

Research



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A 2200-year record of Andean Condor diet and nest site usage reflects natural and anthropogenic stressors

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Understanding how animals respond to large-scale environmental changes is difficult to achieve because monitoring data are rarely available for more than the past few decades, if at all. Here, we demonstrate how a variety of palaeoecological proxies (e.g. isotopes, geochemistry and DNA) from an Andean Condor (*Vultur gryphus*) guano deposit from Argentina can be used to explore breeding site fidelity and the impacts of environmental changes on avian behaviour. We found that condors used the nesting site since at least approximately 2200 years ago, with an approximately 1000-year nesting frequency slowdown from *ca* 1650 to 650 years before the present (yr BP). We provide evidence that the nesting slowdown coincided with a period of increased volcanic activity in the nearby Southern Volcanic Zone, which resulted in decreased availability of carrion and deterred scavenging birds. After returning to the nest site *ca* 650 yr BP, condor diet shifted from the carrion of native species and beached marine animals to the carrion of livestock (e.g. sheep and cattle) and exotic herbivores (e.g. red deer and European hare) introduced by European settlers. Currently, Andean Condors have elevated lead concentrations in their guano compared to the past, which is associated with human persecution linked to the shift in diet.

1. Introduction

Understanding how animal populations respond to environmental changes is often difficult given the general scarcity of long-term data [1] owing to the intensive time, labour and financial requirements of continued wildlife monitoring programs [2]. Consequently, natural variability in animal populations is generally unknown and descriptions of baseline conditions preceding anthropogenic stressors are unavailable. Under certain circumstances, however, sites continually used by animals over many generations may form natural archives of past activity that can offer insight into baseline (often pre-anthropogenic) conditions. Such is the case for communal roosts and nesting sites that often accrue

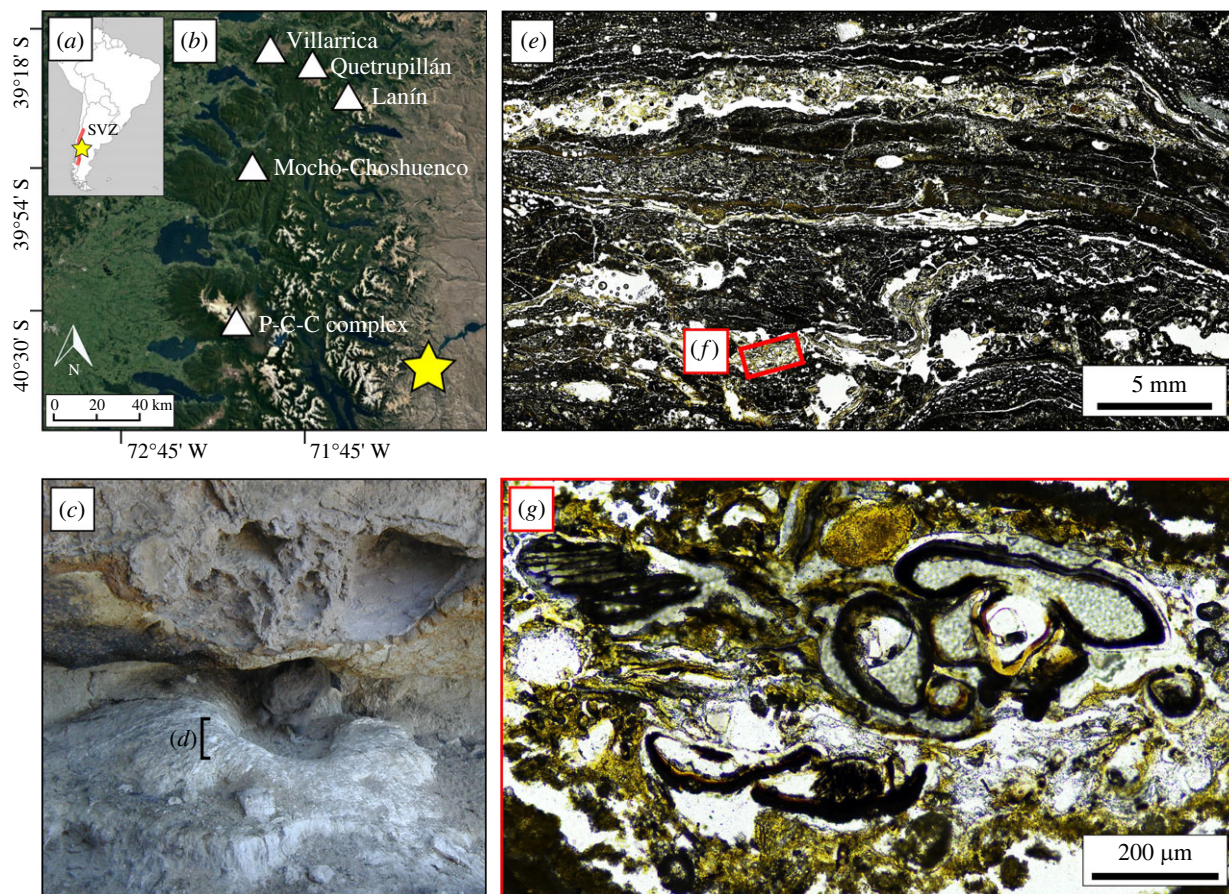


Figure 1. Map of the condor nesting site relative to major volcanoes, alongside photographs and photomicrographs of the Andean Condor deposit. (a) Map of South America, highlighting the Southern Volcanic Zone (SVZ) in red and the location of the Andean Condor deposit with a yellow star. (b) Locations of major, active volcanoes relative to the condor nesting site. Volcanoes in the P–C–C complex, Mocho-Choshuenco, Lanín, Quetrupillán and Villarrica. (c) Photograph of the Andean Condor nesting site, with a nestling condor (photo credit: Lorenzo Simpson, 16 June 2014). (d) Section of the deposit that was collected, about 25 cm in height. (e) Image showing the complex and irregular nature of hydrated phosphate layers forming the deposit walls. (f) Outline of the bone- and detrital grain-rich layers, which are lighter in colour and commonly deformed. (g) A magnified area of (f), illustrating the high concentration of bone fragments reflecting consumed carrion throughout the deposit.

excrement, undigested food, feathers, eggshells and other refuse in a stratigraphically intact manner. These can be analysed to infer, for instance, changes in population dynamics, diet and the surrounding environment (reviewed in [3]).

Palaeoecological analyses of naturally occurring archives have been used to reconstruct population and environmental trends for various animal groups, including rodents (e.g. [4]), fish (e.g. [5]), moths (e.g. [6]), bats (e.g. [7]) and, most commonly, birds (e.g. [8–11]). These approaches are of particular interest for populations experiencing recent declines as palaeoecological data can provide baseline variability before the onset of anthropogenic stressors, which can lead to a better understanding of the factors that modulate populations and thereby guide more effective management practices. For example, an analysis of a guano deposit from insectivorous Chimney Swifts (*Chaetura pelagica*) showed a dietary shift from nutrient-rich Coleoptera (beetles) to nutrient-poor Hemiptera (true bugs), likely as a result of DDT application, which was linked to declines in swifts and other aerial insectivores, providing critical data in conservation efforts [12].

