

# A 45,000 yr record of Adélie penguins and climate change in the Ross Sea, Antarctica

Steven D. Emslie\*

Department of Biology and Marine Biology, University of North Carolina, 601 S. College Road, Wilmington, North Carolina 28403, USA

Larry Coats

Department of Geography, University of Utah, 260 S. Central Campus Drive, Room 270, Salt Lake City, Utah 84112, USA

Kathy Licht

Geology Department, Indiana University-Purdue University Indianapolis,  
723 W. Michigan Street, Room SL118, Indianapolis, Indiana 46202, USA

## ABSTRACT

**Well-preserved remains of bone, tissue, and eggshell of Adélie Penguin (*Pygoscelis adeliae*) have been recovered from numerous abandoned colonies in the Ross Sea region, Antarctica. Radiocarbon dates on these remains provide an occupation history for this species ranging from hundreds to tens of thousands of years ago. We completed 62 new radiocarbon dates on these remains, which now indicate that an open-water marine environment existed in the Ross Sea from ca. 45,000 to 27,000 <sup>14</sup>C yr before present (B.P.) and provide constraints for the timing of the last advance of the Ross Ice Sheet. Penguins did not recolonize the Ross Sea until ca. 8000 calendar years (cal yr) B.P., after the early Holocene retreat of the Ross Ice Sheet. Two subsequent periods of abandonment at 5000–4000 and 2000–1100 cal yr B.P. correlate with cooling episodes that caused unfavorable marine conditions for breeding penguins. Most modern colonies were established only within the past 2000 yr.**

**Keywords:** Adélie Penguin, abandoned colonies, occupation history, Ross Sea, ice sheet.

## INTRODUCTION

The fossil record for living penguin species is relatively poor (Fordyce and Jones, 1990). However, numerous abandoned and active colonies of Adélie Penguin (*Pygoscelis adeliae*) exist in the Ross Sea region, Antarctica, where the cold, dry environment facilitates preservation and mummification of ancient tissue and other remains (bone, skin, feathers, guano, and eggshell; Baroni and Orombelli, 1994a; Lambert et al., 2002; Polito et al., 2002; Emslie et al., 2003; Shepherd et al., 2005). Moreover, since breeding Adélie penguins require ice-free terrain for nesting, open-water access to this terrain, and adequate marine food supplies nearby, abandoned colonies are a proxy for these conditions in the past. Here, we report 62 new radiocarbon dates on Adélie Penguin remains from 21 active and abandoned sites at 11 localities in the Ross Sea, as well as one fossil molt site. The 62 radiocarbon dates, along with previously published dates on this species, provide an occupation history of Adélie penguins that now spans the past 45,000 yr, the longest known for any living species of penguin. By comparing this occupation history with the paleoclimatic record, we show that penguin distributions have shifted over millennia with climate change and sea-ice extent.

## METHODS

Abandoned penguin colonies were excavated following published methods (Emslie et al., 2003). Samples were dated from 23 sites at 11 localities (see the GSA Data Repository<sup>1</sup>). Organic remains were sorted from excavated sediments and submitted to the Rafter Radiocarbon Laboratory, New Zealand, or Beta Analytic, Inc., Coral Gables, Florida, for accelerator mass spectrometry (AMS) radiocarbon analysis.

All radiocarbon dates less than 26,000 years old were calibrated for the marine-carbon reservoir effect using a  $\Delta R = 750 \pm 50$  yr and the CALIB 5.0 software program with the MARINE04 database (Stuiver and Reimer, 1993; Hughen et al., 2004) or by the Pretoria/Beta Analytic calibration program at Beta Analytic, Inc. These calibrations provide a minimum and maximum age for each sample in calendar yr B.P. (cal yr B.P.) with 95% accuracy that the true date of the sample falls within this range. The 62 new radiocarbon dates on penguin remains (GSA Data Repository, see footnote 1) were compared with previously published dates from the Ross Sea region (Harrington and McKellar, 1958; Harrington, 1960; Spellerberg,

1970; Stonehouse, 1970; Speir and Cowling, 1984; Heine and Speir, 1989; Baroni and Orombelli, 1994a; Lambert et al., 2002; Polito et al., 2002; Emslie et al., 2003; Hall et al., 2004; Baroni and Hall, 2004), which were calibrated using the same methods, to develop the occupation history.

