

Pre-Columbian transregional captive rearing of Amazonian parrots in the Atacama Desert

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The feathers of tropical birds were one of the most significant symbols of economic, social, and sacred status in the pre-Columbian Americas. In the Andes, finely produced clothing and textiles containing multicolored feathers of tropical parrots materialized power, prestige, and distinction and were particularly prized by political and religious elites. Here we report 27 complete or partial remains of macaws and amazon parrots from five archaeological sites in the Atacama Desert of northern Chile to improve our understanding of their taxonomic identity, chronology, cultural context, and mechanisms of acquisition. We conducted a multiproxy archaeometric study that included zooarchaeological analysis, isotopic dietary reconstruction, accelerated mass spectrometry radiocarbon dating, and paleogenomic analysis. The results reveal that during the Late Intermediate Period (1100 to 1450 CE), Atacama oasis communities acquired scarlet macaws (Ara macao) and at least five additional translocated parrot species through vast exchange networks that extended more than 500 km toward the eastern Amazonian tropics. Carbon and nitrogen stable isotopes indicate that Atacama aviculturalists sustained these birds on diets rich in marine bird guano-fertilized maizebased foods. The captive rearing of these colorful, exotic, and charismatic birds served to unambiguously signal relational wealth in a context of emergent intercommunity competition.

Atacama desert | exchange | feathers | relational wealth | tropical birds

ne of the most pervasive and unambiguous material symbols of prestige, wealth, and spiritual status in the pre-Columbian Americas were long, slender, and brightly colored feathers often worn in elaborated headdresses (1-4). Feather use and its representation in iconography is recurrently found as a marker of leadership and association with divinity from incipiently stratified communities to consolidated empires (5, 6). In the Andes, the colorful feathers of tropical parrots were often imported from the eastern Amazonian tropical forests by littleunderstood mechanisms of exchange and trade (7-9). Although many feathers were transported and maintained in special containers, some tropical birds might have been taken and moved across the Andes alive. The archaeological finding of actual tropical macaws and amazon parrots in specific ritual and funerary contexts provides a unique opportunity to explore the origin of these birds and the management strategies related to their procurement, handling in captivity, and ceremonial interment. Here we reconstructed some of these practices by conducting a multiproxy study involving direct accelerated mass spectrometry (AMS) radiocarbon dating, stable isotope analysis, and paleogenomic sequencing of an assemblage of macaw and amazon parrot remains recovered from archaeological sites located in the Atacama Desert of northern Chile.

The Atacama Desert provides remarkable conditions for the preservation of organic materials such as bone, tendons, muscles, skin, and feathers (10–12). The evidence associated with the preservation and use of tropical bird feathers in this region has

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been a topic of recurrent discussion regarding the nature of the social interaction between societies located on both sides of the Andes (8, 13). The Andes were not the only place where these birds and their feathers were widely circulated. Scarlet macaws (*Ara macao*) were transported and held captive for feathers to mark status and for ceremonial purposes by Ancestral Pueblo, Mimbres, Paquimé, and other pre-Hispanic societies across the arid southwestern US and northwestern Mexico (14–16). Moreover, recent technical advances in the study of the pre-Columbian avicultural practices open up a series of possibilities for improving our understanding about ancient social, economic, and religious practices in the Americas, as well as of animal husbandry, procurement strategies, feeding ecology, and biogeography of tropical bird species that are presently threatened (17–19).

Feathers and Parrots in the Atacama Desert

Well-preserved red, yellow, blue, and green feathers of parrots and other vibrantly colored neotropical birds from the Amazon are relatively common in Atacama Desert archaeological assemblages. Feathered headdresses and ritual garments are found in cemetery contexts and in dry rock shelters, and their presence has been used to infer interregional movement, interaction, and trade between the Pacific coast and the tropical lowlands of the

Significance

The brightly colored feathers of macaws, amazons, and other neotropical parrots were one of the most important symbols of wealth, power, and sacredness in the pre-Columbian Americas. Andean highland and coastal societies imported these exotic goods from Amazonian tropical forests by little-understood mechanisms of exchange. The study of 27 complete and partially mummified and skeletonized remains of at least six species of parrots from five archaeological sites in the Atacama Desert of northern Chile provides evidence that capturing, transporting, and keeping macaws, amazons, and conures as pets was part of this provisioning system, likely motivated by their significance for producing and representing relational wealth.

