Ornithogenic soils and the paleoecology of pygoscelid penguins in Antarctica

S.D. Emslie [a, *], M.J. Polito [b], R. Brasso [a], W.P. Patterson [c], L. Sun [d]

[a] Department of Biology and Marine Biology, University of North Carolina, 601 S. College Road, Wilmington, NC 28403, USA
[b] Woods Hole Oceanographic Institution, 266 Woods Hole Road MS# 50, Woods Hole, MA 02543, USA
[c] Saskatchewan Isotope Laboratory, 114 Science Place, Saskatoon, SK S7N5E2, Canada
[d] Institute of Polar Environment, University of Science and Technology of China, Hefei, Anhui 230026, China

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ABSTRACT

Ornithogenic or bird-formed soils have accumulated in many coastal regions around Antarctica as a result of breeding activities by pygoscelid penguins, especially the Adélie penguin (*Pygoscelis adeliae*). These soils are often deep, range from hundreds to thousands of years old, and contain a natural archive of penguin tissues and those of their prey. In some regions, these tissues are extremely well preserved by the dry, cold environment and include complete and partial penguin mummies, feathers, bone, and eggshell. Hard parts of prey (fish bones, otoliths, and squid beaks) also commonly occur in these deposits from the penguin guano as it accumulates during soil development. Here, we review how research on these soils and the tissues they contain has progressed since they were first identified and described. These studies have provided not only valuable information on penguin occupation history with climate change since the Pleistocene, but also whole ecosystem responses to perturbations such as the 'krill surplus' that is hypothesized to have occurred following historic depletion of seals and whales in the 18th–20th centuries. New findings in the Ross Sea indicate how penguin occupation and abandonment cycles have progressed over millennia in relation to climate change. In addition, stable isotope analysis of $\delta^{15}N$ and $\delta^{13}C$ in ancient and modern Adélie penguin tissues (feathers, bone, eggshell and membrane) and guano support the 'krill surplus' hypothesis in showing a dietary shift from fish to krill over the past ~200 years. Other recent studies have focused on stable isotope analyses of penguin prey remains, as well as ancient DNA and mercury analyses of penguin tissues recovered from ornithogenic soils. An analysis of fish otoliths recovered from ancient guano provide a means to investigate values of otolith carbonate $\delta^{18}O$, which correlates with other paleoclimatic records, and can be used as a proxy for changing ocean temperatures through time. In addition, measurements of total mercury (Hg) in penguin egg membrane from abandoned colonies up to 800 years old indicate significantly higher mercury levels in the past compared to modern penguins, likely due to a greater reliance on higher trophic prey prior to the proposed 'krill surplus'. All of these studies indicate that ornithogenic soils and the natural archive of tissues they contain provide a unique means to integrate both terrestrial and marine records with ecosystem studies and climate change, past and present, in Antarctica.

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Bleached remains of thousands of penguins were scattered all over the platform, mostly young ones which has succumbed to the severity of the climate. Thousands of years hence, if the species should become extinct, these remains frozen and buried among the debris will be available as a proof of what once existed in these gelid regions, now just habitable, then perhaps not at all.

Louis Bernacchi, upon landing at Cape Adare, Antarctica
17 February 1899.

1. Introduction

On 17 February 1899, Louis Charles Bernacchi, a meteorologist on the Carsten Borkgrevink *Southern Cross* expedition, wrote the above words after stepping on the shores of Cape Adare, Antarctica, for the first time. This cape, located at the entrance to the Ross Sea (Fig. 1), currently supports the largest Adélie penguin (*Pygoscelis adeliae*) breeding colony in Antarctica. Bernacchi and nine other men were about to become the first explorers to spend a winter on the Antarctic continent and his prescient observations are remarkable, given what we know today about these colonies and

* Corresponding author.
  E-mail address: emslies@uncw.edu (S.D. Emslie).

the natural archive of tissues they contain. However, he was not the only one to make these observations as later explorers, including those who were part of Robert F. Scott's *Northern Party* also stopped at Cape Adare and recorded similar impressions (Priestley, 1915). Not known at the time, penguins had been active at this colony for over 2000 years and these activities included the development of a unique type of deposit, an ornithogenic (bird-formed) soil (Fig. 2), that preserves not only penguin bones, eggshell, and feathers, but also a record of penguin diet in guano (e.g., fish bones, otoliths, squid beaks). In addition, lakes and low areas where sediment accumulates near penguin colonies also preserve biological and geochemical evidence of former breeding colonies and have been referred to as ornithogenic sediment to indicate this different origin from ornithogenic soils and this terminology is followed here.

Here, we review the current state of knowledge on ornithogenic soils and the biological archive they contain. Our primary objective is to demonstrate how this record contributes to our understanding of past marine and terrestrial ecosystems in Antarctica and the potential for additional studies on the paleoecology of penguins.

We also present new data on stable isotope analysis ($\delta^{18}O$) of otoliths from ancient penguin guano as a proxy for past sea surface temperatures, and data on mercury in ancient and modern penguin egg membrane in relation to past diet. These studies serve to highlight the expanding value of the natural biological archive stored in ornithogenic soils.

2. Pygoscelid penguins in Antarctica

There are currently five species of penguins that breed in the Antarctic, but the Adélie penguin is the only one to have left an extensive terrestrial record of their former occupation. Not only does this species require ice-free terrain for nesting, it is also the most abundant penguin in Antarctica found in coastal areas around the entire continent. Their habit of collecting pebbles to build or rebuild their nests every year facilitates the deposition of clastic sediment, guano, and organic debris that ultimately develop into ornithogenic soil. Two other pygoscelid penguins, the Gentoo (*Pygoscelis papua*) and Chinstrap penguin (*Pygoscelis antarctica*) co-
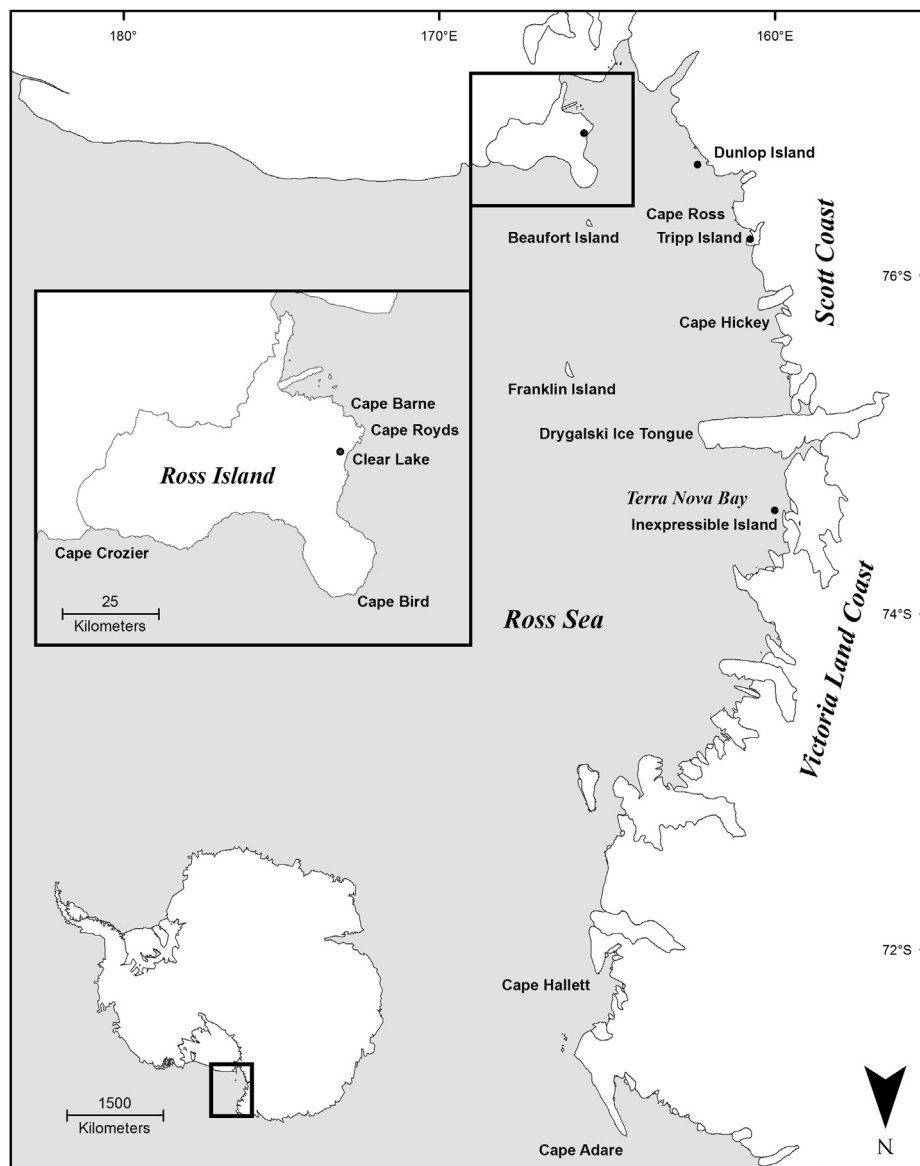