Only dates from ornithogenic (bird-formed) soils, that represent bona fide evidence of former breeding by penguins, or penguin molt layers were used in this analysis. In addition, questionable dates that were far outside the range of dates on associated material and/or were stratigraphically mixed were excluded. These dates included one reported from bottom layers of an abandoned colony at Cape Bird (Speir and Cowling, 1984). The authors reported the age on penguin remains as  $7070 \pm 180$  <sup>14</sup>C yr B.P., but Heine and Speir (1989) reported this same date (by similar laboratory numbers) on penguin bone at  $8080 \pm 160$  <sup>14</sup>C yr B.P. and did not cite the other date. This site was relocated in 2001, based on a map and description in Heine and Speir (1989), and excavated to the base of the ornithogenic sediments. Five radiocarbon dates on penguin bones, selected from the top to bottom of the exposed profile, produced ages ranging between 590 and 140 cal yr B.P. (Emslie et al., 2003). Thus, the two reported dates of 7070 and 8080 yr B.P. are considered invalid. Two dates on guano from ornithogenic sedi-

\*E-mail: emslies@uncw.edu.

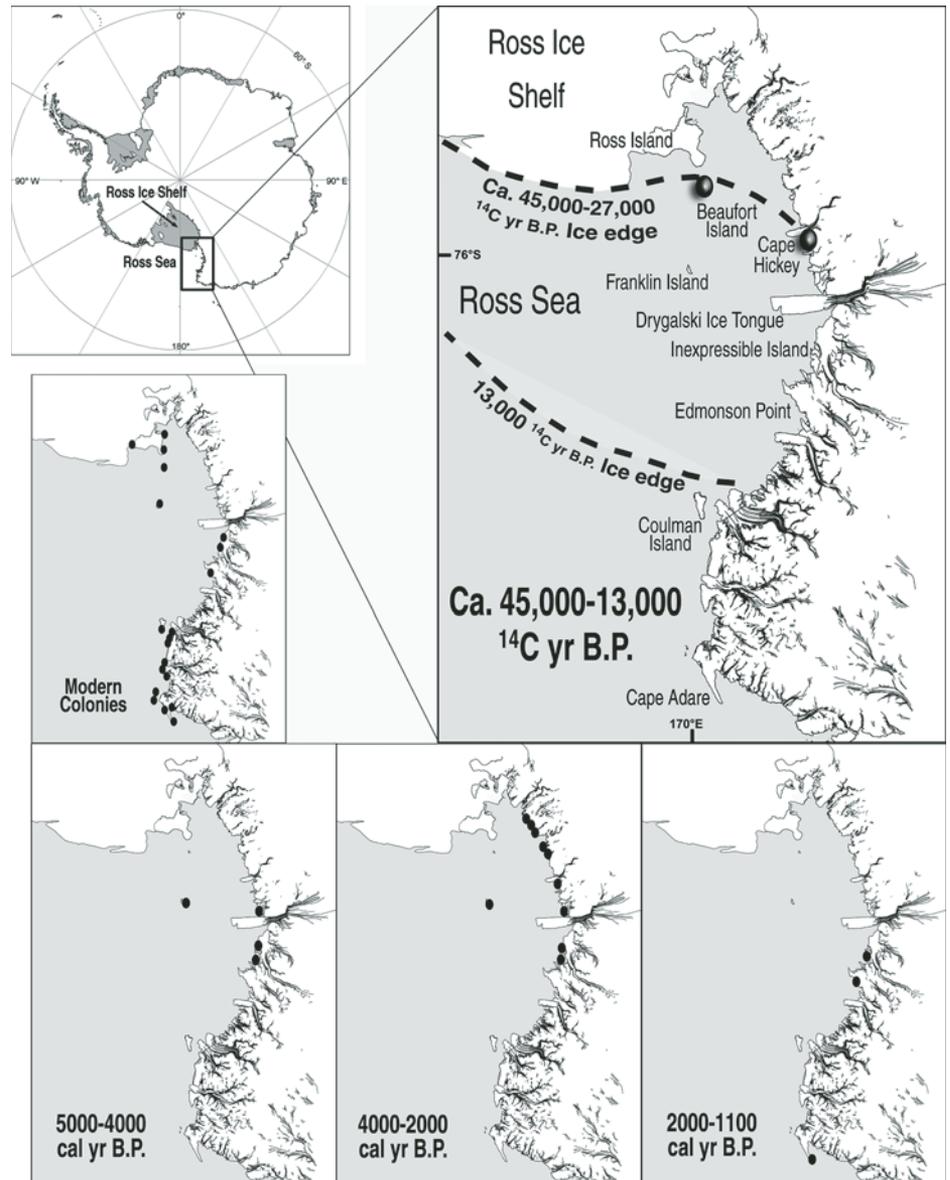
<sup>1</sup>GSA Data Repository item 2007021, location and elevation of sites excavated, and all radiocarbon dates, is available online at [www.geosociety.org/pubs/ft2007.htm](http://www.geosociety.org/pubs/ft2007.htm), or on request from [editing@geosociety.org](mailto:editing@geosociety.org) or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