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eastern Andes (20, 21). Some of the earliest contexts that bear tropical bird feathers correspond to the late Chinchorro mummy complex that emerged during the middle Holocene, ~5,500 y ago (22). For instance, red, yellow, blue, and green feathers were found in elaborate headdresses at the late Archaic Period site of Camarones 15 (23). The occasional presence of bird feathers continued throughout the Formative Period (1000 BCE to 500 CE), generally in association with high-status burials. For instance, parrot feathers have been reported from the villages and cemeteries of Caserones, Caleta Huelén 42, Tarapacá 40, and Topater Cemetery 1 (24, 25). Similarly, in sites linked to the epoch when the highland Tiwanaku State (500 to 1100 CE) maintained certain interaction with coastal Pacific valleys (e.g., Azapa 6, Azapa 71, Azapa 75, Azapa 141), macaw feathers often occur as part of high-status regalia such as gowns in elaborate

burials (26, 27). Tropical feathers became progressively more frequent throughout the Atacama Desert during the Late Intermediate Period (1100 to 1450 CE) in connection with increased reliance on interregional movement facilitated by llama caravans that connected a vast web of dispersed communities settled along the coast, valleys, and quebradas toward the eastern Andes and beyond (28–30). The increased incidence of tropical feathers along with hallucinogenic paraphernalia and other exotic goods suggest that the Late Intermediate Period featured complex regional trade and communication networks that included nodes in oases, such as Pica, Chiu-Chiu, and San Pedro de Atacama (31). During the Late Horizon (1450 to 1532 CE), the Inca enhanced the use of feathers as unequivocal markers of social, religious, and political status.



Fig. 1. Location of Pica 8 and other archaeological sites from northern Chile where parrot remains have been identified in relation to the distribution of the six represented species. Modern species distributions (courtesy of BirdLife International) are noted in different colors: scarlet macaw (red), blue-and-yellow macaw (blue), mealy amazon (green), yellow-crowned amazon (yellow), blue-fronted amazon (cyan), and mitred conure (orange swath). Segmented gray lines are possible movement routes as derived using path and cost distance tools in ArcGIS Pro (*SI Appendix, Extended Methods 1*). Species distribution maps data from ref. 36. Bird images credit: Carlos Capriles Farfán (photographer).

Located in the hyperarid core of the Atacama Desert, Pica is an oasis that became a central node for interregional llama caravan traffic prior to the Inca conquest (8, 32). Pica 8 is a cemetery site that contains an exceptional record of human burials associated with incredibly preserved and diverse organic offerings. The site is approximately 0.5 hectare in size and, although some of its tombs had been looted since at least the 19th century, ~269 well-preserved tombs distributed in 10 sectors were systematically excavated between 1963 and 1965 (33, 34). A recent analysis of paired samples of human and textile fragments for radiocarbon analyses verified that the site was mostly occupied between 900 and 1400 CE (35). Furthermore, stable isotope data suggest that the cemetery included a diverse community of individuals who consumed a wide range of resources that originated



Fig. 2. Mummified parrots from the Atacama Desert. (A) Scarlet macaw recovered from Pica 8 (PI-8-1047). (B) Scarlet macaw recovered from Pica 8 (PI-8-1046). (C) Blue-fronted amazon recovered from Pica 8 (PI-8-1206). (D) Scarlet macaw recovered from Pica 8 (PI-8-0248). (E) Subadult blue-and-yellow macaw recovered from Pica 8 (PI-8-0651). (F) Scarlet macaw recovered from Pica 8 (E2-B2); note the leather strap around its feet. (G) Scarlet macaw head recovered from Camarones 8 (MASMA-1/20107/87).

from the coast, oases, and even highlands, emphasizing the site's regional importance as an interregional exchange node (29).