Fig. 1. Map of the Ross Sea, with enlarged map of Ross Island, showing locations of major geographic regions and sites discussed in the text.

Fig. 2. The formation of ornithogenic soils at an active Adélie penguin colony at Cape Adare, Ross Sea, Antarctica. Nesting activities at this site for ~2000 years have resulted in formation of numerous parallel ridges on the beach that are composed primarily of over 1-m deep ornithogenic soil (top). This soil is clearly differentiated in color and lithology from the volcanic beach gravel and sand that forms the base of the deposits (bottom). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

occur with breeding Adélie penguins in the Antarctic Peninsula, but are found on many sub-Antarctic islands as well. These two species also require ice-free terrain for nesting, but the soils formed at their colonies are not nearly as extensive or as old as those formed by the Adélie Penguin. To date, the oldest soils and tissue remains have been dated at ~1000 calendar years before present (BP; after correction and calibration for the marine carbon reservoir effect, see Emslie 2001) at Byers Peninsula, Livingston Island (Fig. 3; Emslie et al., 2011). The persistent lack of older remains at active and abandoned colonies of these two species may be due in part to the selection by Chinstrap penguins of nesting sites that often are on high exposed ridges or rocky slopes and substrates where sediments do not easily accumulate. It is also possible that pygoscelid penguins have only colonized the Antarctic Peninsula since the late Holocene as no older evidence for their former breeding colonies currently exists in this region. Only a few abandoned colonies on King George and Livingston Island have produced mounds of debris that could be excavated and these were very young in age, less than a thousand years (Emslie et al., 2003a, 2011). More deposits of these species do exist, such as on Deception Island for Chinstrap Penguins, but have not been investigated in detail.

The record left by Adélie penguins is unique in its age and geographic extent. In fact, we know of no other living species of bird that has provided such a well preserved and rich record (including mummified remains of whole carcasses) of its past history, extending to over 40,000 years in age, within the same region that it occupies today. Moreover, climate change in the Antarctic region is well documented with numerous studies of ice cores, marine sediment, and polar lakes (e.g., Ingólfsson et al., 1998, 2003; Masson et al., 2000; Verleyen et al., 2011). Thus, the Adélie penguin record provides a rare opportunity to investigate the paleoecology of this species in relation to climate and changes in marine and terrestrial ecosystems that have occurred before and after the Last Glacial Maximum (LGM; 18,000–20,000 B.P.) and other climatic events that followed during the Holocene.

Adélie penguins, past and present, also are excellent bio-indicators for marine and terrestrial conditions because they can only exist in an area if three conditions are present: ice-free terrain suitable for nesting (including availability of pebbles for nest building), open water for beach access at this location, and sufficient food supplies within a reasonable foraging distance from the colony so that the adults can obtain enough food in a timely manner to sustain their chicks through fledging. As these conditions persist, the colony may expand over time as surviving young will frequently return as breeders to the colony where they hatched. If any of these conditions change, the colony will shrink and disappear from lack of new recruits as the adults die off, thereby becoming an abandoned colony where the ornithogenic soils continue to develop. Alternatively, new colonies may form as conditions become more favorable in coastal areas previously not occupied by breeding penguins. Thus, the formation and abandonment of nesting sites is a very dynamic process, with colonies appearing and disappearing in regions such as the Ross Sea over centuries to millennia. Left behind are mounds of pebbles and debris that document these previous occupations and reflect the marine and terrestrial conditions that once existed there. Next, we discuss the history of these ornithogenic soils, from their first description and early investigations, to how methodologies have advanced over the past decade to include numerous new analyses of penguin tissues and prey remains.

3. Ornithogenic soils

Ornithogenic soils were first named by a Russian biologist, E.E. Syroechkovsky (1959), who was working at the remote Mirnyi observatory in Queen Mary Land, east Antarctica in 1956/1957. An Adélie penguin colony was located on Haswell Island (Fig. 3) near the coast and it was here that Syroechkovsky conducted the first research on penguin guano deposits in Antarctica. At that time, there were over 24,000 nesting penguins on this island that he and other scientists, members of the first Russian winter expedition to Antarctica, were investigating that year. There is no English translation of Syroechkovsky's published work on ornithogenic soils, but a partial translation indicates the study included not only guano deposition, but also plants (primarily lichens and algae) that were growing on and near the penguin colonies. The combination of the enriched sediment from penguin guano with the vegetation led Syroechkovsky to conclude that true soil-forming processes are present in the Antarctic and that these soils should be referred to as "ornithogenic".

Soon after this initial research by Syroechkovsky, study of these soils intensified. J.C.F. Tedrow, F.C. Ugolini, I.B. Campbell, and G.G.C. Claridge all began investigations of various types of Antarctic soils, including ornithogenic, and soil forming processes in the Ross Sea region by the early 1960s. Among the major findings of this work was a clear understanding of how ornithogenic soils begin as a guano layer over unconsolidated sand or other sediment (Campbell and Claridge, 1966, 1987; Tedrow and Ugolini, 1966; McCraw, 1967;
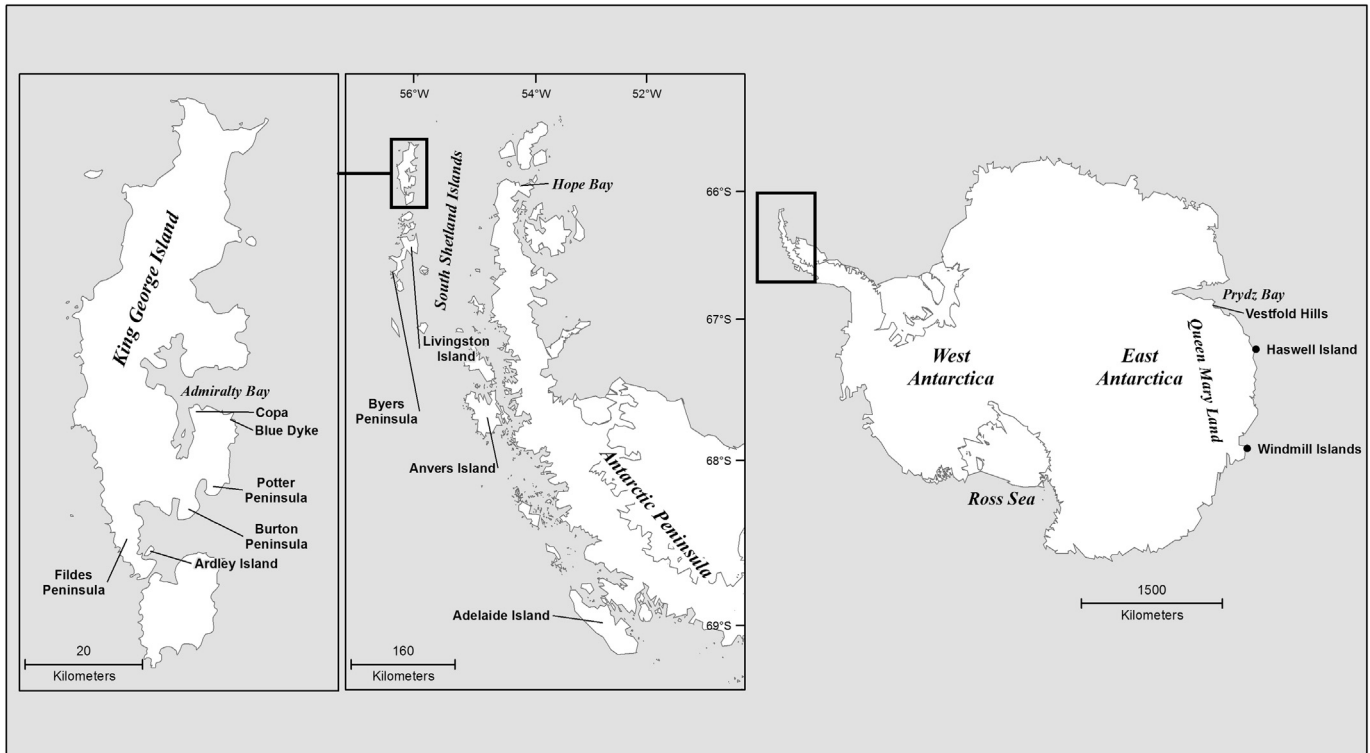
Fig. 3. Location of major regions in continental Antarctica (right) with detail of the Antarctic Peninsula (middle) and King George Island (left) to indicate specific locations discussed in the text.