ments at Cape Hickey are reported as  $11,325 \pm 360$  and  $13,070 \pm 405$  yr B.P. (Baroni and Orombelli, 1994a). Two additional old guano dates also have been reported from this site (Lambert et al., 2002). However, all these dates from Cape Hickey may be contaminated by old carbon and are considered invalid (Hall et al., 2004). Two old dates on guano from Campo Icarus (TO-4966,  $10,180 \pm 150$  yr B.P.) and Gondwana Station (TO-4965,  $9220 \pm 100$  yr B.P.; Lambert et al., 2002) were redated by Baroni and Hall (2004) and were found to be much younger in age than originally reported (OS-27673 and OS-27547, respectively).

### HISTORY OF THE ROSS ICE SHEET

Two sites have produced a series of radiocarbon dates that verify the presence of breeding penguins in the Ross Sea during the mid-Wisconsinan (Fig. 1; GSA Data Repository, see footnote 1). Cape Hickey is a remote site where only a few small pockets of ornithogenic soils from abandoned colonies are exposed. The oldest dates on penguin eggshells from these deposits range from 27,170 to 43,010  $^{14}\text{C}$  yr B.P. and imply that open water existed there during that period. The sites were re-exposed by ca. 4000–3000 cal yr B.P. because dates on penguin remains from upper deposits indicate reoccupation by breeding penguins at that time. In addition, an exposure of laminated layers of penguin tissue and bone under ~20 m of overlying sediments was discovered on Beaufort Island by Seppelt et al. (1999) in 1997 and was described as a possible former breeding colony of Emperor or Adélie penguins. Our visit to the site in 2005 indicated that the deposits are not characterized by ornithogenic soils as found at abandoned colonies, but are dominated by matted layers of pin feathers that are characteristic of molting sites. The feathers and bones have been identified as Adélie Penguin. Two feathers and one bone from these layers dated beyond the range of radiocarbon dating ( $>44,000$  yr old) and are now the oldest known records for this species. This site also implies that open water existed in the Ross Sea in the mid-Wisconsinan. These deposits were probably covered by glacial ice for most of the period following the last advance of the marine-based Ross Ice Sheet.

These pre-Holocene dates on penguin remains are consistent with terrestrial and marine glacial geological data. During the late Quaternary Last Glacial Maximum (LGM), grounded ice from the Ross Ice Sheet extended as far north as Coulman Island in the Ross Sea Embayment (Fig. 1; Anderson et al., 1992; Licht et al., 1996; Conway et al., 1999; Shipp et al., 1999). Previous research has shown that glacial ice did not advance into the mouth of Taylor Valley until after 24,000  $^{14}\text{C}$  yr B.P. (Hall and Denton, 2000). Dates on foraminifera from glacial marine sediments on the western