An initial inventory of materials recovered from the 1960s excavations at Pica 8 included at least 35 artifacts containing feathers (34). Tropical feathers were present in containers, arrow fletching, ornaments, garments, hats, and headdresses. Most remarkably, this collection included eight mummified macaws and amazon parrots deposited as part of funerary offerings, and since then, additional bird remains have been found in Pica as well as other Atacama Desert sites. Between 2015 and 2017, we conducted visits to regional museums and research collections in northern Chile to quantify the archaeological presence of tropical feathers and birds outside of their native ranges and to improve the taxonomic and contextual description of these remains. As part of this work, we completed a multiproxy archaeometric study from a sample of these bird remains to advance our understanding of their chronology, origin, and diet, as well as the interregional exchange networks, management strategies, and ritual behaviors underlying the circulation and deposition of tropical birds in the South Central Andes during pre-Columbian times.

Results

Taxonomic Identification. We documented 27 neotropical parrot (Psittacidae, Arinae) remains from five sites located in the Atacama Desert of northern Chile (Fig. 1) and deposited in at least seven different repositories in Chile and the US (SI Appendix, Table S1). Of these, 14 were either complete or semicomplete mummified specimens (including two that had their heads removed), two nearly complete skeletons, six mummified heads, and five isolated bony beaks (premaxillae) (SI Appendix, Table S2). We were able to directly study 23 of these remains and sample 15 of them, most of which were from the Pica 8 site. The preservation of individual birds varied a great deal, and while there were remarkably well-preserved specimens, likely enhanced by the compositional hardiness of parrot feathers (37), there were also guite damaged ones certainly affected by postdepositional processes and, to a lesser extent, recovery and manipulation (Fig. 2).

Based on a combination of traits, including size of different bones (especially the cranium), but mainly their preserved plumage, we were able to identify these birds to various degrees of taxonomic specificity. At the genus level, the collection includes the remains of 16 macaws of the Ara genus, nine amazons of the Amazona genus, and two conures of the Psittacara genus. At the species level, nine specimens were identified as scarlet macaws (Ara macao) and one was identified as a blue-and-yellow macaw (Ara ararauna), and it seems very plausible that many of the unidentifiable macaws represented by mostly osteologic remains (such as premaxillae), also correspond to scarlet macaws. Specific amazon species included four blue-fronted amazons (Amazona aestiva), two mealy amazons (Amazona farinosa), one yellow-crowned amazon (Amazona ochrocephala), and two indeterminate specimens, which could add the scaly-naped amazon (Amazona mercenarius) to the list, among other species. Finally, two specimens corresponded to mitred conures (*Psittacara mitratus*). There were at least two subadult individuals, including the blue-and-yellow macaw and an identifiable macaw, but the rest of the birds were likely adults.

In terms of their interment, most birds were placed in direct association with human burials, but some did not have good contextual information, as they were recovered as incidental or salvage findings. Many of the well-preserved mummified birds evidenced evisceration, removal of tails including the pygostyle (fused caudal vertebrae that support the tail), and wrapping or bagging in textiles (Fig. 2). Most specimens were left in a resting position with their wings and legs contracted, but some were placed in quite elaborate stances, including forcefully opened beaks with tongues sticking out. This was most common in isolated amazon heads, suggesting an elaborate and likely ritualized mummification process. Two birds had evidence of leather straps on their legs, three had the tip of their beaks cut off, and many had evidence of clipped or plucked wings or feathers while alive. One bird had an overgrown beak, and some birds had evidence of overgrown claws, possibly a consequence of lack of wear and a nutritional deficiency. One scarlet macaw skeleton had healed fractures in the radius and ulna. Nearly all the birds with preserved soft tissue had evidence of excessive down feather buds, which is symptomatic of excessive plucking.