Ugolini, 1970, 1972). Dessication and gradual decay of the guano layer ensues after abandonment, forming a soil rich in nitrogen, phosphorus, salt, uric acid, and other nutrients that provide "an exceptional abundance of organic material in contrast with the rest of the soils of continental Antarctica" (Ugolini, 1972: 190). Young, developing ornithogenic soils have a dark, indurated crust of guano overlying the sediments below, but over time the soil becomes lighter and pinkish in color, largely from the krill in penguin guano. Eventually, a fully formed soil will be dry and even dusty, with a lithology of mostly pebbles of the same approximate size, intermixed with sediment, bones, feathers, and eggshell fragments. The lower boundary is sharply delineated where natural sands, volcanic, or glacial sediment immediately below the ornithogenic soil have a distinctly different color and lithology (Fig. 2). Overall, the soil forming processes in Antarctica occur at different rates (slower in East Antarctica compared to the warmer and moister Antarctic Peninsula) than at lower latitudes and thus allow study of the biochemistry and development of these soils with high organic inputs (Heine and Speir, 1989).

Research on the chemical composition and decay processes in ornithogenic soils continued in the 1980s. Most of this work took place in the Ross Sea region on Ross Island and the Victoria Land coast (Fig. 1; Speir and Heine, 1982; Orchard and Corderoy, 1983; Speir and Cowling, 1984; Speir and Ross, 1984; Heine and Speir, 1989). By investigating active, recently abandoned, and ancient penguin colonies, these studies were instrumental in understanding the soil forming processes that resulted in the rich mineral content of ornithogenic soils. In the Antarctic Peninsula, ornithogenic soils were first investigated by Everett (1976) along with numerous other soil types in the South Shetland Islands (Fig. 3). She described the ornithogenic soil profiles in her study area and noted the high content of salts, potassium, and ammonia. By the 1980s, considerable research was conducted on ornithogenic soil formation and mineral content by Polish scientists stationed at Admiralty

Bay, King George Island (Fig. 3). These studies in particular indicated how the enriched soils were also high in fluorine from krill in penguin guano, especially in the upper layers, and how the mineral content in general influenced the terrestrial ecosystem (Tatur and Barczuk, 1985; Tatur, 1987, 1989; Tatur and Myrcha, 1989). They also identified "ornithogenic relict soils" that were buried under dense vegetation that formed from the enriched nutrient content of the soils. In particular, Antarctic grass (*Deschampsia antarctica*) may grow thick over abandoned colonies in the Antarctic Peninsula, but these grasses do not occur farther south on the continent. Thus, soil formation in the peninsula includes a succession of plant colonizations after a colony is abandoned, altering the structure and color of the soils compared to those in the Ross Sea (Tatur et al., 1997). These authors also completed a survey of the northern Antarctic Peninsula and identified a number of sites where ornithogenic soils were located and described at active and abandoned colonies (Tatur, 1989; Tatur and Myrcha, 1989). Later, Michel et al. (2006) and Simas et al. (2007, 2008) completed more analyses of ornithogenic soils in Admiralty Bay and at active and abandoned penguin colonies near the Copacabana field station (Copa), King George Island (Fig. 2). They provide detailed descriptions of the vegetation and pedogenesis of these soils, including mineral content and biogeochemical cycling.

4. Investigations on the biological archive in ornithogenic soils

4.1. Radiocarbon dating and penguin occupation history

The first use of organic remains preserved in ornithogenic soils for paleoecological research on penguins was for radiocarbon dating to develop an occupation history at specific locations. The earliest published radiocarbon date is by Harrington and McKellar (1958) who dated a single specimen, a mummified carcass found

while bulldozing at Cape Hallett, Ross Sea (Fig. 1), which produced an uncorrected age of 1210 ± 70 radiocarbon years before present (^{14}C BP). This date closely approximates other dates obtained much later on penguin remains from this site (Hofstee et al., 2006; Emslie et al., 2007) and indicates a young age (~500−900 BP) for the occupation of this large Adélie penguin colony (~44,000 breeding pairs; Ainley, 2002). Surprisingly, no other research on abandoned colonies or radiocarbon dating was conducted until Stonehouse (1970) and Spellerberg (1970) both published their results from samples collected at Cape Barne and Clear Lake (near Cape Royds), Ross Island (Fig. 1), respectively. Again the results indicated a relatively young age for occupation of these sites by breeding Adélie penguins at 600 BP and younger.

After this initial research on radiocarbon dating of penguin remains from ornithogenic soils, another long gap (>10 years) occurred where essentially no other research appears to have been conducted or published on these soils. The surge in interest on these soils in the 1980s described above in the Antarctic Peninsula included buried penguin bones under peat deposits dated at 4950 BP on Penguin Ridge near Arctowski Station, King George Island (Tatur and Myrcha, 1989). The sediment described, however, is not *in situ* ornithogenic soil as it includes loam and clay (rather than pebbles) and the bones were deposited secondarily, suggesting that a breeding colony was located nearby. Only one other site, also on King George Island at Potter Peninsula (Fig. 3), has produced penguin bone from geological deposits in raised beaches dating to the mid Holocene (del Valle et al., 2002, 2007), but again no *bona fide* ornithogenic soils have been located that date older than ~1000 BP in the northern Antarctic Peninsula (Emslie, 2001).

By the early 1990s, ornithogenic soils had been well described and penguin remains were being used to obtain radiocarbon dates to determine their age. Depending on the location of the abandoned site, radiocarbon dates can provide minimum ages for the formation of raised beaches, glacial moraines, sea-ice coverage, and deglaciation of a region (Baroni and Orombelli, 1991; Emslie et al., 2003b; Hall et al., 2004; Gardner et al., 2006). A landmark paper by Baroni and Orombelli (1994), however, set the stage for the use of penguin remains from these deposits to assess regional changes in climate. These authors investigated a number of abandoned Adélie penguin colonies in the Ross Sea region to develop an occupation history of Adélie penguins since the late Pleistocene that reflected paleoclimatic conditions over the past 13,000 years. They found that most of their 61 radiocarbon dates fell within the calibrated time period of 4000−3000 BP and referred to this period as the 'penguin optimum' as so many colonies were newly established and occupied along the Scott Coast in the southern Ross Sea at that time. However, these sites are now abandoned. They correlated this period with a warm interval recorded in the Dome C ice-core record that promoted open water access to coastal areas, especially the Scott Coast, which is currently blocked by persistent, multi-year sea ice and has no breeding penguins there today. This research clearly demonstrated the value in studying penguin occupation history as another proxy for paleoclimatic conditions in Antarctica.