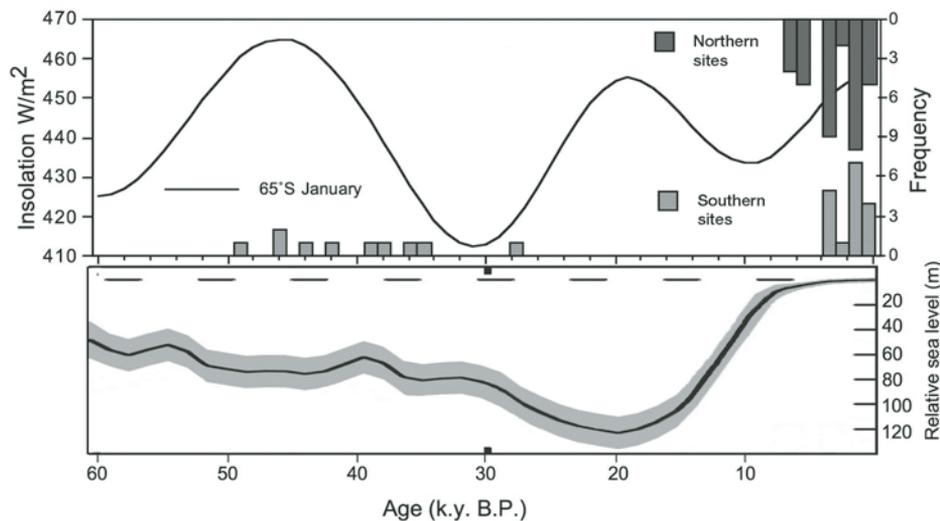


**Figure 1. Location of study region in Antarctica and ages for Adélie penguin occupations (in calendar yr B.P. [cal yr B.P.]) in Ross Sea over 45,000 yr. Locations of Ross Ice Shelf grounding lines since mid-Wisconsinan also are shown in radiocarbon years, ( $^{14}\text{C}$  yr B.P.).**

Ross Sea continental shelf just northward of the LGM grounding line also show that open-water conditions existed there until at least ca. 22,000  $^{14}\text{C}$  yr B.P. (Licht et al., 1996). Additionally, the solar insolation curve for 65°S (Berger and Loutre, 1991) shows a period of above average insolation ( $>440$   $\text{W}/\text{m}^2$ ) from 54,000 to 38,000 yr B.P., suggesting possible solar forcing for this period of open water in the Ross Sea (Fig. 2), particularly considering that a change in external forcing takes 8000–10,000 yr to propagate through the ice mass. Thus, the Ross Ice Sheet, or an ice shelf extending from the grounding line, could not have advanced past Cape Hickey until after ca. 27,000  $^{14}\text{C}$  yr B.P. and reached its LGM grounding line in the western Ross Sea by ca. 18,000–20,000  $^{14}\text{C}$  yr B.P. (Ingólfsson et al.,

1998; Domack et al., 1999). This rate of ice sheet advance is similar to that of its retreat, the latter of which is estimated at ~50–100 m/yr based on marine-sediment data (Licht et al., 1996; Domack et al., 1999; Licht and Andrews, 2002).

No data exist as to where Adélie penguins had breeding colonies during the LGM, or prior to 45,000  $^{14}\text{C}$  yr B.P. We can only speculate that populations were reduced during these periods and that refuges were located on ice-free islands beyond the continental shelf (e.g., Balleny Islands), or on a shallow exposed shelf when sea level was ~80 m lower at this time (Chappell et al., 1996; Waelbroeck et al., 2002). Thus, these earlier sites may now be obliterated, under water, or under existing ice shelves and glaciers.



**Figure 2. A: Solar insolation forcing for 65°S adapted from original in Berger and Loutre (1991). Histogram depicts periods of Adélie penguin occupation with heights of bars providing frequency of radiocarbon dates on penguin remains per time period. Occupation periods indicate open-water conditions in Ross Sea at those times. B: Composite relative sea-level curve (approximates eustatic value) showing confidence interval in gray modified from Waelbroeck et al. (2002). Antarctica's relative sea-level history will be somewhat different because of ice sheet's isostatic effects; however, local data for entire time interval are not available.**

