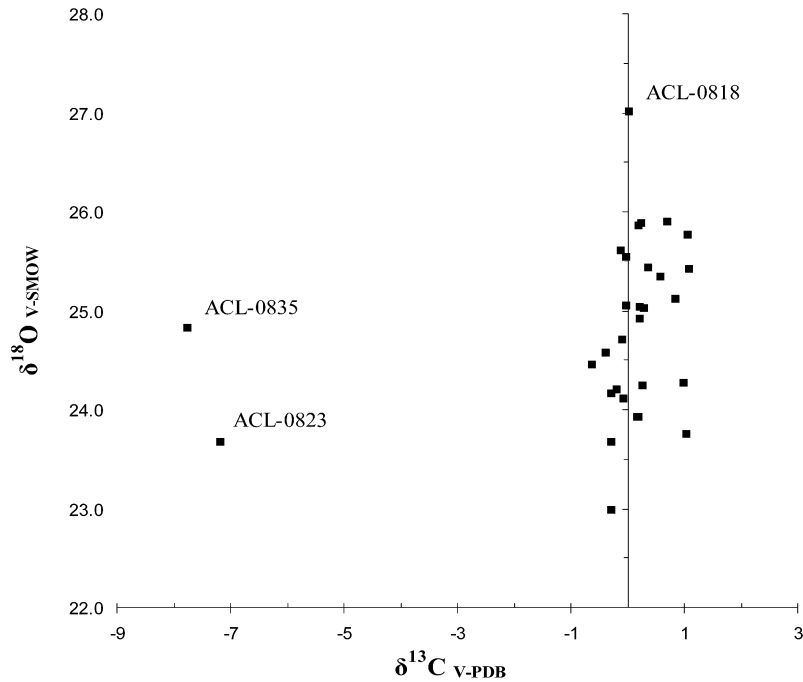


Fig. 4. Macaw carbon and oxygen isotope ratios. The $\delta^{13}\text{C}$ values reflect the relative contribution of C_3 and C_4 plants to the macaws' diet. With the exception of the two negative outliers, the macaws appear to have been primarily C_4 maize consumers. The $\delta^{18}\text{O}$ values reflect the isotopic composition of water imbibed by the macaws. Here, the large range indicates variable fractionation between skeletal elements. Both data sets suggest that the Paquimeños actively bred scarlet macaws. ACL-0818 ACL-0832.

Table 2

Presentation of isotopic data in relation to archeological context and bone type.

