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penguins through the ages

Thanks to their robust bones, which fossilise better than those of most other birds, we have a fairly good record of the evolutionary history of penguins. The earliest remains of *Waimanu manneringi*, a 1.2-metre-tall bird – similar in size to an Emperor Penguin – date back more than 60 million years. Gerald Mayr and colleagues recently reported that an even larger species, standing about 1.5 metres tall, also occurred in New Zealand at about the same time as *W. manneringi* (2017, *Science of Nature* 104: 9). Interestingly, the newly described species shows several features typical of more 'advanced' penguins, suggesting that penguins radiated rapidly after the Cretaceous–Palaeogene mass extinction that saw the demise of the non-avian dinosaurs. At least 12 more species of 'giant' penguins flourished for almost 30 million years. Their disappearance during the Oligocene more or less coincided with the evolution of toothed whales and dolphins, giving rise to speculation that either competition with or predation by these marine mammals (or perhaps a combination of both) led to the giant penguins' demise.

Recent studies show how Adélie Penguin colonies have fluctuated with changes in sea ice extent.

Although we tend to associate penguins with Antarctica, they evolved during a relatively warm period in the earth's history and their adaptation to live in cold conditions came later. Another recent study combining molecular and fossil evidence concludes that the radiation of modern penguins started around 13 million years ago, more recently than previously thought (Gavryushkina et al. 2017, *Systematic Biology* 66: 57–73). This is when the earth's seas started a period of sustained cooling, culminating in the glaciation of Antarctica. The authors suggest that *Aptenodytes* and *Pygoscelis* penguins, which are basal among extant penguins, evolved at this time to take advantage of the newly formed polar environments. Radiations within modern genera occurred even more recently, mainly within the past one to five million years.

At a finer temporal scale, we know that the fortunes of Antarctic penguins have waxed and waned over the past tens of thousands of years. Several studies have reported the repeated colonisation by and extinction of penguins at various sites around Antarctica and linked these events to climate change in the region. For example, carbon-dating studies indicate that Adélie Penguins occupied the Ross Sea from around 45 000 to 27 000 years BP, then again from 8000 to 5000 years BP, 4000 to 2000 BP and, finally, from 1050 to the present. Their absences coincide with cooler periods, when there was insufficient open water for penguins to forage.

However, other factors also affect penguin populations. Stephen Roberts and colleagues recently reported how explosive volcanism has repeatedly impacted a large colony of Gentoo Penguins on Ardley Island, off the Antarctic Peninsula (2017, *Nature Communications* 8: 14914). Analysis of sediments from a lake near the colony reveals how penguin numbers have crashed five times during the past 8500 years, with at least three of these events linked to massive eruptions of the nearby Deception Island volcano. Each time it took the penguin population some 400 to 800 years to recover.

Penguin numbers also may be influenced by human impacts on their competitors. The 'krill surplus' hypothesis proposes that whaling and sealing in the 19th and early 20th centuries reduced numbers of whales and seals to such an extent that large quantities of Antarctic krill were made available to other consumers. This idea has been hard to test, but over the past few years support for the hypothesis has come from stable isotope and trace metal analyses of sub-fossil penguin remains, which show that pygoscelid penguins ate mainly fish before the whaling era, whereas they now rely mostly on krill. More controversially, the recent increases in some Adélie Penguin colonies in the Ross Sea have been attributed to an increase in Antarctic silverfish, thanks to the fishery for Antarctic toothfish, which competes with penguins for silverfish. It goes to show that predicting the impacts of climate change is seldom simple, even in remote areas such as Antarctica.

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