## HOLOCENE PENGUIN OCCUPATIONS

The radiocarbon chronology reveals that the Ross Sea was not reoccupied by breeding penguins until after Ross Ice Sheet began receding at ca. 13,000  $^{14}C$  yr B.P. (Conway et al., 1999; Domack et al., 1999). By ca. 9600  $^{14}C$  yr B.P., most of the northern Ross Sea (defined as north of the Drygalski Ice Tongue at 75°24'S) was open water again (Cunningham et al., 1999; Masson et al., 2000; Licht and Andrews, 2002), and the first Holocene penguin occupations were restricted to the Terra Nova Bay region (North Adélie Cove and Campo Icarus) at ca. 8000 cal yr B.P. (Baroni and Orombelli, 1994a; Lambert et al., 2002). By ca. 5000–4000 cal yr B.P., only a few sites were occupied along the central Victoria Land Coast (Prior Island to Terra Nova Bay), as well as Franklin Island (Fig. 1). This limited occupation correlates with a cooling period documented in the geologic and hydrologic records. Data from ice cores and raised beaches indicate that a Holocene “optimum,” or period of warming and glacial retreat, occurred from ca. 7000 to 5000 cal yr B.P. in the Ross Sea (Ingólfsson et al., 1998; Masson et al., 2000; Baroni and Orombelli, 1994b), although Steig et al. (1998) and Cunningham et al. (1999) place the age for this retreat at 6000 cal yr B.P. The cooling period that followed this “optimum” may have caused extensive permanent sea ice or unfavorable marine conditions that prevented penguins from occupying sites along the Scott Coast; glacial readvancements also are documented in the Antarctic Peninsula, indicating a widespread climatic event at this time (Ingólfsson et al., 1998). However, open water

must have existed in the Terra Nova Bay region by at least 5000–4000 cal yr B.P. to allow penguins to reach breeding colonies in this area as well as at Franklin Island; this supports marine sedimentary data for a mid-Holocene origin of the Terra Nova polynya that persists in this region today (Berkman et al., 1998).

From ca. 4000 to 3000 cal yr B.P., there was extensive occupation by Adélie penguins along the central to southern coastlines, which was associated with climate warming. This occupation period has been referred to as the “penguin optimum” (Baroni and Orombelli, 1994a). Our data support this optimum, but with one occupation enduring at Marble Point in the southern Ross Sea until ca. 2000 cal yr B.P. After that time, the southern Ross Sea was abandoned by breeding penguins for ~900 yr, probably due to extensive permanent sea-ice coverage at that time that blocked access to ice-free terrain along the Scott Coast (Emslie et al., 2003). In concordance with this abandonment, the record now shows the earliest known occupation at Cape Adare in the northern Ross Sea, with continued occupation of Inexpressible Island in Terra Nova Bay (Fig. 1). Another new occupation occurred at Edmonson Point shortly after these. Cape Adare now has the largest Adélie Penguin colony in Antarctica with an estimated size of ~85,000–135,000 nests (Woehler, 1993; Ainley, 2002). The colony is located on a broad flat beach only 1–2 m above present sea level. Parallel-trending ridges and mounds on this beach that extend for hundreds of meters have been described as raised beaches (Colhoun et al., 1992), but are composed of basal beach sediments

capped entirely by ornithogenic soils formed by breeding penguins. Thus, these extensive ridges are all bird-formed and are not the result of any geological or glaciological processes.

Until now, no penguin remains have been dated from Cape Adare, contrary to what has been inferred in the literature (Ingólfsson et al., 1998; Cunningham et al., 1999; Licht et al., 1999). Dates presented here on the ornithogenic sediments from the mounds on the beach as well as abandoned sites on a terrace 300 m above the beach indicate that penguin occupation at this colony did not begin until ca. 2000 cal yr B.P. This late Holocene occupation coincides with extensive abandonment to the south (Emslie et al., 2003) and may be interpreted as a shift in the population center for Adélie penguins to the northern Ross Sea at the end of the “penguin optimum.” Most of the currently active penguin colonies in the northern Ross Sea have been dated to no older than ca. 2000 cal yr B.P., while the oldest in the southern Ross Sea do not predate ca. 1100 cal yr B.P. (Polito et al., 2002; Emslie et al., 2003). Only one colony at Inexpressible Island appears to have had a continuous occupation for the past ~7000 yr, perhaps in association with the inception of the Terra Nova Bay polynya. While most active colonies in the southern Ross Sea have been dated, at least ten others in the northern Ross Sea, located on Coulman Island and north to Cape Adare, have not yet been dated and warrant further investigation.