At the same time that this work was being completed, a taphonomic study on how bones are deposited at active penguin colonies was conducted by Emslie (1995). Systematic survey and collection of bones at active and abandoned Adélie, Chinstrap, and Gentoo penguin colonies over two field seasons at Copa, King George Island (Fig. 3), indicated that these colonies accumulate primarily bones of chicks and juveniles (>70%) with certain elements (especially humeri, furcula, femora, and tibiotarsi) being most prevalent. As bones of chicks and juveniles are easily distinguished from those of adults by their incomplete ossification and porosity, fossil and subfossil ornithogenic deposits should retain this signature, allowing differentiation from other, geological bone

deposits such as in raised beaches or at molt sites where the bones are primarily those of adults. This information thereby allows precise determination of penguin occupation history of a region by using radiocarbon dates only from remains found at former breeding colonies.

Since this initial work on regional climate change using data from abandoned colonies, there have been numerous papers on how penguin occupation has shifted over millennia with climate change or other factors (e.g., changes in sea ice conditions, presence of polynas). Most of this research has been focused on the Ross Sea, where the record for Adélie penguins now extends to the last interglacial (~27,000−44,000 ^{14}C BP), before the Ross Ice Shelf (RIS) moved northward to its maximum extent in the LGM by 18,000 to 20,000 ^{14}C BP At that time, the entire Ross Sea was abandoned by breeding penguins and was not reoccupied until about 8000 ^{14}C BP. when the RIS had receded sufficiently to allow access to ice-free coastal terrain by breeding penguins (Emslie et al., 2007; Lambert et al., 2010). This initial occupation occurred in the Terra Nova Bay region where a polynya helps maintain open water that facilitates this occupation today. The data also suggest that this polynya developed soon after the retreat of the RIS, allowing for the longest continuous occupation of this area by breeding penguins in the Ross Sea (Emslie et al., 2007).

The evidence for interglacial occupation of the Ross Sea by Adélie penguins, prior to the advance of the RIS to its LGM grounding line, is so far limited to just a few sites where ornithogenic deposits have managed to survive: Cape Hickey, Cape Ross, Dunlop Island (Emslie et al., 2007), and a new site discovered in 2011−2012 at Tripp Island (Fig. 1). A single radiocarbon date from this last site, based on multiple eggshell fragments recovered from shallow ornithogenic soils that were sampled there, provided an uncorrected date of 26,620 ± 150 ^{14}C BP (UGAMS 11370). In addition, a buried molt layer exposed under deep deposits at Beaufort Island, first reported by Seppelt et al. (1999), has yielded dates in excess of >44,000 ^{14}C BP, or beyond the range of radiocarbon dating, providing further evidence that Adélie penguins were thriving in the Ross Sea prior to the LGM (Emslie et al., 2007). While this deposit is comprised primarily of layers of matted feathers from molting birds, a few eggshell fragments suggest that ornithogenic soil may also be present at this site, but are more deeply buried or eroded away (J. Smykla, pers. comm.).

Only two other regions in Antarctica have ornithogenic soils that document a long-term occupation history by breeding Adélie penguins. The Windmill Islands, East Antarctica (Fig. 3), have dozens of large abandoned pebble mounds have been located in the area around the current Adélie penguin colonies near Casey Station, some with ornithogenic deposits more than a meter deep. Sampling and radiocarbon dating of many of these sites have indicated a continuous occupation of this area over the past 9000 years, or soon after deglaciation of the region (Emslie and Woehler, 2005). A similar long-term occupation has been suggested at Prydz Bay (Fig. 3) near Davis Station, based on sediment core dates on deposits near the present Adélie penguin colony on Gardner Island (Huang et al., 2009, 2010), but excavations of abandoned colonies and ornithogenic soils are needed to further document this occupation history. Ongoing research continues to add to the occupation history of pygoscelid penguins in Antarctica. The absence of ornithogenic soils older than ~1000 years in the northern Antarctic Peninsula remains an enigma that future investigations may resolve (Emslie, 2001).

4.2. Prey remains

Besides the often rich and well preserved archive of penguin tissues that are found in ornithogenic soils, they often include

abundant remains of hard parts of prey in penguin guano that forms the basic ingredient of the soil. The fish bones, otoliths and squid beaks that preserve in the soil provide a record of the marine environment, sampled for us by penguins from hundreds to thousands of years ago. Despite this abundance in the soils, these prey remains were unknown or ignored in early research efforts, probably because most are not visible with the naked eye. Until the soils were excavated and carefully washed through fine-mesh screens did these remains begin to receive attention.

Using a combination of both archaeological and paleontological methods, Emslie (1995) recovered prey remains from excavations of ornithogenic soils at an active Chinstrap penguin colony at Blue Dyke, King George Island (Fig. 3). Although only ¼ inch (63.5 cm) and 1/8 inch (2 mm) mesh screens were used at that time, two squid beaks were recovered and identified as *Chiroteuthis* sp.; one beak of this species also had been recovered from a stomach lavage of a Chinstrap penguin near the same location in 1994. Some of the soil from this site also was panned for otoliths, but none were recovered. Although these results were limited, they indicated that prey remains could be preserved and recovered from ornithogenic soils. Thus, the methodology was refined with a third and smaller mesh screen (0.25 mm^2) added in subsequent excavations of six abandoned colonies near Palmer Station, Anvers Island, in 1996/1997 (Fig. 3; Emslie et al., 1998). At each site, a 1 m^2 pit was excavated in arbitrary 5–10-cm levels until the bottom of the ornithogenic soil was reached as indicated by a change in color and texture when natural beach or glacial sediment was encountered. All sediment from each level was measured by volume using a 20-l bucket and then washed through the three nested screens. Penguin bones, feathers and eggshell, as well as prey remains (squid beaks) were sorted from the top two screens with the naked eye, while smaller organic remains (fish bones, otoliths) were recovered from the finer sediment after drying and with the use of a low-power stereomicroscope. Two control excavations were conducted to determine if prey remains in ornithogenic soils were really from penguin guano and not 'background debris' from other species that may use the same ice-free terraces. The first control excavations were completed at three active colonies (one Chinstrap and two Adélie) to help assess the number and kinds of organic material recovered from the abandoned sites. The second control was completed at four locations on a marine terrace not used by breeding penguins, past or present, but where southern elephant seal and fur seals frequently haul out to molt and rest in summer. These two control excavations were important as this was the first time that abundant prey remains were recovered from ornithogenic soils and the controls would help verify their source from penguin guano.

This excavation of ornithogenic soils at Palmer Station produced hundreds of squid beaks and otoliths representing at least five taxa of squid and seven of fish. By far the most abundant species were glacial squid (*Psychroteuthis glacialis*) and Antarctic silverfish (*Pleuragramma antarcticum*). Lantern fish (*Electrona antarctica*) was the second most abundant fish, but was far less abundant than *Pleuragramma* while most of the other taxa were represented by only 1–3 otoliths each (Emslie et al., 1998). These prey species were also abundant in soils excavated at the active penguin colonies, but sparsely represented or absent from the marine terrace samples, verifying their presence in the soils directly from penguin guano and thus penguin diet. The number of squid beaks in these samples was surprising as squid were rare to absent in stomach lavage samples at this same area (W. Fraser, pers. comm.). It is likely that squid is consumed by the penguins late in the breeding season, while they are still returning to the colony and depositing guano, but after the chick-rearing period when stomach lavages are taken.