Here, we used a suite of palaeoecological approaches to examine ecological and dietary changes in the Andean Condor (*Vultur gryphus*) based on a guano deposit from a breeding site in northern Patagonia, Argentina (figure 1). The Andean Condor is at risk of extinction in the wild and is currently listed as ‘Vulnerable’ by the IUCN Red List

[13], with key threats being chemical contamination (e.g. [14,15]) and human persecution [16,17]. To provide shelter from the elements, humans and other predators, condors use montane caves or rock shelves on large cliffs as isolated nests or communal roosts [18–20]. If the nesting site has been protected from adverse weather over significant periods, guano and other refuse can accumulate [21]. The presence of a thick, doughnut-shaped guano deposit around our focal nest (figure 1c) thus represents continual use over many generations and can be used to determine changes in environmental conditions, diet and potentially, health.

Although limited palaeoecological research has been completed on waste deposits to track environmental changes in the environment, considerable preliminary work has validated the overall approach. For example, Ainley *et al.* [22] analysed changes in isotopes from laminated deposits of stomach oil from Snow Petrel (*Pagodroma nivea*) in Antarctica to determine how changes in past climate may have caused shifts in forage prey. Similarly, Burnham *et al.* [23] analysed isotopes from Gyrfalcon (*Falco rusticolus*) faecal deposits to understand avian colonization and dietary differences based on geographical location.

The condor guano deposit we analysed is located in the Neuquén Province of Argentina within Nahuel Huapi National Park (Spanish: Parque Nacional Nahuel Huapi), at approximately 40°44 S, 71°06 W (yellow stars in figure 1a,b).

Nahuel Huapi National Park is an IUCN category II protected area, meaning the local ecosystems are cared for, but also that the development of recreational tourism and livestock farming is supported in some areas. The climate of the Neuquén Province is temperate and dry [24]. The deposit is approximately 225 km east of the Pacific Ocean and accumulated in a grotto of an ignimbrite cliff. The home range of Andean Condor is large and variable (2700–53 000 km²; average = 16 300 km²) [25]. The surrounding ecosystems are an ecotone of Andean Patagonian Forest and Steppe. Importantly, the deposit is protected from rain and snow by a rock overhang and it therefore stays dry and does not get washed away (figure 1c). The overhang and relatively cold and dry climate provide the conditions that lead to slow decomposition, which helped preserve and protect the various biological and geochemical proxies archived in the deposit.

A small portion of the deposit was collected before the breeding season, on 9 August 2014, by sawing out a *ca* 25 cm deep cross-section of the outer edge (figure 1d). The cross-section was refilled with surrounding debris to minimize the impact on condor nesting in the future. One half of the section was used for photomicrography and X-ray diffraction (XRD) analysis, and the other half was segmented into 14 equal samples, approximately 1.75 cm thick, used for the remaining analyses. We also collected dried faeces from an adult and nestling condors near the deposit. Adult and nestlings' faeces can be distinguished based on condor behaviour; an adult in the nest during the breeding season will generally defecate between 30 and 100 cm from the nest, whereas the nestling will defecate on the interior edges of the nest. This behaviour was also observed before collecting the samples (L. Simpson 2020, personal communication).

To better understand the historical ecology of Andean Condors, we reconstructed past changes in condor diet and local environmental conditions using various physical, chemical and biological proxies identified from the guano deposit and contemporary, dried faecal samples. The proxies included photomicrographs and XRD analysis to visually identify the physical and mineralogical makeup of the guano deposit; ¹⁴C dating to determine the age and accumulation of the guano; fossil sterols and stanols to track biological inputs; change in the isotope ratios of organic carbon (expressed as $\delta^{13}\text{C}_{\text{org}}$) and stable nitrogen ($\delta^{15}\text{N}$) to identify shifts in diet between terrestrial-derived carbon and marine-derived nitrogen; environmental DNA to detect the presence of emblematic prey; geochemistry to identify environmental changes and potential trace metal uptake by condors; and finally, sub-fossil diatoms (Class: Bacillariophyceae) to track changes in the local nesting conditions. With these palaeoecological data, we had three main objectives: (i) to determine nesting site usage history; (ii) to explore the potential effects of long-term environmental changes on condors and (iii) to provide historical context to changes in diet. The varied palaeoecological approaches that we showcase here can be extended to other accumulations of animal excrement and refuse to understand long-term dynamics unavailable with traditional monitoring alone.

2. Materials and methods

(a) Deposit composition and photomicrography

Photomicrographs were collected in plane- and cross-polarized light to identify the composition and layering of the deposit. To

do so, a segment of the deposit's wall was cut with a diamond saw blade perpendicular to the layering. Five samples were cut from this longitudinal section and manufactured into polished thin sections. Thin sections were examined in stratigraphic order using standard transmitted light petrographic techniques on a Nikon Eclipse LV100N-POL with a Nikon Digital Sight Ri2 Ultra-High Resolution Digital Camera and NIS-Elements imaging software v.5.20.01. To confirm petrographic mineral determinations, we also performed bulk powder XRD of three samples. Samples were analysed on a Panalytical Empyrean Series 2 X-ray diffractometer with a Pixel 3 X-ray detector across scattering angles from 0° to 90° using a copper X-ray target source.

(b) Chronology

To ensure a robust chronology, 10 samples of various material types, including vegetation picked from samples, condor nestling down feathers and bulk sediment, were analysed using accelerator mass spectrometry (AMS) ¹⁴C dating at the André E. Lalonde AMS laboratory in Ottawa, Ontario, and Keck Carbon Cycle AMS Facility in Irvine, California. The ¹⁴C data were calibrated using a South Hemisphere calibration (SHCal20) [26] and the chronology and accumulation rate were determined using the package 'rBacon' v.2.5.5 [27] in the R workspace [28]. All dates are presented in calendar years before the present (yr BP), where 0 BP is 1950 common era (CE).