## CONCLUSIONS

The Adélie Penguin record indicates major shifts in this species' population in the Ross Sea during the Holocene, including two periods of large-scale abandonment at 5000–4000 and 2000–1100 cal yr B.P. These population shifts are in accord with ancient DNA data from this species that evince a high rate of microevolution over the past 6000 yr in the Ross Sea, perhaps in response to mega-icebergs and a constantly changing sea-ice regime over millennia (Shepherd et al., 2005). Our data reveal that the current distribution of Adélie penguins in the Ross Sea is a relatively recent phenomenon resulting from thousands of years of climate change. We expect that population shifts by Adélie penguins will remain a dynamic process in this region of Antarctica.

## ACKNOWLEDGMENTS

This research was funded by grants 9909274 and 0125098 from National Science Foundation (NSF) Office of Polar Programs. Radiocarbon samples were completed at the Rafter Radiocarbon Laboratory, New Zealand, and Beta Analytic, Inc., Florida. We thank Raytheon Polar Services and the Italian Antarctic Program for logistical support, and E. Cavallerano, S. Loiacono, M. Polito, and J. Smykla for assistance in the field. C. Baroni and D. Ainley provided valuable comments on an earlier version of this paper. Comments by H. Conway, W. Fraser, and one anonymous reviewer also improved the manuscript.