Four screen traps placed randomly in the active colonies and left over the winter were subsequently collected, washed to recover fresh (up to one year old) guano and verified that penguins were depositing squid beaks and otoliths late in the breeding season. These data also indicated that Adélie penguins may have shifted their diet over time, based on relative abundances of otoliths and squid beaks from dated levels at the sites in relation to warming and cooling trends since the Little Ice Age (LIA, AD 1500–1850); there was a greater proportion of squid in levels dated prior to AD 1500 and more fish during the LIA.

Research on prey remains continued at many other locations after this initial work at Palmer Station. Excavations at Rothera Station, Adelaide Island (Fig. 3) in 1999/2000 also produced abundant remains of fish and squid from abandoned colonies dating as old as 6000 BP (Emslie and McDaniel, 2002). Results here were similar to those at Palmer Station—the most abundant prey items were *P. glacialis* and *P. antarcticum*, with relative abundances for each fluctuating with warm and cool periods in the past. However, squid remains were largely restricted to sites of younger ages, possibly as a result of preservational factors such as freeze-thaw over time that could grind and destroy the chitinous beaks in older sediments. The occupation history also fit well with geological data for deglaciation of this region. Measurements of recovered *Pleuragramma* otoliths and *Psychroteuthis* beaks were added to the analyses to estimate size of the fish and squid in life revealing significant shifts in prey size selected by penguins through time (McDaniel and Emslie, 2002). Excavations of active Adélie penguin colonies on Ross Island, Ross Sea, with deposits dating up to 1000 years old also were sampled using the same methods as described above (Polito et al., 2002). Again, the same two prey species were most prevalent, though it was found that *Pleuragramma* became less abundant in the sites after about 600 BP to the present. *Psychroteuthis* was present, but less abundant than in sites from the Antarctic Peninsula, implying different foraging strategies by Adélie penguins in these two regions.

The preference by Adélie penguins for *Psychroteuthis* and *Pleuragramma* (besides krill, which lacks hard parts and does not preserve in ornithogenic soils) appears to be a circum-Antarctic pattern as shown by excavations of 17 abandoned colonies near Casey Station, Windmill Islands (Emslie and Woehler, 2005). As mentioned above, this location has one of the longest continuous occupations by breeding penguins spanning the past 9000 years. Abundant prey remains recovered from the sites were, as expected, dominated by *Psychroteuthis* beaks and *Pleuragramma* otoliths. These prey also fluctuated significantly through time, though squid was relatively rare at most sites except one dated at 5700–6100 BP where it was extremely abundant. This result suggests a shift in prey preferences, perhaps due to a period of warming at that time that may have impacted marine conditions and relative prey numbers (Emslie and Woehler, 2005), but this is in need of additional investigation.

One other study on prey remains from abandoned colonies in the Ross Sea was completed by Lorenzini et al. (2009). These authors investigated a 7000 year-old Adélie penguin record and recovered hundreds of otoliths, primarily of *Pleuragramma*. They were able to show shifts in prey abundance and size throughout this period, the longest so far analyzed in this manner for the Ross Sea region. They found a peak in abundance of *Pleuragramma* in sediment during the period from 2000 to 4000 BP ('penguin optimum') when Adélie penguins were most abundant in the southern Ross Sea. Since this study was published in 2009, most studies on past diet and dietary fluctuations in penguins in Antarctica turned to the use of stable isotope analysis of tissues preserved in abandoned colonies. However, another application of stable isotope analysis with otoliths is currently in development (see below).

4.3. Stable isotope analysis of penguin tissues

Stable isotope analysis is now a common tool in trophic ecology studies as the ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in animal tissues reflect diets at the time of synthesis (Inger and Bearhop, 2008; Boecklen et al., 2011; McMahon et al., 2013). Specifically, studies have commonly estimated shifts in trophic position based on the observation that $\delta^{15}N$ values increase (~3.4‰) with each trophic level (Minagawa and Wada, 1984). As $\delta^{13}C$ values only increase slightly (~0−1‰) in consumer tissues, these values tend to track the isotopic composition of primary producers at the base of the food web (DeNiro and Epstein, 1978). These methods have now been applied in a number of studies of seabirds since the 1980s (Bone and Jones, 2009). Recovery of prey remains to determine past penguin diets from ornithogenic soils requires systematic excavations, screen washing of hundreds of liters of sediment, and careful sorting using a stereomicroscope to recover all the remains, especially otoliths. This procedure is quite time-consuming, but stable isotope analysis provides a less time-consuming avenue to investigate diet in penguins, past and present. Its application to ancient tissues is more recent, but allows assessment of dietary shifts through time if a sufficient record of tissues can be recovered. Although there are some inherent problems in these analyses, such as unknown isotopic shifts in prey base over time, variations due to the Suess Effect, and diagenetic effects (Bone and Jones, 2009; Huang et al., 2014), these problems can now be addressed so that this methodology can provide useful information on how climate change may impact prey populations, predator diet and dietary shifts.

The first application of these methods in Antarctica to assess dietary shifts in Adélie penguins over millennia was completed by Emslie and Patterson (2007) who analyzed hundreds of tissue samples from abandoned colonies. They found little change in diet over the past 44,000 years and indication of a high-trophic diet primarily of fish. However, the data further indicated a sharp decline in both $\delta^{13}C$ and $\delta^{15}N$ within the past 200−300 years suggesting a major dietary shift to primarily krill. This shift was hypothesized to be related to a 'krill surplus' that developed in the Southern Ocean following the removal and near extinction of many krill-eating whales and seals during the historic whaling and sealing era in the 19th−20th centuries (Sladen, 1964; Laws, 1977, 1985; Fraser et al., 1992).

Using the same 7000-year record of Adélie penguin remains reported by Lorenzini et al. (2009), these authors applied stable isotope analysis to fossil and modern eggshell ($\delta^{13}C$ only) and guano samples ($\delta^{13}C$ and $\delta^{15}N$; Lorenzini et al., 2010) to assess dietary shifts through time. Their subsequent study indicated high $\delta^{13}C$ values in eggshell from 2000 to 7000 BP, possibly from high fish exploitation during that time, but more variable results from 230 to 1300 BP when penguin diets were clearly changing. Most of the shift towards lower trophic prey (e.g., krill) occurred in modern samples in support of the 'krill surplus' hypothesis. Guano samples, however, did not exhibit this shift in $\delta^{13}C$ values as found in eggshell while $\delta^{15}N$ was up to 10‰ higher in ornithogenic soils compared to modern guano. The authors attributed this difference to ammonia volatilization of old guano, which can affect soil nitrogen values, though it has been shown that volatilization does not impact the $\delta^{15}N$ values of penguin tissues preserved in these soils (see Emslie et al., 2013).

The 'krill surplus' hypothesis continued to be tested with additional stable isotope analyses of penguin and prey tissues in Antarctica. Huang et al. (2013) completed $\delta^{15}N$ analysis of Adélie penguin feathers and bones recovered from ornithogenic sediment as old as 8000 years at the Vestfold Hills, East Antarctica (Fig. 3), to investigate dietary shifts through time. They found evidence for increased krill abundance (low $\delta^{15}N$ values in penguin tissues) during cold periods (~5700−6300 and 7600−8500 BP) and the reverse during warm events (~2200−4800 and 6300−7500 BP) throughout the Holocene. In addition, they documented low $\delta^{15}N$ values in modern Adélie tissues in accordance with the 'krill surplus' hypothesis. All of these studies have indicated remarkable consistency in showing a decline in $\delta^{15}N$ values in Adélie Penguin tissues and guano within the past 200 years (Fig. 4), providing strong support for the 'krill surplus' hypothesis.