(c) Sterols and stanols

Deposit and faecal samples were analysed for 11 sterols and stanols, including: 5 β -cholestan-3 β -ol (commonly referred to as coprostanol), 5 β -cholestan-3 α -ol (epi-coprostanol), 5 β -cholestan-3-one (coprostanone), cholest-5-en-3 β -ol (cholesterol), 5 α -cholestan-3 β -ol (cholestanol), 5 α -cholestan-3-one (cholestanone), 3 β -cholesta-5,24-dien-3-ol (desmosterol), campest-5-en-3 β -ol (campesterol), stigmasta-5,24-dien-3 β -ol (fucosterol), β -sitosterol (sitosterol) and 5 α -stigmastan-3 β -ol (stigmastanol). To measure the sterol concentrations, all samples were first freeze-dried and homogenized. Next, 0.1 g of copper powder was cleaned with dichloromethane (DCM) and added to each sample in a 1 : 1 ratio. Samples were also spiked with known concentrations of deuterated recovery surrogate (*d*₆-cholesterol; Cambridge Isotope Laboratories, Tewksbury, MA, USA) and extracted by sonication with three rounds of 10 ml DCM. Extracts were pooled and evaporated using N₂, then further cleaned using 1 g Supelclean™ LC-Si solid-phase extraction cartridges that were preconditioned with 6 ml of DCM. Samples were then eluted with 30 ml DCM, evaporated and derivatized using 0.1 ml BSTFA + 1% TCMS (N,O-bis(trimethylsilyl)trifluoroacetamide + 1% trimethylchlorosilane; Sigma Aldrich, St. Louis, MO, USA), heated to 60°C for 2 h. Once cooled, 0.9 ml toluene was added to the samples and spiked with *p*-terphenyl-*d*₁₄ (Cambridge Isotope Laboratories, Tewksbury, MA, USA) as an internal standard and analysed using gas-chromatography-mass spectrometry. Sterol and stanol concentrations are displayed as relative abundance per sample. Method detection limits were determined using methods outlined in Loconto [29], following the equation:

$$\text{MDL} = \frac{(\text{IDL} \times \text{VE} \times 100)}{(\text{VS} \times \% \text{ recovery})}$$

where IDL is the instrument detection limit, VE is the volume of the final extract, VS is the volume of the sample and % recovery is the per cent recovery. IDL is determined as the mean minimum detectable signal plus 3 × the standard deviation above instrument background, divided by the slope of the calibration curve. The detection limits of all measured sterols and stanols are provided in the electronic supplementary material, table S4.

(d) Geochemistry

Elemental concentrations were analysed at the Queen's University Analytical Services Unit (ASU) in Kingston, ON. We measured 30 elements per sample using inductively coupled plasma-mass spectrometry (ICP-MS) and ICP-optical emission spectrometry (OES), including (with detection limits in $\mu\text{g g}^{-1}$): Ag (0.1), Al (10), As (0.5), B (10), Ba (1.0), Be (0.05), Cd (0.05), Ca (100), Cr (1.0), Co (0.1), Cu (2.0), Fe (20), K (50), Mg (20), Mn (1.0), Mo (0.5), Na (75), Ni (0.5), P (20), Pb (0.5), S(25), Sb (1.0), Se (0.25), Sn (0.2), Sr (1.0), Th (0.025), Ti (1.0), U (0.025), V (0.1) and Zn (5.0). We also measured mercury (Hg) concentrations using cold vapour atomic absorption spectroscopy. One-sided one-sample *t*-tests with a Bonferroni adjustment for multiple tests were used to determine if the concentration of adult and nestling faeces was elevated compared to the rest of the deposit. Below detection limit values were replaced with the detection limit divided by the square root of 2 [30].

(e) Diatoms

Diatoms were prepared following methods described in Wilson *et al.* [31]. Briefly, approximately 0.05 g material was mixed in 10% HCl to remove carbonates. Next, the slurry was digested in a 1:1 molecular weight ratio of sulfuric and nitric acid for 2 h at 80°C to remove the organic component. Each sample was then repeatedly rinsed with deionized water until reaching a neutral pH. Aliquots of the slurries were then pipetted onto coverslips and mounted with Naphrax®. At least 250 diatoms were identified to the species level per sample using light microscopy. Diatoms were not present in the contemporary condor faecal samples.

(f) Eruption history

Given the volatile eruptive history of Argentina and established effects of volcanic activity on condors (e.g. [32–34]), we explored the potential impacts of volcanic inputs using geochemistry and diatom assemblages. For geochemistry, we focused on trends in S, K and Na. Volcanic eruptions commonly produce high levels of SiO₂, K₂O, and distinctively for eruptions near the nest, Na₂O [35,36]. For the diatom assemblage, we focused on two of the most abundant taxa in the deposit with well-established ecological optima: *Pinnularia borealis* and *Aulacoseira distans*. Both species are heavily silicified and found on soils, rocks and walls, but *P. borealis* is dry-tolerant, whereas the *A. distans* species complex requires relatively wetter conditions [37]. These taxa have been found in the Quelccaya Ice Caps (in the Peruvian Andes), where *A. distans* was more abundant in wetter conditions and *P. borealis* were more abundant in drier conditions [38]. As volcanic activity tends to reduce precipitation [39], an examination of the ratio of these diatoms enables us to infer changes in humidity around the nest site that may be linked to eruptions.

We compared the trends in proxies related to volcanic eruptions to eruption histories catalogued and confirmed by the Smithsonian Institution National Museum of Natural History, Global Volcanism Program [40]. We focused on volcanos in the Southern Volcanic Zone (SVZ)—the nearest chain of active volcanoes to the deposit. The SVZ is within 200 km of the deposit and within range to impact the condor's nest and prey that they may scavenge. Also, we only considered eruptions with a Volcanic Explosivity Index (VEI) greater than 3, which has appreciable ashfall at 500 km from the eruption.

(g) Isotopes

The stable isotope ratios of carbon (¹³C: ¹²C; as $\delta^{13}\text{C}$) and nitrogen (¹⁵N: ¹⁴N; as $\delta^{15}\text{N}$) in the deposit material were determined

using standard methods of the Queen's Facility for Isotope Research (QFIR) in Kingston, ON. Samples were weighed into tin capsules and the carbon and nitrogen isotopic compositions were measured using a Costech ECS 4010 coupled to a Thermo-Finnigan Delta^{Plus} XP Continuous-Flow Isotope Ratio Mass Spectrometer (CF-IRMS). To measure the carbonate components, samples were first powdered, and then 1 mg of material was reacted with 100% anhydrous phosphoric acid at 72°C for 4 h. The CO₂ released was analysed using a Thermo-Finnigan Gas Bench coupled to a Thermo-Finnigan Delta^{Plus} XP CF-IRMS. Our data were reported in δ notation (i.e. deviations from standards in parts per mille (‰)), relative to Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$ and atmospheric N₂ for $\delta^{15}\text{N}$. Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were accurate to 0.1‰ s.d. For our faecal samples collected in 2014, we applied a correction factor to pre-1840s values on the $\delta^{13}\text{C}$ values using the methods presented in Schelske & Hodell [41] to account for the Suess Effect (i.e. $\delta^{13}\text{C}$ depletion due to human industrialization [42]). When used in dietary analyses, depleted $\delta^{13}\text{C}_{\text{org}}$ indicates terrestrial origins, whereas enriched $\delta^{13}\text{C}_{\text{org}}$ indicates marine origins. $\delta^{15}\text{N}$ values reflect changes in trophic level.