## REFERENCES CITED

- Ainley, D.G., 2002, *The Adélie Penguin*: New York, Columbia University Press, 310 p.
- Anderson, J.B., Shipp, S.S., Bartek, L.R., and Reid, D.E., 1992, Evidence for a grounded ice sheet on the Ross Sea continental shelf during the late Pleistocene and preliminary paleodrainage reconstruction: *Antarctic Research Series*, v. 57, p. 39–62.
- Baroni, C., and Hall, B.L., 2004, A new Holocene relative sea-level curve for Terra Nova Bay, Victoria Land, Antarctica: *Journal of Quaternary Science*, v. 19, p. 377–396, doi: 10.1002/jqs.825.
- Baroni, C., and Orombelli, G., 1994a, Abandoned penguin rookeries as Holocene paleoclimatic indicators in Antarctica: *Geology*, v. 22, p. 23–26, doi: 10.1130/0091-7613(1994)022<0023:APRAHP>2.3.CO;2.
- Baroni, C., and Orombelli, G., 1994b, Holocene glacier variations in the Terra Nova Bay area (Victoria Land, Antarctica): *Antarctic Science*, v. 6, p. 497–505.
- Berger, A., and Loutre, M.F., 1991, Insolation values for the climate of the last 10 million years: *Quaternary Science Reviews*, v. 10, p. 297–317, doi: 10.1016/0277-3791(91)90033-Q.
- Berkman, P.A., Andrews, J.T., Björck, S., Colhoun, E.A., Emslie, S.D., Goodwin, I.D., Hall, B.L., Hart, C.P., Hirakawa, K., Igarashi, A., Ingólfsson, O., López-Martínez, J., Lyons, W.B., Mabin, M.C.G., Quilty, P.G., Taviani, M., and Yoshida, Y., 1998, Circum-Antarctic coastal environmental shifts during the late Quaternary reflected by emerged marine deposits: *Antarctic Science*, v. 10, p. 345–362.
- Chappell, J., Omura, A., Esat, T., McCulloch, M., Pandolfi, J., Ota, Y., and Pillans, B., 1996, Reconciliation of late Quaternary sea levels derived from coral terraces at Huon Peninsula with deep sea oxygen isotope records: *Earth and Planetary Science Letters*, v. 141, p. 227–236, doi: 10.1016/0012-821X(96)00062-3.
- Colhoun, E.A., Mabin, M.C.G., Adamson, D.A., and Kirk, R.M., 1992, Antarctic ice volume and contribution to sea-level fall at 20,000 yr BP from raised beaches: *Nature*, v. 358, p. 316–319, doi: 10.1038/358316a0.
- Conway, H., Hall, B.L., Denton, G.H., Gades, A.M., and Waddington, E.D., 1999, Past and future grounding-line retreat of the West Antarctic Ice Sheet: *Science*, v. 286, p. 280–283, doi: 10.1126/science.286.5438.280.
- Cunningham, W.L., Leventer, A., Andrews, J.T., Jennings, A.E., and Licht, K.J., 1999, Late Pleistocene–Holocene marine conditions in the Ross Sea, Antarctica: Evidence from the diatom record: *The Holocene*, v. 9, p. 129–139, doi: 10.1191/095968399675624796.
- Domack, E.W., Jacobson, E.A., Shipp, S., and Anderson, J.B., 1999, Late Pleistocene–Holocene retreat of the West Antarctic Ice Sheet system in the Ross Sea: Part 2. Sedimentologic and stratigraphic signature: *Geological Society of America Bulletin*, v. 111, p. 1517–1536, doi: 10.1130/0016-7606(1999)111<1517:LPHROT>2.3.CO;2.
- Emslie, S.D., Berkman, P.A., Ainley, D.G., Coats, L., and Polito, M., 2003, Late-Holocene initiation of ice-free ecosystems in the southern Ross Sea, Antarctica: *Marine Ecology Progress Series*, v. 262, p. 19–25.
- Fordyce, E., and Jones, C.M., 1990, Penguin history and new fossil material from New Zealand, in Davis, L.S., and Darby, J.T., eds., *Penguin Biology*: San Diego, Academic Press, p. 419–446.
- Hall, B.L., and Denton, G.H., 2000, Radiocarbon chronology of Ross Sea drift, eastern Taylor Valley, Antarctica: Evidence for a grounded ice sheet in the Ross Sea at the Last Glacial Maximum: *Geografiska Annaler*, v. 82A, p. 305–363.
- Hall, B.L., Baroni, C., and Denton, G.H., 2004, Holocene relative sea-level history of the southern Victoria Land coast, Antarctica: *Global and Planetary Change*, v. 42, p. 241–263, doi: 10.1016/j.gloplacha.2003.09.004.
- Harrington, H.J., 1960, Adélie penguin rookeries in the Ross Sea region: *Notornis*, v. 9, p. 33–39.
- Harrington, H.J., and McKellar, I.C., 1958, A radiocarbon date for penguin colonization of Cape Hallett, Antarctica: *New Zealand Journal of Geology and Geophysics*, v. 1, p. 571–576.
- Heine, J.C., and Speir, T.W., 1989, Ornithogenic soils of the Cape Bird Adélie penguin rookeries, Antarctica: *Polar Biology*, v. 10, p. 89–99, doi: 10.1007/BF00239153.
- Hughen, K.A., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J.W., Bertrand, C.J.H., Blackwell, P.G., Buck, C.E., Burr, G.S., Cutler, K.B., Damon, P.E., Edwards, R.L., Fairbanks, R.G., Friedrich, M., Guilderson, T.P., Kromer, B., McCormac, F.G., Manning, S.W., Bronk, R.C., Reimer, P.J., Reimer, R.W., Remmele, S., Southon, J.R., Stuiver, M., Talamo, S., Taylor, F.W., van der Plicht, J., and Weyhenmeyer, C.E., 2004, Marine04 Marine radiocarbon age calibration, 26–0 ka BP: *Radiocarbon*, v. 46, p. 1059–1086.