Emslie et al. (2013) expanded the investigation of the 'krill surplus' hypothesis to Gentoo penguins using egg membrane from active and abandoned colonies in the South Shetland Islands (Fig. 3). These authors investigated three study sites on King George and Livingston Islands and found considerable variation in $\delta^{13}C$ and $\delta^{15}N$ values in ancient and modern tissues, with a weak decline of these values in modern egg membrane in support of a dietary shift and the 'krill surplus' model. The weaker relationships compared to those in Adélie penguins (Emslie and Patterson, 2007) were probably due to the greater importance of fish in the diet of Gentoo penguins, past and present, than in Adélies. As yet, no ancient Chinstrap tissues are available to further test this model with this species. Recent advances in compound-specific stable isotope analyses may allow more exact tests of the 'krill surplus' hypothesis by extracting specific amino acids for analysis from prey as well as penguin tissues, ancient and modern. Such analysis can help resolve whether or not isotopic values have shifted in prey populations in the past that could, at least in part, explain the large decline in $\delta^{13}C$ and $\delta^{15}N$ values recorded in modern versus ancient Adélie penguin tissues.

Finally, Lorenzini et al. (2011) used stable isotope analyses of $\delta^{18}O$ on ancient and modern Adélie penguin eggshell carbonate to assess variation in fresh water input in seawater to investigate paleoenvironmental change in the Ross Sea region during the Holocene. They analyzed 858 fossil and 65 modern eggshells from ancient and active penguin colonies in the Terra Nova Bay region, Ross Sea, spanning the past 8000 years in age. While much variation occurred in the $\delta^{18}O$ values, they noted a shift from generally lower values from 8000 to 2000 BP, to higher values after 2000 BP. The authors attributed this shift to decreased snowmelt and freshwater input into seawater that could be related to dietary shifts in fish and krill in Adélie penguins as proposed by Lorenzini et al. (2009). The $\delta^{18}O$ results also are in accordance with a cool period that began at the end of the 'penguin optimum' at 2000 BP (Emslie et al., 2007).
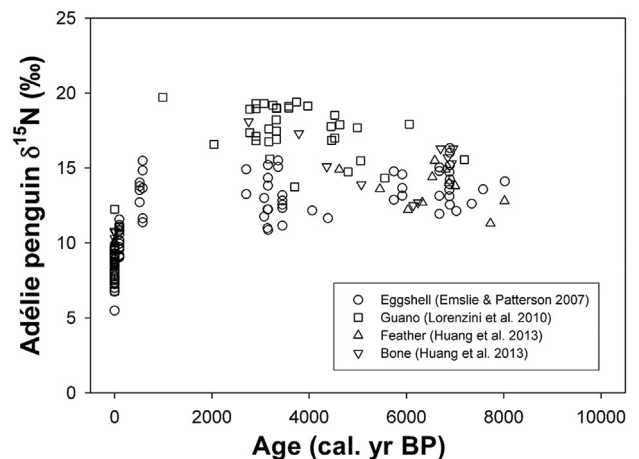

Fig. 4. Synthesis of $\delta^{15}N$ values reported on ancient and modern Adélie penguin tissues and guano in Antarctica. The lower values within the past ~200 years indicate a major shift in diet in support of the 'krill surplus' hypothesis.

4.4. Otolith $\delta^{18}O$ analysis as a measure of ocean temperatures

The application of stable isotope analyses on tissues preserved in ornithogenic soils continues to expand. The large number of *Pleuragramma* otoliths spanning the past 9000 years in age recovered from ornithogenic soils at the Windmill Islands provided an opportunity to apply this methodology to penguin prey remains as well. Stable oxygen isotope values ($\delta^{18}O$) from otoliths have been used as a proxy for ocean temperature and environmental conditions for time periods as far back as the Jurassic, 172 Ma (Patterson, 1999). During growth, otoliths record environmental information such as water temperature, metabolism, and diet (e.g., Radtke et al., 1996; Campana, 1999; Ivany et al., 2000). Thus, otoliths can be an excellent indicator of ocean temperatures, past and present (e.g., Andrus et al., 2002). Juvenile *P. antarcticum* of the size class preyed upon by penguins (95–110 mm standard length; McDaniel and Emslie, 2002) are most abundant in the upper 100 m of the water column (Nast et al., 1987), or well within the average foraging depth of diving pygoscelid penguins (<40 m; Williams, 1995). Therefore, we hypothesized that $\delta^{18}O$ values of their otoliths recovered from ornithogenic soils could provide a proxy of upper water column temperatures over time, independent of penguin and other paleoclimatic records.

To test this hypothesis, we determined $\delta^{18}O$ from 114 *P. antarcticum* otoliths recovered from ornithogenic soils in the Windmill Islands (Supplementary Data Table 1). We averaged the $\delta^{18}O$ values by time periods (estimated by midpoint of 2σ calibrated ranges in calendar years BP from radiocarbon-dated levels) and found significant variation in $\delta^{18}O$ values through time (Fig. 5). The fluctuations in these values matched temperature trends based on other paleoclimatic records from marine and lake sediment in the Windmill Islands (Kirkup et al., 2002; Cremer et al., 2003) and nearby Bunger Hills regions (Melles et al., 1997; Kulbe et al., 2001; Verkulich et al., 2002) during the middle and late Holocene. In particular, early Holocene warming peaks at 4000 ^{14}C BP, followed by a cooling period prior to late Holocene warming that follow similar trends in the oxygen isotope record provided by the otoliths. These results indicate that, with additional refinement of this methodology, otoliths recovered from ornithogenic soils can increase the resolution of radiocarbon-dated episodes of ocean temperature changes to other paleoclimatic records and are worthy of additional investigation in Antarctica.

4.5. Geochemical analyses

Geochemical analyses of ornithogenic sediments and soils use methodologies that allow stratigraphic assessment of mineral and nutrient content and how it changes with depth. These analyses are particularly useful in determining the impact of penguin guano on sediment accumulation in lakes and low areas surrounding penguin colonies. Moreover, these studies can indicate stratigraphically how penguin impacts have fluctuated over time with periods of occupation and abandonment. While mineral content of ornithogenic soils had been studied and documented early on in the investigations of these soils as described above, the first one to use this information to help reconstruct the occupation history and size of past penguin populations was Zale (1994). He used a nearly 3 m deep sediment core from Lake Boeckella, Hope Bay (Fig. 3), at the tip of the Antarctic Peninsula to estimate that Adélie penguin occupation of this region began by the mid Holocene, or ~5550 ^{14}C BP. This site currently supports the second largest Adélie penguin colony in the peninsula with over 120,000 breeding pair (though the size of the colony is believed to have declined from human impacts from research stations established there beginning in 1945). Zale (1994) found that elements abundant in penguin
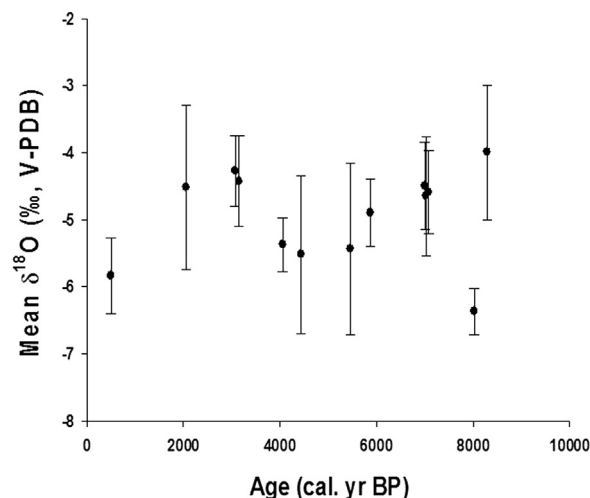
Fig. 5. Mean $\delta^{18}O$ values determined from 114 Antarctic silverfish (*Pleuragramma antarcticum*) otoliths from ornithogenic soils excavated at abandoned Adélie penguin colonies spanning 9000 years in age from the Windmill Islands, East Antarctica. See Supplementary Table 1 for sample size by time period.

guano, especially P and Cu, were significantly higher in concentration in the core samples than background levels from lakes not associated with penguin colonies. The author suggested that the penguin population began increasing at this site, with guano deposits washing into the lake, in the mid Holocene and continued to increase in the 20th century due to a krill surplus in the Southern Ocean as baleen whales were being removed from the marine ecosystem.