Specimen number	Provenience	Age	Bone	Notes	$\delta^{13}\text{C}_{\text{v-PDB}}$	$\delta^{18}\text{O}_{\text{v-SMOW}}$
ACL-0812 CG-240	Plaza 3–12	Immature	Humerus	Multiple burial – 2 scarlet	0.9	25.1
ACL-0813 CG-227	Plaza 3–12	Newfledged	Femur	Single articulated plaza burial	-0.6	24.5
ACL-0814 CG-49	Rm 36–11	Adult II	Humerus	Multiple burial – 3 scarlet, 2 ind macaw species	0.4	25.4
ACL-0815 CG-237	Plaza 3–12	Immature or older	Humerus	Single articulated plaza burial	0.2	23.9
ACL-0816 CG-272–3	Plaza 3–12	Immature	Femur	Multiple burial – 2 scarlet	-0.1	25.6
ACL-0817 CG-258	Plaza 3–12	Immature	Humerus	Multiple burial – 3 scarlet	0.0	25.0
ACL-0818 CG-68	Plaza 6–12	Immature	Tibio tarsus	Multiple burial – 3 scarlet, 1 ind macaw species	0.0	27.0
ACL-0819 CG-46	Rm 36–11	Immature	Tibio tarsus	Multiple burial – 3 scarlet, 2 ind macaw species	-0.4	24.6
ACL-0820 CG-0a	Plaza 3–12	Immature	Humerus	Multiple burial – 5 scarlet, 4 ind macaw species	0.2	23.9
ACL-0821 CG-244	Plaza 3–12	Immature	Femur	Single articulated plaza burial	1.0	23.8
ACL-0822 CG-364.1	Plaza 3–11	Immature	Femur	Multiple burial – 8 scarlet	-0.1	24.1
ACL-0823 CG-0b	Plaza 3–12	Nestling	Humerus	multiple burial – 5 scarlet, 4 ind macaw species	-7.2	23.7
ACL-0824 CG-255	Plaza 3–12	Immature or older	Humerus	Multiple burial – 2 scarlet, 1 military	0.0	25.5
ACL-0825 CG-248	Plaza 3–12	Adult I	Humerus	Multiple burial – 1 scarlet, 1 ind macaw species	0.2	25.9
ACL-0826 CG-305	Rm 2–18 Platform	Immature	Humerus	Multiple burial – 6 scarlet	0.7	25.9
ACL-0827 CG-89	Plaza 3–11	Immature	Humerus	Multiple burial – 3 scarlet, 1 ind macaw species	0.2	25.9
ACL-0828 CG-259	Plaza 3–12	Immature or older	Femur	Multiple burial – 3 scarlet	-3	23.7
ACL-0829 CG-325	Rm (Plaza) 19–8	Adult II	Humerus	Without head; multiple burial – 29 scarlet, 4 military, 1 ind macaw species	1.0	24.3
ACL-0830 CG-257	Plaza 3–12	Immature or older	Femur	Multiple burial – 3 scarlet	0.3	24.2
ACL-0831 CG-267	Plaza 3–12	Immature or older	Femur	Single articulated plaza burial	-0.1	24.7
ACL-0832 CG-319	Rm (Plaza) 19–8	Immature	Humerus	At feet of human burial	-0.3	23.0
ACL-0833 CG-110	Plaza 3–12	Immature	Femur	Single articulated plaza burial	-0.2	24.2
ACL-0834 CG-75	Plaza 5–12	Immature	Femur	Multiple burial – 2 scarlet, 1 ind macaw species	-0.3	24.2
ACL-0835 CG-109	Plaza 3–12	Immature or older	Femur	Multiple burial – 1 scarlet, 1 ind macaw species; buried with Dosinia armet fragment	-7.8	24.8
ACL-0836 CG-79	Plaza 5–12	Immature	Humerus	Single articulated plaza burial	0.3	25.0
ACL-0837 CG-246	Plaza 3–12	Immature	Femur	Single articulated plaza burial	0.2	24.9
ACL-0838 CG-297	Rm 28–8	Immature	Humerus	Single subfloor burial	0.6	25.3
ACL-0839 CG-82	Plaza 3–11	Newfledged	Humerus	Multiple burial – 5 scarlet, 1 ind macaw species, 1 military	1.1	25.4
ACL-0840 CG-70	Plaza 6–12	Adult II	Humerus	Multiple burial – 3 scarlet, 1 ind macaw species	0.2	25.0
ACL-0841 CG-245	Plaza 3–12	Immature	Humerus	Single articulated plaza burial	1.1	25.8

stage of development (McKusick, 1974). Hence, the macaw leg bones exhibit an isotopic signal representative of earlier conditions in the individuals' lives than do bones involved with flight, such as

the humeri. Since the femora values presented here exhibit significantly more negative $\delta^{13}\text{C}_{\text{ap}}$ values than the humeri and because the femora are expected to mineralize before the humeri, maize