(h) Environmental DNA

We used droplet digital polymerase chain reaction (ddPCR) to assess potential taxonomic shifts in condor diet based on the DNA analysis of guano deposit and faecal samples. Based on contemporary condor diet [43], we *a priori* selected and tested primer pairs for South American camelids (*Lama* spp.), sheep (*Ovis* spp.) and cattle (*Bos* spp.) to represent likely food sources before (guanaco) and after (sheep, cattle) the introduction of livestock to Patagonia. For all groups, we designed custom primer pairs using Primer3 v.4.1.0 [44] to amplify approximately 100 BP segments of the mitochondrial cytochrome *b* (*Cytb*) gene (electronic supplementary material, table S2). *Cytb* has demonstrated effective resolution to genus or species (e.g. [45,46]). We examined primer specificity *in silico* using BLAST [47] and Primer-BLAST [48].

To examine primer accuracy and potential cross-amplification, we performed pilot ddPCR testing with high-quality DNA extracted from llama tissue, sheep blood and cattle blood. Sheep and cattle blood were provided by local farmers (Kingston, ON) and tissue samples were provided by colleagues at Queen's University (Kingston, ON). Genomic DNA was extracted from blood samples using the Qiagen DNeasy Blood and Tissue Kit (Qiagen Inc., Hilden, Germany) according to the manufacturer's protocol. Tissue sample DNA was extracted using a salt extraction procedure following Aljanabi & Martinez [49], with minor modifications detailed in the electronic supplementary material, text. DNA from these samples was pooled and diluted to obtain high-quality positive controls for ddPCR protocol testing. For deposit and faecal samples, DNA was extracted using the Qiagen DNeasy PowerSoil Pro Kit (Qiagen Inc., Hilden, Germany) according to the manufacturer's protocol.

To assess diet, we ran multiple ddPCR tests for each focal prey taxonomic group of interest. Each test used group-specific primers to amplify DNA from the condor deposit and faecal samples, with corresponding standards included (i.e. llama standards were used for tests with camelid primers). All ddPCR amplifications were performed in triplicate for samples (deposit, faeces), standards (prey group) and blank controls (water). The results are presented in copy numbers per extraction. All ddPCR was performed using the QX200 Droplet Digital PCR System (Bio-Rad Laboratories Canada, Mississauga, ON). Detailed ddPCR cocktail and thermal cycling profile are presented in the electronic supplementary material.

3. Results

(a) Guano deposit structure and chronology

The guano deposit is an accumulation composed of primarily dried faeces, with small portions of condor nestling down feathers and vegetation. The plant material was leaves from cordilleran cypress (*Austrocedrus chilensis*), a conifer endemic to Argentina and Chile [50] that is abundant in the area surrounding the deposit. The deposit walls are composed of compacted layers of poorly crystalline-hydrated phosphate (figure 1e). The semi-arid climate and sheltered location have prevented the formation of minerals such hydroxyapatite, brushite, taranakite and ardealite, which are produced as bird guano is altered in wetter climates [51,52]. Millimetre-thick layers were discontinuous and recorded individual defecation episodes. With time, the circular walls of the nest were produced through the accumulation of guano from multiple condor generations. The presence of deformed layers indicates that the guano was disturbed by adults and nestlings before hardening (figure 1e). Some layers contain bone fragments and detrital grains, suggesting the guano deposit possesses a temporal record of condor diet (figure 1f,g). There is no visible evidence for breaks in guano accumulation that can produce hiatal surfaces or unconformities that eroded into underlying layers.

The ^{14}C ages indicate a stratigraphically intact guano profile with no reversals, regardless of material type (figure 2a). The mean basal age of the guano deposit based on the modelled dating profile is 2150 BP (figure 2a). Our oldest sample, however, is a mixture of down feathers and vegetation aged 3140–3270 BP, suggesting that the basal date may be older than modelled (electronic supplementary material, table S1). The accumulation rate of the deposit was slow in the first two intervals from approximately 25 to 22 cm (approx. $0.006\text{ cm year}^{-1}$) and then increased to an average of $0.080\text{ cm year}^{-1}$ from 22 to 10 cm. After, the accumulation rate dramatically slowed to approximately $0.003\text{ cm year}^{-1}$ from 10 cm to 6 cm (figure 2b). This four-cm interval represents approximately 1000 years from 1650 to 650 BP. The accumulation rate again increased to approximately $0.014\text{ cm year}^{-1}$ in the top 4 cm. From the bottom of the nest accumulation, we observed declines in Al and Ti, two conservative lithogenic elements that indicate the development of the deposit, from a large influx of material from the surrounding ignimbrite to predominantly condor faeces (figure 2c,d). Also, from the bottom of the nest deposit, there is a decline in the relative abundance of *Orthoseira* spp., an aerophytic diatom predominantly found on wet walls of caves and rocks [53], reflecting a shift to drier conditions and higher nutrients as expected from guano deposit development (figure 2e).

(b) Temporal changes in the condor guano deposit

(i) Sterols and stanols

Although we measured the concentrations of 11 sterols and stanols, coprostanone, cholestanone, desmosterol, campesterol and fucosterol were all below detection and excluded from further analysis. The remaining six sterols and stanols were grouped as zoosterols (coprostanol, epi-coprostanol, cholesterol and cholestanol) and phytosterols (sitosterol and stigmastanol; figure 3). We found that only coprostanol and epi-coprostanol were higher in the recent adult and nestling faeces compared to in the deposit (figure 3). Coprostanol,

for example, was approximately 506% higher in the faeces compared to the mean deposit measurement ($147.3\text{ }\mu\text{g g}^{-1}$; $24.3\text{ }\mu\text{g g}^{-1}$) and epi-coprostanol was approximately 355% higher in the faeces ($21.4\text{ }\mu\text{g g}^{-1}$; $4.7\text{ }\mu\text{g g}^{-1}$). Cholestanol, the derivative product of cholesterol, was below detection in the faecal samples and had no notable trends in the deposit (mean = $20.2 \pm 11.1\text{ }\mu\text{g g}^{-1}$ s.d.; figure 3). Phytosterols were nearly absent in both the current faeces and guano deposit, and when present, they were in very low concentrations (figure 3). Finally, we also show phosphorus concentrations alongside sterols and stanols as it is commonly introduced by bird guano and illustrates that the nest is an accumulation of condor faeces. The condor deposit samples have P concentrations 267% higher than in the faeces samples (11.0 mg g^{-1} ; 3.0 mg g^{-1}), likely due to P diagenesis in the deposit through time (figure 3). The results of the sterol and stanol analysis indicate that the nest is largely an accumulation of condor faecal material, not an accumulation of plant growth associated with succession or a rock structure associated with erosion of the surrounding material. This result provides support for our subsequent analyses linking changes in the nest with the condors.