Carbon and Nitrogen Stable Isotopes. Carbon and nitrogen stable isotopes were analyzed from 14 birds from Pica 8, one bird from Camarones 8, and a feather from a tabard recovered from Azapa 6 to examine dietary diversity within the assemblage and the potential origin of the birds (SI Appendix, Table S3). Specifically, we obtained results from 21 samples (including five paired samples) that consisted of eight wing feathers, five body feathers, one head feather, three soft tissue samples, two vertebrae, and two ribs. Values of δ^{13} C and δ^{15} N standardized to collagen (38) sorted by taxa and overlying human remains from Pica 8 (35) and Camarones 8 (39) showed a wide dietary diversity, which can be summarized in three nonoverlapping groups (Fig. 3). The first group is characterized by low $\delta^{13}C$ (mean \pm SD, $-18.5 \pm 0.8\%$); n = 3) and low δ^{15} N (mean \pm SD, $8.9 \pm 0.5\%$) and includes a mealy amazon bone, a scarlet macaw bone, and a scarlet macaw feather. A second group features relatively high $\delta^{13}C$ (mean \pm SD, $-9.1 \pm 1.2\%$; n = 3) and low $\delta^{15}N$ (mean \pm SD, 8.8 \pm 1.0%) and consists of two samples of soft tissue of a mitred conure and the scarlet macaw feather from the Azapa 6 tabard. Finally, the third group consists of both very high δ^{13} C (mean \pm SD, $-6.6 \pm 1.4\%$; n = 15) and δ^{15} N (mean \pm SD, $21.7 \pm 3.3\%$) and includes three blue-fronted amazon feathers, a feather and bone of an indeterminate amazon, two blue-and-yellow macaw



Fig. 3. Carbon and nitrogen stable isotopes of the studied species. Circles represent feathers; squares, bone collagen; and triangles, soft tissue. All values were standardized to collagen (38). Dashed lines correspond to paired samples from the same individual birds, and significant differences between some specimens could be related to drastic dietary changes resulting from geographic translocation and management (*SI Appendix, Extended Methods 1*). Human remains stable isotope data of Pica 8 are from ref. 40 and those of Camarones 8 are from ref. 39.

on December 28.

feathers, six scarlet macaw feathers, a scarlet macaw bone from Camarones 8, and a Pica 8 scarlet macaw soft tissue.

Radiocarbon Dates. We analyzed 21 direct AMS radiocarbon dates to determine the chronology associated with the studied birds. A Bayesian phase sequence model incorporating 17 dates from Pica suggests that the mummified parrots were deposited between 1251 to 1376 and 1424 to 1484 CE (*SI Appendix*, Fig. S1). The Camarones 8 scarlet macaw (1230 to 1296 CE) overlaps with the beginning of this phase, but the Azapa 6 tabard (1156 to 1218 CE) and a mitred conure from Pica (994 to 1151 CE) are a few centuries older (*SI Appendix*, Table S4). Thereafter, there seems to be a sequential but cumulative process of deposition at Pica, albeit with most birds deposited during the latter portion of the sequence.

Archaeogenomics. The archaeogenomic component of our study was designed to examine phylogenetic relationships between the Atacama macaws, improve our taxonomic identifications based on morphological characters, and potentially reveal some of the management strategies involved in the capture and circulation of these birds. We decided to focus our genetic study on the scarlet macaws because they were the most common taxon, and also because we could rely on previous archaeogenomic work conducted on this species in the southwestern US (17). Specifically, we assessed the maternal relationship to determine whether these birds had single or multiple proveniences, to identify potential breeding colonies, and to characterize the range of variation within our sample by comparing it with modern reference specimens.

The four complete mitogenome sequences support the A. macao taxonomic identification and a Bayesian phylogenetic tree indicated that all four sequences cluster with the A. m. macao subspecies that is currently distributed in South America (Fig. 4). All four sequences were also identified as part of Haplo4, the only known haplogroup distributed across the Amazon and South America in general (*SI Appendix*, Table S5). Furthermore, the four specimens correspond to unique haplotypes within this haplogroup, suggesting significant heterogeneity and potentially diverse source populations, but these results are hampered by our small sample size and the complex genetic diversity of haplo4 (SI Appendix, Fig. S2). We ran permutation analyses to test whether there were significant differences in nucleotide diversity and haplotype frequency between the Atacama group and modern geographic reference groups (SI Appendix, Table S6). The results suggest that the Atacama nucleotide diversity is nominally higher than that of all other reference groups, but there is no significant difference between the groups after 1,000 permutations. Our ancient results support the demographic scenario that South American scarlet macaw populations are more stable and less divergent than those of Central America (44). However, we note that these results could be a product of multiple origins from entry points along the Andes Mountain ranges in Peru and Bolivia. The relatively high genetic diversity in the Atacama sample is an aspect that merits further research.