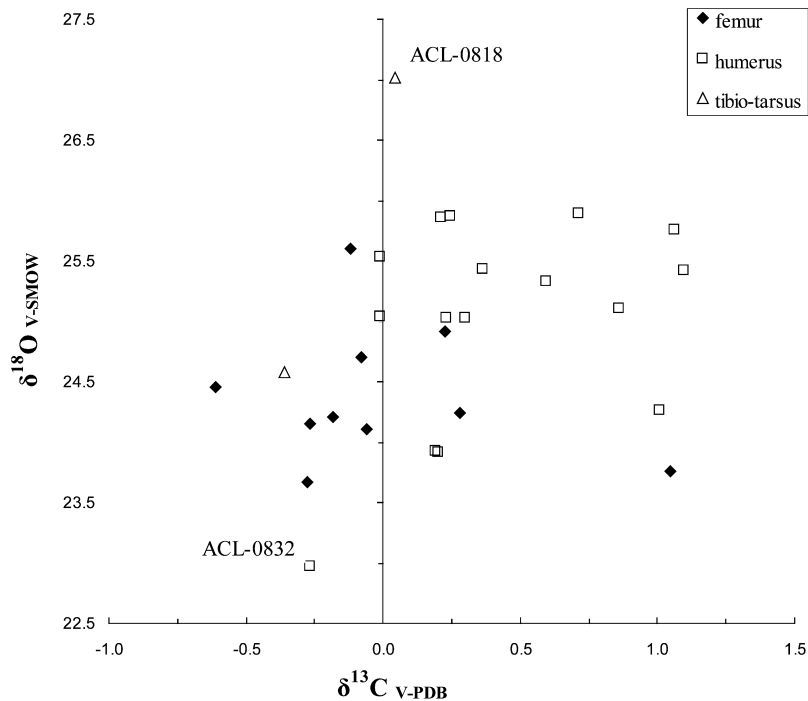


Fig. 5. Graph of macaws sorted by bone element with outliers excluded. The femora, leg bones that ossify early in the macaws' life, are more depleted in both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values than the humeri. The tibiotarsal leg bones should have similar values to the femora. Yet, one tibiotarsus (ACL-0818) exhibits the most positive $\delta^{18}\text{O}_{\text{ap}}$ value of the sample set, suggesting a possible import from the humid lowland forests of Mesoamerica.

appears to have been a much more important element in the diet of the macaws after the nestling period. It is possible that foods with more vitamins and minerals than maize, such as mashed squash, were provided to the nestlings in their first few weeks to months.

The macaw bone samples exhibit a range of $\delta^{18}\text{O}_{\text{ap(v-SMOW)}} = 23.0\text{--}27.0\text{‰}$ with a mean of $\delta^{18}\text{O}_{\text{ap(v-SMOW)}} = 24.8\text{‰} \pm 0.88\text{‰}$ ($n = 30, 1\sigma$; Fig. 4; Table 2). Within this relatively large range, there is no correlation between the $\delta^{18}\text{O}_{\text{ap(v-SMOW)}}$ values and site provenience, burial treatment, or the age of the birds. However, sorting the macaws by bone element once again reveals a difference between the humeri and femora values (Fig. 5). An independent samples *t*-test demonstrates that the humeri are significantly ($p = 0.033$) more enriched in their $\delta^{18}\text{O}_{\text{ap}}$ values than the femora, which mineralize earlier in the macaw's life and reflect environmental conditions during that period. Although the isotopic difference between the humeri and femora might indicate trade and geographic relocation over the lifespan of the macaws, these differences are not consistent with the hypothesis that they were imported from the humid lowland forests of Mesoamerica.

The temporal difference in ossification between the femora and humeri, while causing a bimodal distribution of the oxygen isotope values, is fortunate in that it allows for interpretations to be made concerning the nature of macaw procurement at Paquimé. If the scarlet macaws were kept captive, maize most likely would have composed a large percentage of their diet regardless of their location. That is, macaws raised in captivity in lowland Mesoamerica would probably exhibit similar $\delta^{13}\text{C}_{\text{ap}}$ values to macaws raised at Paquimé. The carbon data presented here is thus not sufficient to demonstrate that the Paquimeños were breeding the macaws instead of importing them. The differences in $\delta^{18}\text{O}_{\text{ap}}$ between the femora and humeri, however, allow the case to be made for local breeding. As discussed above, lowland Mesoamerican water values are expected to be more enriched in ^{18}O than the meteoric water values of northern Chihuahua, and if the macaws were indeed imported from areas near their natural habitat, their femora would

exhibit higher $\delta^{18}\text{O}_{\text{ap}}$ values than the humeri. Here we find that the inverse is true.

Two scenarios may explain this phenomenon. First, scarlet macaws are seasonal breeders that, as Rizo (1998), p. 54 estimates for Chihuahua, would have laid their eggs in February and, following a 28 day period of incubation, the nestlings would have hatched in March. The majority of these birds were then sacrificed about 1 year later on the vernal equinox. This lifecycle corresponds with the seasonal precipitation pattern of Chihuahua where the majority of rain falls during the months of the summer monsoon. This precipitation from June, July, and August is more enriched in ^{18}O than the spring rains of the macaw hatching season (IAEA, 2006; Fig. 6). Since the macaws were born in a season of low $\delta^{18}\text{O}$ values for precipitation and the precipitation was most likely incorporated into drinking water sources, their femora and tibiotarsi, which develop during the nestling phase (McKusick, 1974), would have incorporated these lower $\delta^{18}\text{O}$ values into their bone apatite during mineralization. The humeri, which begin to mineralize several weeks to months later, would exhibit higher $\delta^{18}\text{O}$ values due to the isotopically heavier rains that occurred later in the macaws' lives. This seasonal variability in the $\delta^{18}\text{O}$ values of precipitation in Chihuahua may explain the significantly different $\delta^{18}\text{O}_{\text{ap}}$ values of the macaw femora and humeri. This scenario is probably the more likely of the two.