(ii) Volcanic activity

Five main volcanoes/volcanic complexes in the SVZ may have impacted the condor deposit and condor behaviour, including the Puyehue–Cordón–Caulle complex (P–C–C) (approx. 86 km from the deposit), Mocho-Choshuenco (approx. 119 km), Lanín (approx. 126 km), Quetrupillán (approx. 147 km) and Villarrica (approx. 162 km; figure 1b). Of these, only PCC, Lanín and Quetrupillán erupted with a VEI > 3 within the time range encapsulated in the condor deposit [40]. There was increased volcanic activity in the SVZ from ca 2000 to 1300 BP, a relatively short period in geological timescales, with seven eruptions nearby the nesting site (two with VEI > 4, 5 VEI uncertain; figure 4e). During this period of increased activity, we measured distinct peaks ca 1740 and ca 1630 BP in the concentrations of S (12.9 and 17.1 mg g^{-1} , respectively), K (20 and 27 mg g^{-1} , respectively) and Na (7.2 and 7.4 mg g^{-1} , respectively) (figure 4a–c). Coevally, we measured a potential dry period as suggested by the diatom ratio ca 1630 BP (figure 4). We also measured peaks in S, K and Na ca 400 BP, but there was no change in the diatom ratio (figure 4).

(iii) Isotopes

Before ca 1500 CE, $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{15}\text{N}$ values in the deposit were generally unchanging ($\delta^{13}\text{C} = -23.7 \pm 0.24\text{‰}$ s.d.; $\delta^{15}\text{N} = 5.5 \pm 0.38\text{‰}$ s.d.; figure 5a). Notably, after ca 1500 CE, $\delta^{13}\text{C}_{\text{org}}$ declined to -26.2‰ , and $\delta^{15}\text{N}$ values declined to 4.9‰ . Additionally, $\delta^{13}\text{C}_{\text{org}}$ values measured in the adult and nestling faeces follow the depletion trends of the rest of the condor deposit (adult $\delta^{13}\text{C}_{\text{org}} = -25.9\text{‰}$; nestling $\delta^{13}\text{C} = -28.6\text{‰}$). The $\delta^{15}\text{N}$ values of the nestling's faeces were similar to values recorded in the deposit ($\delta^{15}\text{N} = 4.1\text{‰}$), but the adult's were relatively elevated ($\delta^{15}\text{N} = 7.8\text{‰}$), potentially indicating that the condor recently fed on a high-trophic organism.

(iv) Environmental DNA

Our custom primers for sheep, cattle and camelid demonstrated relatively high specificity. *In silico* analyses indicated that primers would not produce amplicons near our target

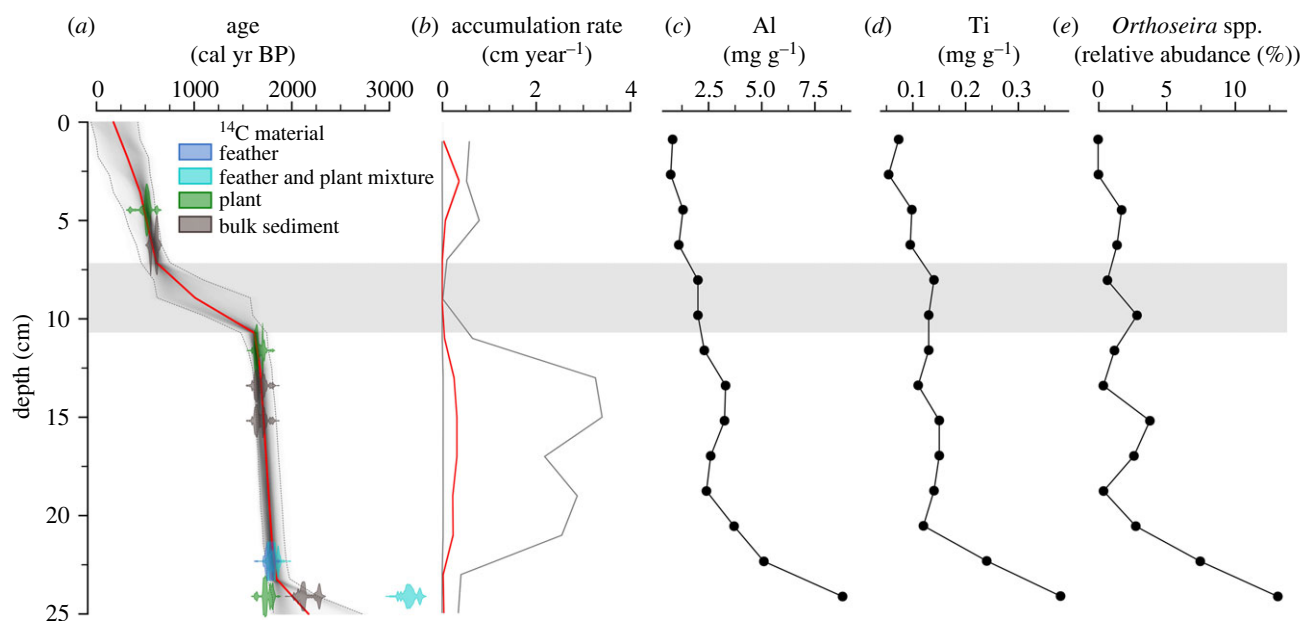


Figure 2. Condor deposit dating profile, accumulation rate and proxies of nest build-up. (a) The modelled mean age–depth relationship, with 95% confidence intervals. (b) Changes in accumulation rate, with 95% confidence intervals. (c,d) Changes in the concentrations of Al and Ti, two conservative lithogenic elements. (e) Changes in the per cent relative abundance of the diatom *Orthoseira* spp., typically found on the rockfaces of caves. The grey bar indicates the period of inferred nesting frequency slowdown.