- Ingólfsson, O., Hjort, C., Berkman, P., Björck, S., Colhoun, E., Goodwin, I., Hall, B., Hirakawa, K., Melles, M., Möller, P., and Printice, M., 1998, Antarctic glacial history since the Last Glacial Maximum: An overview of the record on land: *Antarctic Science*, v. 10, p. 326–344.
- Lambert, D.M., Ritchie, P.A., Millar, C.D., Holland, B., Drummond, A.J., and Baroni, C., 2002, Rates of evolution in ancient DNA from Adélie penguins: *Science*, v. 295, p. 2270–2273, doi: 10.1126/science.1068105.
- Licht, K.J., and Andrews, J.T., 2002, The <sup>14</sup>C record of late Pleistocene ice advance and retreat in the central Ross Sea, Antarctica: *Arctic, Antarctic, and Alpine Research*, v. 34, p. 324–333, doi: 10.2307/1552491.
- Licht, K.J., Jennings, A.E., Andrews, J.T., and Williams, K.M., 1996, Chronology of late Wisconsin ice retreat from the western Ross Sea, Antarctica: *Geology*, v. 24, p. 223–226, doi: 10.1130/0091-7613(1996)024<0223:COLWIR>2.3.CO;2.
- Licht, K.J., Dunbar, N.W., Andrews, J.T., and Jennings, A.E., 1999, Distinguishing subglacial marine diamictons in the western Ross Sea, Antarctica: Implications for a Last Glacial Maximum grounding line: *Geological Society of America Bulletin*, v. 111, p. 91–103, doi: 10.1130/0016-7606(1999)111<0091:DSTAGM>2.3.CO;2.
- Masson, V., Vimeux, F., Jouzel, J., Morgan, V., Delmotte, M., Ciais, P., Hammer, C., Johnsen, S., Lipenkov, V.Y., Mosley-Thompson, E., Petit, J.-R., Steig, E.J., Stievenard, M., and Vaikmae, R., 2000, Holocene climate variability in Antarctica based on 11 ice-core isotopic records: *Quaternary Research*, v. 54, p. 348–358, doi: 10.1006/qres.2000.2172.
- Polito, M., Emslie, S.D., and Walker, W., 2002, A 1000-year record of Adélie penguin diets in the southern Ross Sea: *Antarctic Science*, v. 14, p. 327–332, doi: 10.1017/S0954102002000184.
- Seppelt, R.D., Green, T.G.A., and Skotnicki, M., 1999, Notes on the flora, vertebrate fauna and biological significance of Beaufort Island, Ross Sea, Antarctica: *Polarforschung*, v. 66, p. 53–59.
- Shepherd, L.D., Millar, C.D., Ballard, G., Ainley, D.G., Wilson, P.R., Haynes, G.D., Baroni, C., and Lambert, D.M., 2005, Microevolution and mega-icebergs in the Antarctic: *Proceedings of the National Academy of Sciences of the United States of America*, v. 102, p. 16,717–16,722, doi: 10.1073/pnas.0502281102.
- Shipp, S., Anderson, J., and Domack, E., 1999, Late Pleistocene–Holocene retreat of the West Antarctic Ice Sheet system in the Ross Sea: Part 1. Geophysical results: *Geological Society of America Bulletin*, v. 111, p. 1486–1516, doi: 10.1130/0016-7606(1999)111<1486:LPHROT>2.3.CO;2.
- Speir, T.W., and Cowling, J.C., 1984, Ornithogenic soils of the Cape Bird Adélie penguin rookeries, Antarctica: 1. Chemical properties: *Polar Biology*, v. 2, p. 199–205, doi: 10.1007/BF00263625.
- Spellerberg, I.F., 1970, Abandoned penguin rookeries near Cape Royds, Ross Island, Antarctica and <sup>14</sup>C dating of penguin remains: *New Zealand Journal of Science*, v. 13, p. 380–385.
- Steig, E.J., Hart, C.P., White, J.W.C., Cunningham, W.L., Davis, M.D., and Saltzman, E.S., 1998, Changes in climate, ocean and ice-sheet conditions in the Ross embayment, Antarctica, at 6 ka: *Annals of Glaciology*, v. 27, p. 305–310.
- Stonehouse, B., 1970, Recent climatic change in Antarctica suggested from <sup>14</sup>C dating of penguin remains: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 7, p. 341–343, doi: 10.1016/0031-0182(70)90100-8.
- Stuiver, M., and Reimer, P.J., 1993, Extended <sup>14</sup>C database and revised CALIB radiocarbon calibration program: *Radiocarbon*, v. 35, p. 215–230.
- Waelbroeck, C., Labeyrie, L., Michel, E., Duplessy, J.C., McManus, J.F., Lambeck, K., Balbon, E., and Labracherie, M., 2002, Sea-level and deep water temperature changes derived from benthic foraminifera isotopic records: *Quaternary Science Reviews*, v. 21, p. 295–305, doi: 10.1016/S0277-3791(01)00101-9.
- Woehler, E., 1993, *The distribution and abundance of Antarctic and Subantarctic penguins*: Cambridge, UK, Scientific Committee on Antarctic Research, 75 p.

Manuscript received 8 June 2006

Revised manuscript received 3 September 2006

Manuscript accepted 7 September 2006

Printed in USA