Secondly, a physiological reason may explain this phenomenon. All parrot species hatch as ectothermic poikilotherms and are unable to control their body temperature for the first few weeks of life (Kattan and Gomez, 1992). In ectothermic organisms, the measured $\delta^{18}\text{O}$ values in bone reflect an organism's body temperature at the time of ossification as oxygen isotopes fractionate with increasing temperature. Under the assumption that more negative bone $\delta^{18}\text{O}_{\text{ap}}$ values indicate warmer body temperature and more positive $\delta^{18}\text{O}_{\text{ap}}$ values indicate colder body temperature (Kolodny et al., 1983), previous studies have tested dinosaur homeothermy by measuring $\delta^{18}\text{O}_{\text{ap}}$ values from bones of the core and of the limbs (Barrick and Showers, 1994, 1995). Although the sampled

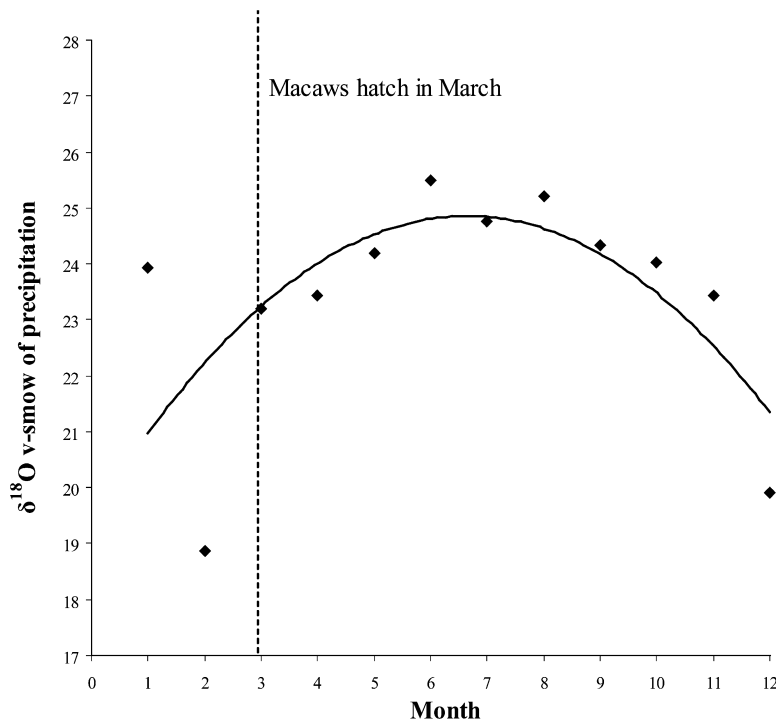


Fig. 6. Graph of average $\delta^{18}\text{O}$ values for monthly precipitation from Chihuahua, Mexico. Dashed line indicates month when the macaws from Paquimé would have hatched. The summer rainy season is more enriched in ^{18}O than the spring months when the macaws from Paquimé would have been born. Data from IAEA GNIP 2006.

dinosaurs were found to be homeothermic, slight inter-bone isotopic variation was discovered; the warmer core regions had slightly more negative $\delta^{18}\text{O}_{\text{ap}}$ values and the more distal limb elements exhibited slightly more positive $\delta^{18}\text{O}_{\text{ap}}$ values. Since nestling macaws do not leave the nest and spend most of their time resting on their hind limbs, the femora are expected to mineralize in warmer conditions than the more exposed and less muscled humeri. Neither of the two explanations presented here support reliance by Paquimé on constant parrot importation from the lowlands of Mesoamerica. Nevertheless, several sampled macaws exhibit unexpected isotope ratios, suggesting a more complicated picture of Paquimé's acquisition and care of scarlet macaws.