An additional study using mineral concentrations in sediment cores to estimate past penguin populations was completed at Ardley Island, King George Island, Antarctic Peninsula (Fig. 3; Sun et al., 2000). These authors used a lake sediment core taken near an active Gentoo penguin colony to analyze relative concentrations of 'bio-elements' (Zn, F, Sr, Ba, S, P, Cu, Se, Ca) at 1-cm intervals with depth using a Q-mode factor analysis, a common geochemical method to analyze numerous variables collectively. An increased concentration of these elements indicated increased guano input and thus more penguins, while a decrease in elements was related to fewer penguins and more tundra vegetation. Data indicated that penguin population size fluctuated over the past 3000 years and was lowest at 1800–2300 BP during a relatively colder period (Sun et al., 2000). Besides the bio-elements, the ratio of $^{87}Sr/^{86}Sr$ in the acid-soluble fractions was found to be more accurate in the reconstruction of historical penguin population changes from ornithogenic sediments (Sun et al., 2005). This research was elaborated upon at both Ardley Island and on the nearby Barton Peninsula by Sun et al. (2004) and Zhu et al. (2005), also from sediment cores from depressed areas and one lake near the active colonies. These studies, also based on Q-factor analysis of bio-elements and changes in vegetation, documented similar oscillations in penguin populations over the past 3000 years with evidence for rapid expansion of the Gentoo colony over the last 60 years. Wang et al. (2007) added two more lake cores from Ardley Island to these analyses to investigate fecal sterols and *n*-alkanols as proxies for the presence of penguins or vegetative cover, respectively. Variations in these proxies throughout the cores indicated that penguin populations were highest at 1800–1360 BP, similar to results by Sun et al. (2000).

In the Ross Sea, Liu et al. (2013) conducted a geochemical analysis of 22 bio-elements and carbon isotope distributions in five sediment cores taken in depressed areas near active Adélie penguin

colonies on Ross (Capes Bird and Crozier) and Beaufort Islands (Fig. 1). The combined analyses provided a strong proxy for the influence of penguin guano versus algal biomass on the geochemistry of the sediment, and thus relates to relative changes in the penguin populations through time. Importantly, they found that these patterns were similar to seabird-influenced sediment in other parts of the world so that this methodology could be applied across a larger geographic scale. The cores from Cape Bird were further studied by Hu et al. (2013) for fecal sterols and *n*-alkanols as a further means to detect changes in Adélie penguin populations through time at this site. Their analysis indicated more sterols and an increase in penguin populations during the Little Ice Age. However, local emigration or movements of existing colonies to new areas could also account for the increased sterols (Hu et al., 2013).

Finally, Liu et al. (2011) investigated rare earth elements (REEs) from ornithogenic sediment on Ardley Island to determine if they also showed distribution patterns in relation to penguin occupation periods (via guano input into the sediment). These elements were compared to the distribution of bio-elements from guano in the sediments and a negative correlation was observed. Nie et al. (2014) studied rare earth elements in the cores from Cape Bird and Beaufort Island in comparison with background media including bedrock, algae, and guano. As at Ardley Island, these authors found a negative correlation between REEs and bio-elements from penguin guano. They also determined that most REEs in the sediment are from bedrock sources, while smaller proportions were derived from algae and guano. REEs, then, can be added to the growing list of geochemical signals in ornithogenic sediment that can serve as a proxy for penguin occupation based on guano inputs into the sediment (also see Sun et al., 2013). In summary, these types of mineral bio-element analyses on ornithogenic sediment and soils will continue to add new information on the long-term record of penguin occupations in Antarctica.

4.6. Ancient DNA

Recovery of ancient DNA from penguin tissues to assess genetic change and evolutionary rates is a relatively new field of study that was first investigated by New Zealand scientists in the Ross Sea (Lambert et al., 2002). These authors were able to sequence ancient DNA from 96 well-preserved bones of Adélie penguin that were recovered from abandoned colonies as old as 6424 BP. Using data on mitochondrial haplotypes, Lambert et al. (2002) were able to demonstrate rates of evolution in this species that were two to seven times higher than previous estimates. In addition, research by Ritchie et al. (2004) using fossil bone and blood samples from live Adélie penguins revealed two distinct monophyletic lineages in this species, one in the Ross Sea (RS lineage) and one associated with all other locations in Antarctica (A lineage). Both lineages occur in the Ross Sea today and probably colonized this region soon after deglaciation at the end of the Pleistocene. This research clearly demonstrated the value of tissues preserved in abandoned colonies to investigate genetic evolution in a living species.

The research was taken a step further by Shepherd et al. (2005) who were able to extract and genotype ancient DNA at nine microsatellite loci to determine microevolutionary rates using Adélie penguin bones dated as old as 6000 BP that were recovered from Inexpressible Island, Ross Sea. The authors compared these data with living penguins at the same site, resulting in a unique study of changes in gene frequencies over geologic time. Millar et al. (2008) also investigated mutation rates using the mitochondrial genome in this species, again using modern and subfossil remains up to 37,000 years old from the Ross Sea. It is rare to have DNA samples of the same species through geologic time and these authors were

able to demonstrate that mutation and evolutionary rates did not differ over this 37,000 year period in contrast to other studies that found a time-dependency relationship with these rates. Subramanian et al. (2009) continued on this theme and used fossil remains of Adélie penguins up to 44,000 years old to investigate mitogenomic rates and time dependency. These authors were able to demonstrate that the two Adélie penguin lineages (A and RS) experienced statistically similar evolutionary rates, though the RS lineage rate was slightly higher, probably due to mutational processes. This research also indicated that these rates have remained constant over geologic timescales relative to modern rates in Adélie penguins. Thus, this body of work on ancient DNA from Adélie penguins has been invaluable in testing hypotheses on rates of evolution that can now be applied to evolutionary rates in other avian species.

Ancient DNA is also useful for identifying the species of penguin that occupied an abandoned site, an important tool when the recovered remains are too fragmentary for direct identification from bones or feathers. For example, excavation of abandoned colonies in the Copa area, King George Island, by Emslie et al. (2003a) produced fragmentary remains that could not be identified to species as all three pygoscelid penguins currently breed at this locality. Thus, precise identification of the subfossil remains was essential to reconstruct the occupation history of this region. Nine bones from five abandoned sites had sufficient DNA for species identification verifying that all three species had colonized this island by 500–600 BP. At Byers Peninsula, Livingston Island (Fig. 2), Emslie et al. (2011) also used ancient DNA from to identify Gentoo penguin remains, based on one feather and six egg membrane fragments preserved in the ornithogenic soils of abandoned colonies near an active Gentoo colony at this site. The penguin remains were up to ~1000 BP in age and are the oldest now known for this species in the Antarctic Peninsula.

4.7. Mercury in penguin tissues and seal hair

One of the more recent uses of ancient tissues preserved in sediment and ornithogenic soils in Antarctica is to examine temporal changes in mercury availability in the Southern Ocean. While numerous studies on current background levels of mercury have been completed in the Antarctic Peninsula (Favaro et al., 2004; Dos Santos and Silva-Filho, 2006; Brasso et al., 2012) and Ross Sea (Bargagli et al., 1993, 1998a, 1998b, 2005, 2007; De Mora et al., 1993; Vandal et al., 1998; Riva et al., 2004; Brasso and Polito, 2013), research on past mercury levels using biological tissues has been rare. The first investigation using ancient tissue samples was completed in the Antarctic Peninsula with seal hairs from deposits up to 2000 years old (Sun et al., 2006). The seal hairs were recovered from a sediment core on Fildes Peninsula, King George Island (Fig. 3), where southern elephant seals (*Mirounga leonina*) currently haul out for molting. Hairs were extracted at 0.5 cm intervals from this core and analysis documented considerable variation in mercury concentrations through time, with high values correlating with the rise of prehistoric civilizations and low values with their decline. The authors explained this relationship relative to anthropogenic activities associated with these cultures, including gold and silver mining that would have released more mercury into the atmosphere.