Discussion

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Based on the identification of 27 complete or partial bird remains from five different archaeological sites, we verify pre-Columbian complex transregional circulation, captive rearing, and ritual use of translocated neotropical macaw and amazon parrots in the Atacama Desert of northern Chile. Their associated archaeological context suggests that highly elaborate and ritualized mummification processes were carried out at the time of their death and interment. In particular, all birds from known provenience were found in funerary contexts, some either wrapped or bagged in textiles and most placed in specific positions, including resting or with their beaks wide open. Of the well-preserved mummified birds, most were eviscerated and had their tails removed as well as many other primary and secondary feathers, likely saved for making ritual artifacts.

Nearly all well-preserved birds were covered by down feather buds, suggesting that they were plucking themselves, possibly as a stress or disease symptom, or that they were frequently plucked by their owners. Our preliminary survey of museum collections and published literature suggests that tropical bird feathers are present in nearly 30 sites in the Atacama Desert. A possible sign that some of these feathers were harvested locally is the faded color of some feathers, such as the reds of the scarlet macaws. More than a postdepositional process, this was likely caused by nutrient deficiency, such as a deficit of beta-carotene. Together, this evidence suggests that maintaining the birds while alive involved various practices, such as strapping their feet, plucking their feathers, and sometimes even breaking their wings. However, human care is also observed in the clipping of their overgrown beaks and claws as well as healing of their fractures, underscoring the complexity of avicultural practices and human-bird interactions.

Direct radiocarbon dating verified that the that these birds were translocated and interred during the Late Intermediate Period (1100 to 1450 CE). This interval brackets the period between the disintegration of the Tiwanaku state and the incorporation of this region into the expanding Inca Empire (45–47). Certainly, this is the period during which caravanning and interregional interaction flourished in the Atacama Desert's oases and elsewhere in the South Central Andes (28–31, 48). The oldest samples dated in the sequence are a mitred conure from Pica and a scarlet macaw feather from the Azapa 6 tabard. The latter is contemporaneous with other dates from this cemetery, initially thought to date to the regional expansion of the Tiwanaku state (26) but that actually might correspond to the period immediately after its disintegration (49).

Our ancient DNA results verify the possibility of extracting and sequencing molecular data from the Atacama tropical parrots. Although we were able to reliably sequence only four ancient mitogenomes, the results verified the potential for making interspecific taxonomic identifications as well as assessing intraspecific variation. Specifically, all the sequenced scarlet macaws align with the South American *A. m. macao* subspecies and represent different haplotypes within the South American haplo4 haplogroup, suggesting that the translocated scarlet macaws might have originated from different populations and geographic locations.

Although the scarlet macaw, an iconic species for pre-Columbian societies across the Americas, was the dominant species in the assemblage, at least five other parrot species were represented. Like the scarlet macaw, the yellow-and-blue macaw, the mealy amazon, and the yellow-crowned amazon are ecologically distributed in tropical forests and savannas located several hundred kilometers to the northeast of the Atacama Desert (50, 51). In contrast, the mitred conures, and to a lesser extent the blue-fronted amazons, are native to the dry valleys east of the Andes, where they typically prey on agricultural maize fields (51). Nevertheless, all these birds had to be transported across what today is the Bolivian Altiplano (Fig. 1). The nearest region where all six species are sympatric is the foothills of the eastern Andes between the Bolivian departments of Beni, La Paz, and Cochabamba. Taking Pica 8 as the reference point, this region is >500 km toward the northeast, but a least cost model suggests that the most efficient pathway to the modern distribution of the yellow-crowned amazon extends ~900 km away. Although llama caravans can travel as much as 25 km per day, longer journeys require longer breaks, and ethnographic records suggest that a 400-km journey could take as long as 2 to 3 mo, suggesting that multi-month trips were required for the direct procurement of these birds (52-54). The natural sturdiness and adaptability of parrots would have been critical attributes helping them endure and survive over these extended journeys (55). Nevertheless, it is