Macaw outliers at Paquimé

Macaw specimen ACL-0818, represented by a tibiotarsus, has the most positive $\delta^{18}\text{O}_{\text{ap}}$ value of the sample set. The measured value of $\delta^{18}\text{O}_{\text{ap(V-SMOW)}} = 27.0\text{‰}$ makes this macaw one of two specimens that differ from the population mean by more than two standard deviations (Figs. 4 and 5). As anticipated, the other tibiotarsus (ACL-0819), due to its early ossification, most closely resembles the femora values. Because this bone mineralized early in the macaw's life, the $\delta^{18}\text{O}_{\text{ap}}$ value reflects the water consumed from its nestling location, which due to the relatively positive value, may have been a more southern location. Indeed, the measured value of ACL-0818 is about 3‰ more enriched than the leg bone average, which is within the expected range of difference expected between Chihuahua and the lowlands of Mesoamerica (Bowen and Revenaugh, 2003; Wassenaar et al., 2009). Therefore, ACL-0818 may be a tropical import, although its $\delta^{13}\text{C}_{\text{ap}}$ value indicates a diet extremely heavy on C_4 plants. Perhaps this macaw spent its nestling and juvenile months in Mesoamerica and was traded north to Paquimé when it reached an age suitable for transportation. This $\delta^{18}\text{O}_{\text{ap}}$ value tentatively suggests that the Paquimeños occasionally imported additional macaws from Mesoamerica to supplement their reproducing population.

With a $\delta^{18}\text{O}_{\text{ap(V-SMOW)}}$ value of 23‰, macaw specimen ACL-0832 has the most negative $\delta^{18}\text{O}_{\text{ap}}$ value of the sample set and is the second of two samples that have $\delta^{18}\text{O}_{\text{ap}}$ values more than two standard deviations from the population mean. Moreover, the $\delta^{13}\text{C}_{\text{ap(V-PDB)}}$ value of 0.3‰ is the third most depleted carbon value of the set. Because of these relatively negative isotope ratios, this individual falls far outside the cluster of other humeri (Fig. 5). Notably, this specimen was the only analyzed macaw of the study to have been interred with a human burial. The primary individual was a mid-adult male buried under the plaza of Unit 8 and macaw ACL-0832 was one of seven macaws, two military and five scarlet, that were located at his feet (Di Peso et al., 1974, p. 300, 378). With such a negative $\delta^{18}\text{O}_{\text{ap}}$ value, this macaw is not likely to have been a tropical import. However, it is important to note that other northern Chihuahua sites contained evidence of limited macaw keeping and possible breeding. Minnis et al. (1993) report finding macaw cage-entrance stones at multiple sites in Chihuahua; most were found within a 30 km radius of Paquimé, but several were found in west-central Chihuahua as well. It has been suggested that Paquimé, as the primate center of the regional system, produced the macaws and distributed the feathers and birds to followers in the surrounding environs (Whalen and Minnis, 2001, p. 339). Although far from conclusive, this low $\delta^{18}\text{O}_{\text{ap}}$ value may indicate that macaw ACL-0832 was imported to Paquimé from another highland Chihuahua site that bred parrots, suggesting a complicated picture of macaw movement and trade.

Interestingly, ACL-0835, the most ^{13}C -depleted bird of the sample set ($\delta^{13}\text{C}_{\text{ap(V-PDB)}} = -7.8\text{‰}$) and one of the two major carbon outliers, was the only macaw included in this study that came from a burial with grave artifacts. In fact, only three bird burials from Paquimé contained any sort of offering (Di Peso et al., 1974, p. 296). This multiple burial included the remains of one indeterminate macaw and the analyzed scarlet macaw. A dosinia armlert fragment, made of marine shell imported a great distance from the coast, was found within the burial (McKusick, 1974). Perhaps at an early age this macaw was chosen for a specific ritual sacrifice

and fed a special diet consisting of foods other than maize. Alternatively, this macaw may have been a tropical import from Mesoamerica where it would have consumed more C_3 plants. Yet, its $\delta^{18}O_{ap(V-SMOW)}$ value falls close to the mean of the sample set, providing no evidence for a Mesoamerican origin.

The second major carbon outlier, ACL-0823, was the only nestling (hatching–7 weeks) bird included in this study. The measured value of $\delta^{13}C_{ap(V-PDB)} = -7.2\text{‰}$ indicates that, like ACL-0835, this macaw had a diet much less dependent on C_4 plants than the rest of the population. It is not likely that this nestling was traded from the humid lowlands as its feathers would not yet have developed and its body temperature would be difficult to control during the long over-land journey (McKusick, 1974). Instead, this low value may reflect different feeding practices for nestling birds. As discussed above, the $\delta^{13}C_{ap}$ data from sampled femora suggest that nestlings had access to a wider variety of foods than did the older macaws. As one of the youngest macaws excavated from Paquimé, ACL-0823 is the most representative example of the nestling and juvenile diet. Although the greater inclusion of C_3 foods in this individual's diet may suggest a Mesoamerican origin, the measured $\delta^{18}O_{ap}$ value plots on the more negative end of the sample spectrum, which would not be expected of a tropical import. Thus, this macaw was probably local but, like most of the nestlings from Paquimé, had not yet been fed a pure maize diet.