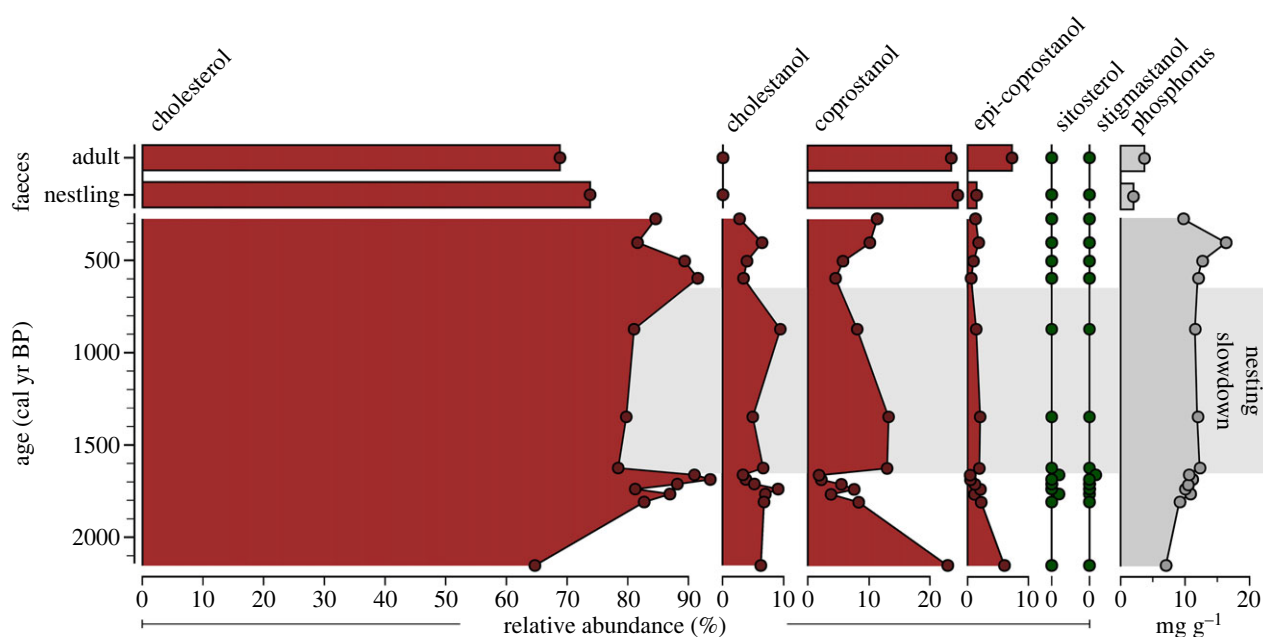


Figure 3. Proportions of the main sterol and stanol (expressed as relative percentages) and phosphorus concentrations (expressed as mg per gram dry weight) in the condor faeces and guano deposit. Zoosterols are represented in red and phytosterols are represented in green. Phosphorus, which is generally representative of nutrient inputs, is in grey. The horizontal grey bar indicates the period of inferred nesting frequency slowdown.

size for non-target species or non-target amplification would be limited to species unlikely to contribute to condor diet (e.g. species outside of range). Despite DNA in faeces generally being poorly preserved, we were able to identify genus-level changes in condor diet (figure 5). The beginning of the record, from *ca* 2150 to 1670 BP, was marked by native camelids (*Lama* spp.; figure 5c), with a high level of repeatability among samples. During this period, we also recorded relatively minor signals of sheep DNA, which is likely a by-product of small amounts of internal contamination, as these species were not present in the area until the past two centuries [54]. Because of the irregular nature

of accumulation in this guano deposit (figure 1e), some internal contamination in highly sensitive proxies, such as DNA, is expected, and thus several corroborative proxies are needed for accurate conclusions. After 500 BP, we observed a cluster of positive detections for sheep and cattle, as well as the continued presence of camelids. Whereas the adult and nestling faeces had sheep and cattle DNA, camelids were only detected in the faeces of the adult condor.

(v) Geochemistry

Several elements were elevated in the individual condor faeces compared to the guano deposit (electronic supplementary

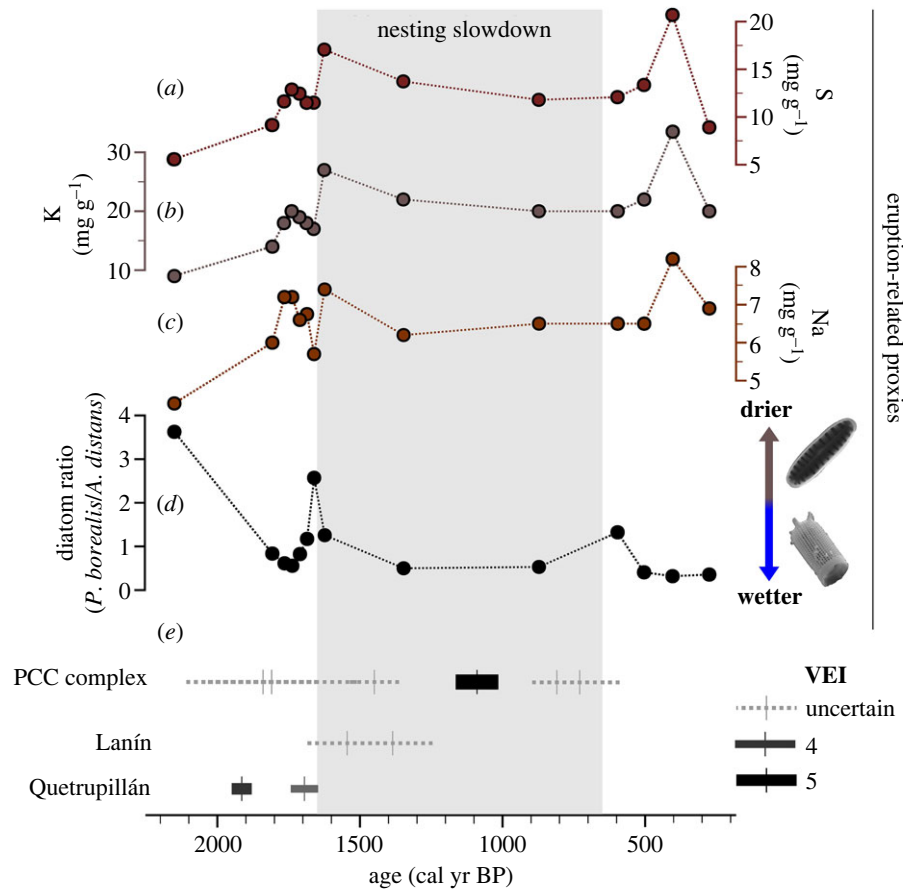


Figure 4. Volcano-related proxies and eruption history in the Southern Volcanic Zone (SVZ). (a–c) Geochemistry related to volcanic eruptions, including concentrations of sulfur, potassium and sodium. (d) A ratio of the diatoms *Pinnularia borealis* to *Aulacoseria distans*, representative of humidity around the nest site. (e) Known volcanic eruptions in the SVZ. The widths of the bars depict the Volcanic Explosivity Index (VEI) from the Smithsonian Institute [40]. The vertical grey bar indicates the period of inferred nesting frequency slowdown.

material, table S2). Due to the limited number of samples, we focused on Pb and Hg as elements of concern as they have well-established anthropogenic sources. For Pb, adult and nestling faeces were elevated compared to the deposit (deposit = $0.63 \mu\text{g g}^{-1}$; adult = $2.4 \mu\text{g g}^{-1}$, one-sample t -test, $p < 0.001$, $t = -17.54$; d.f. = 13; nestling = $31 \mu\text{g g}^{-1}$, one-sample t -test, $p < 0.001$, $t = -319.6$; d.f. = 13; figure 6). Mercury concentration was only elevated in the adult guano (9.93 ng g^{-1}) and was below the detection limit throughout the guano deposit and nestling faeces (i.e. $< 5.0 \text{ ng g}^{-1}$).