Fig. 4. Complete mitogenome phylogenetic relationships among four ancient Atacama macaw haplotypes; a single ancient *A. m. cyanoptera* from Pueblo Bonito, NM; closely related extant *Ara* species; and a *Primolius couloni* outgroup member (*SI Appendix*, Table 57). The Atacama scarlet macaws cluster within the South American *A. m. macao* clade and differ from other extant species, including *A. m. cyanoptera*. All sequences were aligned using multiple alignment fast Fourier transform (41), and the best nucleotide substitution model was determined using jModelTest (42). The unpartitioned Bayesian consensus tree was created in BEAST2 (43) using the Markov chain Monte Carlo method (HKY+I+G with four gamma-distributed rate categories) and 10 million generations, enforcing a relaxed molecular clock parameter. The phylogeny represents all alienable positions with gaps and missing positions included in the analysis. Bayesian posterior probabilities are displayed at major branch nodes (>0.7). Haplogroup designations correspond to groups reported in ref. 44.

likely that these birds were procured from various regions using different routes and also through different mechanisms, including indirect procurement and down-the-line trade, as supported by the documented interspecies and intraspecific diversity. Until the beginning of the 20th century, the people of Pica traded parrots and monkeys with traveling traders from eastern Bolivia that were often kept as pets in their homes or in a small zoo in the central square of this oasis village (56).

Managing the diet of these allochthonous birds was critical for facilitating their transregional transportation and captive rearing. Based on carbon and nitrogen stable isotopes, three different dietary groups were identified among the studied specimens. A first group included low carbon and nitrogen values, which is the expected signature for a diet based on seeds and fruits from C_3 tropical vegetation (57). A second group included birds with low nitrogen values and high carbon values, suggesting the consumption of C₄ plants such as maize (16) and corresponds with the two oldest radiocarbon-dated specimens of the assemblage. The third and final group includes both high carbon and nitrogen values and although the high δ^{13} C values strongly suggest the consumption of maize, the extremely high $\delta^{15}N$ values are indicative of very high trophic level positioning through the potential consumption of marine foods. Given that neotropical parrots are primarily frugivores and granivores (55), the consumption of marine resources is unlikely. Furthermore, whereas a few wild edible plants from the hyperarid Pacific desert coast (around 90 km to the west) have a relatively high carbon and nitrogen isotopic composition, it is unlikely that consuming these plants alone could produce the observed extreme values (58). A more plausible explanation is that these birds were fed cultigens and specifically maize fertilized using marine bird guano, as has been documented historically (10) and verified by isotopic studies on plant remains and human populations buried in coastal and desert pre-Columbian cemeteries, including both Pica 8 and Camarones 8 (39, 58–60).

Isolated remains of macaws and parrots have been documented in a broad range of funerary and other ritual contexts across the Andes (61-64). Nevertheless, the Atacama Desert archaeological evidence suggests a pre-Columbian procurement system of tropical parrots potentially comparable to that observed in the ancient southwestern US (14, 18). However, the reduced genetic diversity of the archaeological scarlet macaws from Chaco Canyon suggests that most birds were procured from a single breeding colony, likely as an effect of the strong religious hierarchical system that strictly controlled the circulation of ritual goods (17). In contrast, the diversity of translocated tropical birds represented in the Atacama Desert assemblages suggests that emerging regional elites participated in and promoted exchange networks extending into the tropical forests powered by llama caravans to enhance their relational wealth. In this sense, while it is certainly possible that many of the studied birds were acquired from a single but highly diverse region, it seems more likely that these tropical birds originated from multiple geographic locations embedded in a complex network of prestigious good circulation that connected the communities of the Atacama Desert with those of the highland Andes, Amazonian tropics, and beyond.