Nie et al. (2012) were the first to study mercury concentrations in ornithogenic sediment as well as in seal hairs using five sediment cores from Ross and Beaufort Islands, Ross Sea (Fig. 1). These authors found relatively higher concentrations of mercury associated with high total organic carbon and phosphorus, a bio-element from penguin guano. A section of one core with abundant seal hairs and excrement also exhibited relatively higher mercury levels

indicating that penguin guano and seal excrement can act as bio-vectors of mercury from the marine to terrestrial ecosystem. None of the mercury levels were high enough to be considered adverse to penguins and seals. These studies not only demonstrate correlations in mercury availability in Antarctica with anthropogenic events, but also reveal the potential role of penguin guano and seal excrement in increasing mercury levels in terrestrial sediment.

To further highlight the utility of mercury analyses of tissue recovered from ornithogenic soils, we completed a study using ancient and modern Gentoo penguin egg membrane. The egg membranes were recovered from excavations of abandoned colonies at King George (Copa area and Ardley Island) and Livingston Islands (Byers Peninsula), as well as from modern eggshell collected at active Gentoo colonies at these sites. Eggshell membranes were thoroughly cleaned with dH$_2$O and analyzed for total mercury (ppm, dry weight) using a Tri-Cell DMA-80 Direct Mercury Analyzer. Mercury concentrations in eggshell membranes from modern Gentoo colonies were found to be significantly lower than in eggshell membranes from ancient, abandoned colonies ($F_{1,152}$ = 245.7, p < 0.0001; Fig. 6). Mercury concentrations in ancient eggshell membranes did not vary among breeding colonies; however, among modern colonies, mercury concentrations at Ardley Island were significantly higher than those at Admiralty Bay (Tukey's HSD, p < 0.05). By combining dietary analysis from stable isotopes (δ^{15}N; Fig. 7) with mercury data from both ancient and modern penguin tissues, we were able to test the hypothesis that elevated mercury in ancient tissues was the result of foraging at an elevated trophic position. As discussed above, there is now evidence of a dietary shift in the diet of *Pygoscelis* penguins approximately 200 years ago in which penguins shifted from a fish-based to krill-based diet (Emslie and Patterson, 2007; Emslie et al., 2013; Huang et al., 2013). More specifically, Emslie et al. (2013) found the diet of modern Gentoo penguins, at the breeding colonies examined, to be dominated by *Euphausia superba* (65.7% of diet) while ancient populations consumed similar proportions of fish and krill (46% and 54%, respectively). The preferred prey fish of Gentoo penguins in the Antarctic Peninsula (*P. antarcticum* and *Lepidonotothen squamifrons*) occupy an elevated trophic position relative to Antarctic krill (*E. superba*; Polito et al., 2011) and owing to the process of biomagnification, an increase in the proportion of fish consumed should result in increased exposure to mercury. Our findings support this hypothesis as reflected by elevated mercury concentrations in ancient tissues relative to modern penguins (Figs. 6 and 7). While the difference in δ^{15}N between ancient and modern Gentoo populations was <1.0‰, the diet of ancient populations included an average of 12% more fish than modern which
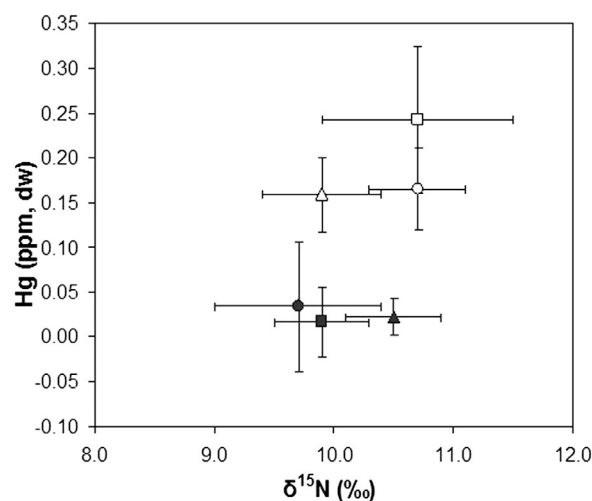
Fig. 7. Ancient Gentoo penguin populations (open symbols) foraged at a higher trophic position relative to modern populations (filled symbols) providing explanatory power to the eleavted mercury concentrations in the former relative to the latter. Triangles = Admiralty Bay, King George Island; squares = Ardley Island, King George Island, and circles = Byers Peninsula, Livingston Island.

could certainly provide explanatory power to the trend detected. Ultimately, the preservation of avian tissues, such as eggshell membrane and feathers in ornithogenic soils provide a unique opportunity to examine historical patterns of mercury availability in this remote ecosystem. Pairing mercury concentrations with stable isotope analysis allowed the source of variation in mercury concentrations between ancient and modern tissues to be resolved—in this case, the elevated trophic position (δ^{15}N) of ancient Gentoo penguins appears to provide sufficient explanatory power to the higher mercury concentrations found in ancient tissues.

5. Conclusions

We have reviewed the current state of knowledge on ornithogenic soils and provided new evidence into how the natural biological archive they contain can provide remarkable insight on the paleoecology and paleobiology of pygoscelid penguins, especially the Adélie penguin, in Antarctica. We know of no other region in the world where a living species of bird has a nearly continuous, well preserved record of tissues dating from over 44,000 years ago to the present. We not only have detailed information on the occupation history of Adélie penguins and how it has been influenced by climate change over millennia, but also have shown how this research can provide high-resolution data on past marine and terrestrial environments. Moreover, well preserved penguin tissues extracted from these soils provide a rare opportunity to investigate evolutionary and mutation rates, as well as lineage divergence, in these penguins from ancient DNA. New directions in stable isotope analyses of prey remains hold promise for providing independent data from the marine and lake sediment and ice-core records on climate and sea surface temperature change and how penguins have responded to both natural and anthropogenic environmental changes. Some problems still remain unresolved, including the inability to date younger (late Holocene) penguin remains due to the marine carbon reservoir effect (see Emslie, 2001) and the need for more precise information on penguin populations changes through time that geochemical evidence cannot provide. However, considerable research has been completed on these soils and the tissues they contain since Louis Bernacchi first made his observations in 1899, but that was only 115 years ago and we predict many
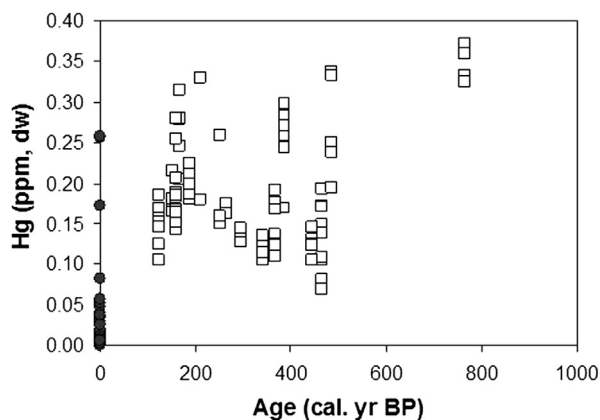

Fig. 6. Mercury concentrations in eggshell membrane from ancient (squares) and modern (circles) Gentoo penguins on King George Island, Antarctic Peninsula.

more new and innovative studies of this natural archive will be developed in the future.

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2014.07.031.

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