4. Discussion

Our analyses of the Andean Condor guano deposit revealed responses to major and long-term changes in the environment. Based on our chronology, Andean Condors have used this nest site for at least approximately 2200 years (figure 2). Nesting activity was markedly reduced for an approximately 1000-year period from *ca* 1650 to 650 BP as inferred by extremely low accumulation rates (figure 2). We explored a variety of potential causes for the nesting frequency slowdown and determined the most likely driver was a series of volcanic eruptions and their associated ecological impacts. We emphasize, however, that the following discussion is based on a single deposit and the conclusions may be strengthened by additional research on other nests. The condor deposit is located within the SVZ of the Andes between 33°S and 46°S latitude, which is historically an

active volcanic area caused by the convergence of the Nazca and Southern American tectonic plates [55]. Before the condors temporarily abandoned the nesting site *ca* 1650 BP, there were at least four high-impact eruptions, producing a distinct signal within the guano deposit (figure 4). Moreover, at least three other large eruptions occurred in the following 350 years (figure 4e).

Eruptions in the SVZ generally produce large plumes of gas and ash that drift southeast, which can directly impact a nesting site, but more importantly, can have devastating impacts on the entirety of receiving ecosystems [32,56]. For example, following the 2011 eruption of the PCC volcanic complex, researchers noted that Andean Condors suffered acute respiratory abnormality (e.g. irritated pharyngitis), lowered concentrations of proteins in the blood (e.g. albumin) and elevated concentrations of trace metals (e.g. As, Cd) in the blood [33]. Although volcanism creates a pulse in the available carrion for scavenging condors [32], the large-scale die-off of available prey populations should have negative long-term effects on reproductive success and survival. Ash-affected areas can suffer reduced herbivore abundance [57] and habitat disruption [58,59], leading to a reduction in available carrion. Following such disturbances, remaining wildlife will typically emigrate if critical survival thresholds are at risk [60]. The rate of ecosystem succession following an eruption depends on the persistence and growth of surviving species [61], but can take several decades to approach equilibrium (e.g. [62,63]). In northwestern Patagonia, condors likely only returned to the nesting site following the reappearance of herbivores (and

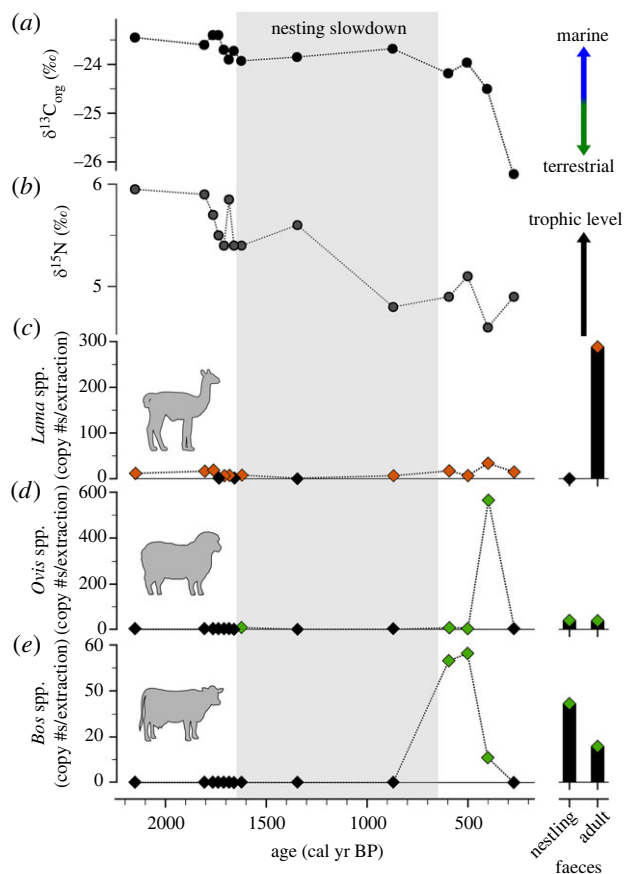


Figure 5. Temporal changes in proxies related to diet. (a,b) Shifts in the values of $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{15}\text{N}$, respectively. (c–e) Shifts in ddPCR-detected DNA presence (presented DNA copies per extraction) in the Condor guano deposit and faecal samples. Intervals that were measured but had no target species DNA are identified in black. Native fauna DNA (*Lama* spp.) are shown in orange and introduced fauna (*Bos* spp. and *Ovis* spp.) are in green. Faecal samples were collected near the nest and are thus shown independently from the rest of the deposit. The vertical grey bar indicates a potential volcano signal preserved in the deposit consistent in all proxies.

thus carrion) and amelioration of the environmental conditions caused by volcanic activity.

The peaks in S, K and Na concentrations occurring *ca* 400 BP may have been caused by a single-large eruption that left a signal in the nest but did not cause a long-term change in the environment, leading to the lack of response in diatoms or nesting behaviour (figure 4d). A potential candidate is the volcano Villarrica (approx. 162 km from the deposit; figure 1b), which is highly active and regularly erupts with mild-to-moderate explosivity [64]. However, historical observations note a short period of increased activity from 1558 to 1562 CE that destroyed the nearby settlement of Villarrica and produced a plume that travelled hundreds of kilometres [65]. The town was then rebuilt a few years later in the same location and renamed Pucón. Such a large eruption may have produced a distinct eruptive signal in the nest deposit (figure 4d) but did not result in ecosystem changes, as earlier described, following approximately 700 years of continuous volcanic activity.

Other environmental factors likely also had minor influences on condor nesting behaviour and may have contributed to the nesting frequency slowdown. Climate reconstructions of Northern Patagonia following condor abandonment *ca* 1650 BP indicate that the area was cooler [66] and drier

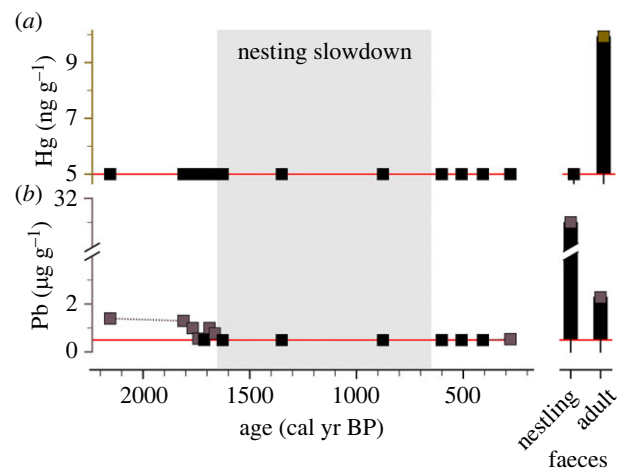


Figure 6. Temporal changes in potentially toxic metals. Intervals that were measured but were below the detection limit are identified in black. Faecal samples were collected near the nest and are thus shown independently from the rest of the deposit. The vertical grey bar indicates a potential volcano signal preserved in the deposit consistent in all proxies. The red line is the detection limit.