Conclusions

The combination of zooarchaeological analysis, dietary stable isotopes, AMS radiocarbon dating, and ancient DNA analysis is a powerful approach for addressing complex questions regarding ancient animal utilization, biogeography, species translocation, and even domestication. In the case of birds, this approach has been successfully applied to identify the ecological niche of the passenger pigeon (Ectopistes migratorius) (65), reconstruct the past distribution of the sacred ibis (Threskiornis aethiopicus) (66, 67), differentiate the various species of wild and domestic turkeys (Meleagris gallopavo) (68-70), and determine whether red jungle fowl (Gallus gallus) or pheasants (Phasianus colchicus) were present in northern China during the Neolithic (71, 72). Here we applied this multiproxy approach to study an assemblage of neotropical parrots (Psittacidae, Arinae) from the Atacama Desert of northern Chile.

The preserved remains of 27 complete and partial parrots from five different archaeological sites verifies that at least six different species were taken from >500 km to the east in the tropical lowlands of what is present-day Bolivia. These macaws, amazons, and conures were successfully captured and transported across the Andes by means of extensive caravan trade networks during the Late Intermediate Period (1100 to 1450 CE), and they were kept alive in agricultural villages in the hyperarid desert conditions of the Atacama Desert as living producers and reproducers of social and religious prestige. Scarlet macaws were the dominant species in the assemblage, and given their genetic diversity, they might have originated from different populations and breeding colonies, underscoring the importance of decentralized procurement strategies for accessing tropical birds by the emerging consumer elites in the oases of the Atacama Desert.

Materials and Methods

We analyzed bird remains from the site of Pica 8 and additional sites from the Atacama Desert of northern Chile. Direct zooarchaeological examination of each bird specimen was carried out to determine the most specific taxonomic identification possible, as well as any information about human care and interment. Following the description of the specimens, we collected available feather, dry soft tissue (e.g., dry skin, muscle), or bone specimens for archaeometric studies. Pretreatment for radiocarbon and stable isotope analyses were carried out at The Pennsylvania State University (PSU) Human Paleoecology and Isotope Geochemistry Lab (SI Appendix, Extended Methods 1). Desiccated soft tissue and keratinous feather samples were processed using a series of acid-base-acid treatments, whereas bone collagen was processed using ultrafiltration and XAD purification. Pretreated organic material was sampled for carbon and nitrogen isotopes, and aliquots were combusted, graphitized, and subsequently measured for ¹⁴C at The Pennsylvania State University Radiocarbon Laboratory (PSUAMS) and W.M. Keck Carbon Cycle Accelerator Mass Spectrometer at the University of California, Irvine (UCIAMS). The results were calibrated using SHCal20 (73) in Oxcal 4.4.2 (74) (SI Appendix, Supplementary Text 1).

DNA extraction and isolation were conducted at the PSU Ancient DNA Laboratory using protocols specified by George et al. (17). Detailed

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laboratory and computational methods are presented in SI Appendix, Extended Methods 2, along with comprehensive results in SI Appendix, Table S5, analysis in SI Appendix, Table S6, and damage profiles in SI Appendix, Fig. S3. DNA sequencing libraries were constructed, indexed, and amplified at the Smithsonian Institution's Museum Support Center. Sequenced reads were demultiplexed at the NYU Medical Center. All haplotype consensus sequences were aligned with published Ara (SI Appendix, Table S7) and Amazona species. Individual haplogroups were assigned using 104 partial sequences from published modern and historic A. macao reference database and two ancient scarlet macaws from Pueblo Bonito (17, 44, 75, 76) that differentiated the A. m. macao subspecies haplogroups in Central and South America (Haplo4 and Haplo7) and the A. m. cyanoptera subspecies in Mexico and Central America (SI Appendix, Table S8).

Data Availability. Raw sequence data for Atacama macaw samples have been deposited in the National Center for Biotechnology Information (NCBI) Sequence Read Archive under BioProject PRJNA675137 (accession nos. SAMN16690475-SAMN16690478). Genome assemblies, MapDamage outputs, and consensus sequences are available in the Dryad Digital Repository (https://datadryad.org/stash/dataset/doi:10.25349/D95C99). Annotated consensus sequences have been deposited in NCBI GenBank (accession nos. MW584234-MW584237).

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