Conclusions

Iconographic sources show that Mesoamerican peoples placed high value on the scarlet macaw as early as the first millennium BC. At Paquimé, lying outside of Mesoamerica, the ritual importance of the scarlet macaw is suggested by its representation on polychrome ceramics and frequent sacrifices at a young age, often paired with military (green-feathered) macaws (Creel and McKusick, 1994; Di Peso et al., 1974; Hargrave, 1970; McKusick, 1974). Leaders in a regional center remote from the tropical lowlands such as Paquimé could have imported macaws routinely, but the $\delta^{13}C_{ap}$ and $\delta^{18}O_{ap}$ data from the sampled macaw bone carbonate support the hypothesis that the Paquimeños went further, actively breeding scarlet macaws so that they did not have to engage in trade to acquire the tropical birds. Within a prestige goods economy, the act of reproducing the birds for their ritually and socially valuable feathers can be seen as a form of import substitution. Economists view import substitution as a strategy whereby local production takes the place of importation, increasing the efficiency of both production and distribution (Oka and Kusimba, 2008, p. 361). In the case of Paquimé, this process also had the effect of extending the range of the scarlet macaw species to an area outside of its natural habitat. Even before Paquimé formed as a regional center, people in the American Southwest had adopted the ancient Mesoamerican practice of using scarlet macaw feathers in ritual practices. The Paquimé breeders extended the infrastructure for raising the birds to Northwest Mexico and were probably themselves agents of trade who increased the availability of the feathers and the birds in the North American Southwest. They were also among the most avid consumers of these products anywhere in Northern Mexico or the American Southwest.

Helms (1993) observes that leaders in many societies legitimize their power by controlling production or acquisition of exotic materials with special properties that have sacred symbolic connotations. Frequently the raw materials are obtained from great distances, and Helms argues that the ability to connect with distant sources may in itself be a demonstration of power. The extensive breeding program at Paquimé may have been fueled by competition between local kin groups and aspiring elites to constitute social power through the production of exotic symbols related to

distant, watery places. The ability to produce colorful feathers for gifts or personal adornment and the spectacle involved in sacrificing the macaws to bring the dry season to an end would have provided great social legitimacy to those responsible for group well-being at Paquimé. One sample (ACL-0818) provides evidence that a few macaws were imported to supplement ongoing parrot breeding at Paquimé, simultaneously maintaining a physical connection with the place of the birds' origin. Scholars have debated whether Paquimé's exchange was controlled by agents of distant empires (Di Peso et al., 1974) or was an independent enterprise (Minnis, 1989). Our evidence suggests independence but continued connection with distant sources of symbolically important resources.

The carbon isotope data from this study adds clarity to inferences already made about the care that the macaws were given in captivity from the bones, cages, feces, and eggshell fragments. As nestlings, the birds had access to more C_3 foods, but, soon after, their diet was limited to almost exclusively C_4 foods, presumably maize. This suggests a tradition of macaw keeping at Paquimé where specialists were familiar with the needs of the parrots and put them on a pure maize diet only after the delicate nestling phase of development. Although the observed variation in $\delta^{18}O_{ap}$ values can be explained by climatological or physiological reasons, further studies of strontium isotope analysis will provide a clearer picture of the trade and breeding practices of scarlet macaws in Northwest Mexico and the North American Southwest.

This study lends weight to the more general inference that humans had an active role in altering species distributions long before the industrial age. Indeed, humans have been translocating animal populations intentionally and unintentionally since at least the Pleistocene (Grayson, 2001). While not an example of the introduction of a species that could survive autonomously, this case demonstrates the human capacity to alter distributional boundaries without the benefit of mechanized transportation or modern animal science. This is significant as large-scale modern macaw breeding was not possible until the 1970s due to the difficulty of sexing the birds (Rizo, 1998). Finally, this study highlights the importance of using the same bone element for studies of migration and mobility as dietary, climatological, and physiological changes through the organism's life can significantly alter the intra-skeletal isotopic values.

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