[67–69] than the present, and experienced elevated fire frequency [70]. Such semi-arid conditions potentially slowed plant succession and the return of herbivores, and even more following volcanic activity. Other factors that can influence populations, such as human interference, likely did not affect the Andean Condors at this time. In Patagonia, human density was historically low. Moreover, Traditional Ecological Knowledge offered by local Indigenous communities and archaeological evidence indicate that the Andean Condor was considered sacred for many South American cultures, and was not persecuted as they are today before European colonization [71]. Andean Condor displacement by intraspecific competition is unlikely as condors have no natural predators [20] and the remote location of their nests makes them generally inaccessible to predators. Following the condors' return to the nest *ca* 650 BP, guano began to accumulate as it had before the period of volcanic activity (figure 2). In the following centuries, we noted a decline in $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{15}\text{N}$ values, indicating a dietary shift towards carrion that is increasingly terrestrial in origin and at a lower trophic level (figure 5). Moreover, the disappearance of guanaco DNA and the appearance of sheep and cattle DNA indicate a distinct shift in diet to introduced animals. As condors are obligate scavengers, their diet reflects changes in the available prey, and thus in the ecosystem makeup. Our results show a temporal shift in the Andean Condor diet from mixed terrestrial and marine carrion (e.g. local fauna and beached mammals) to nearly exclusively terrestrial carrion (e.g. exotic livestock and game species), as previously suggested [43]. Currently, the Andean Condor's diet in this area is *ca* 98.5% exotic species, *ca* 57% of which is livestock and *ca* 41% game species [72]. The introduction and proliferation of exotic mammals in southwestern Patagonia is well-established and occurred between the eighteenth and nineteenth centuries [54]. Although European settlement was documented in northern Patagonia in the mid-seventeenth century when Jesuits introduced livestock near Nahuel Huapi Lake [73], intensive farming and ranching only began in the late nineteenth century. In the past 150 years, cattle and sheep in Patagonia rapidly increased in numbers, reaching estimates of 350 000 cattle and 16 million sheep [74].

Before European settlement, condors scavenged the carrion of native animals such as guanaco (*Lama guanicoe*) and beached marine life [20,43]. Yet, after the introduction, colonization and rapid dispersal of livestock and game animals, native herbivores were displaced and their populations declined. The dietary shift we observe here is also supported by a retrospective isotope analysis of condor feathers [43], which suggested that the diet shift could have been explained by global declines in marine life linked to whaling since the late-seventeenth century [75] and more recently, reduced scavenging behaviour in condors due to urban development along beaches [76]. A reduction in marine-derived carrion forced condors to fly further to access marine resources or to feed on higher proportions of terrestrial prey [43]. The terrestrial prey is now, however, predominantly introduced animals such as livestock and game, which creates tensions with farmers who incorrectly believe that condors kill and/or harm their economically valuable animals [16,17]. As a result, condors are persecuted through the use of poisoned carcasses, traps and hunting [15,16].

We measured elevated Pb and Hg concentrations within the adult or nestling faeces compared to the historical record in the guano deposit, mirroring results that indicate that Andean Condors are being poisoned with metals [15]. Trace metals in the tissues of birds are commonly excreted in feathers and eggshells, by uropygial and salt glands, and importantly, in faeces [77]. Metal concentrations in bird faeces are an effective measure for exposure in wild populations [78]. Elevated lead concentrations in faeces mainly occur via indirect poisoning because condors are shot with lead bullets and they consume the carcasses of animals that have been shot using lead bullets [14,79]. Other potential drivers of elevated Pb concentrations, such as leaded gasoline or high Pb concentrations in the ground, are not considered major factors for Andean Condors because they feed in areas with low human density, gasoline has been free of lead for more than a decade and the ground is naturally low in Pb [79]. Mercury is also on the rise in Patagonia following increased anthropogenic activities following industrialization, including urbanization and land development [80]. The presence of elevated Pb in the condor nestling and adult, as well as elevated Hg in the adult, is a warning sign of potentially deleterious effects on long-term condor survival.

5. Conclusion

Andean Condors have returned to this same nesting site for approximately 2200 years despite disruptive volcanic activity, turnover in their diet and recent human persecution. The long-term usage of this nest demonstrates the importance of quality nesting locations for condors and implies a potential paucity in nature. Nest site fidelity is a known behavioural trait among Andean Condors and the protective qualities of

nesting and roosting sites are essential to their reproduction. Yet, most of these nesting and communal roosting sites are outside protected areas [25,81]. In the light of our results, it is clear that quality breeding sites are critical for this species' survival. To support effective conservation efforts, nesting and roosting sites need extensive protection.

Our study demonstrates the power of palaeoecological techniques to determine baseline conditions that are otherwise not available using traditional monitoring techniques. This approach should be used on other Andean Condor deposits in the region to either strengthen or challenge our interpretations of the regional influences described in the results of our study, such as identifying the potential impacts of volcanic activity on condor nesting. Also, these approaches can be applied to other species that form guano deposits, such as Oilbirds (locally Guácharo; *Steatornis caripensis*) or Guanay Cormorants (*Leucocarbo bougainvilliorum*), among many other taxa. Moreover, palaeoecological studies across a range of habitats can be the basis for metapopulation studies in response to long-term environmental change. These techniques can unlock a wealth of ecological and population information that will directly inform on population baselines, leading to more effective conservation and management of at-risk species.

Data accessibility. All data associated with this manuscript are available in the electronic supplementary material [82].

Authors' contributions. M.P.D.: conceptualization, data curation, investigation, methodology, visualization, writing—original draft and writing—review and editing; C.G.: conceptualization, formal analysis and writing—review and editing; L.S.: formal analysis and writing—review and editing; J.M.B.: supervision and writing—review and editing; D.D.: formal analysis and writing—review and editing; W.F.: formal analysis and writing—review and editing; K.M.H.: formal analysis and writing—review and editing; M.L.J.: formal analysis, supervision and writing—review and editing; L.E.K.: formal analysis; S.A.L.: investigation and writing—review and editing; D.L.-M.: formal analysis and writing—review and editing; S.C.L.: resources, supervision and writing—review and editing; J.M.: writing—review and editing; N.M.: investigation and writing—review and editing; P.K.P.: formal analysis, resources and writing—review and editing; A.V.: formal analysis and writing—review and editing; J.P.S.: conceptualization, project administration, supervision, writing—original draft and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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