Penguin evolution and conservation

Penguins are one of the most distinctive and charismatic bird orders. Supremely adapted for flipper-propelled diving, they are the most aquatic of all birds and hold the records for the deepest and longest dives. A new study by Theresa Cole and a large team of researchers (*Nature Communications*, doi: 10.1038/s41467-022-31508-9) provides unprecedented insights into how they adapted to a life at sea.

Emperor (above) and Adélie penguins (left and above), the two species best adapted to extreme polar conditions, also show the fastest rate of evolution, presumably linked to being forced to adapt to changing conditions during glacial–interglacial cycles.

Thanks to their dense bones and aquatic habitats, penguins are well represented in the fossil record. In addition to the 19 extant species, nearly 50 other penguin species are known from fossil or sub-fossil remains. Cole's team combined data from fossil species with genomic evidence from all extant and recently extinct penguins to infer their evolutionary history.

By comparing the genomes of penguins with those of other birds, the researchers were able to identify the genes responsible for a suite of marine adaptations. These include genes that enhance dive duration by promoting oxygen storage in the muscles and by improving tolerance to low blood oxygen concentrations. Penguins also have lost the gene for green cones in their retina and have blue-shifted their colour vision to enhance visual acuity in extremely low light levels.

Penguins share with other flightless birds genes that are linked to shortening of the wing bones. They also selected for genes associated with tendon and bone development, necessary for the development of rigid flippers and dense bones for 'flying' underwater. Other adaptations include the formation of a subcutaneous white fat layer to keep warm while diving and a reduced sense of taste, which they share with marine mammals.

Most of these adaptations probably evolved early on in the evolution of penguins. The first penguins appear in the fossil record more than 60 million years ago, shortly after the mass extinction event that saw the demise of all non-avian dinosaurs. At least eight species are known from the early Paleogene, all of which were large compared to most modern penguins. They almost certainly evolved in Zealandia, the ancient continent, now mostly submerged, that includes New Zealand. Further diversification was associated with the colonisation of South America and Antarctica and subsequent dispersal back to Zealandia.

The evolution of modern penguins occurred some 14–15 million years ago, linked to the mid-Miocene cooling and intensification of the Antarctic Circumpolar Current. The first penguin fossils in Africa date back 10–12 million years. By five million years ago, when sea levels were 90 metres higher than they are today, at least two species of penguins bred at islands off the Cape coast, including one large species related to the *Pygoscelis* penguins (Adélie, Chinstrap and Gentoo). It is thought that their subsequent disappearance resulted from a shortage of safe breeding islands once the sea level fell.

The genus *Spheniscus*, which includes the African Penguin and its South American cousins, evolved some three million years ago. The African Penguin is sister to the Magellanic Penguin, whereas the Galápagos Penguin is an offshoot from the Humboldt Penguin, but there is genetic evidence of recent hybridisation among all four species.

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Although the Macaroni Penguin is the most abundant penguin species in the world, numbers have apparently been decreasing for more than 100 000 years.

Interestingly, the genomic data can be used to estimate historical trends in penguin populations. Numbers of African and Humboldt penguins (and other species including King and Chinstrap penguins) peaked during the last glacial maximum, some 30–40 thousand years ago. Subsequent warming has seen their numbers decrease. By comparison, Magellanic Penguins decreased during the last glacial maximum and then increased as the planet warmed. Still other species, including the tiny population of Galápagos Penguins and the Macaroni Penguin, which remains the most abundant penguin species, have experienced steady population decreases during at least the past 100 000 years.

Given their long history with little morphological change, it is perhaps not surprising that penguins are characterised by a slow rate of evolution. They have the lowest mutation rate among all bird orders, tying only with the albatrosses and petrels. This reflects their conservative life histories, with associated long generation times, as well as their aquatic lifestyle. It is not clear why waterbirds generally evolve more slowly than terrestrial species, but this pattern is shown by several bird orders. For example, the rate of evolution among ducks and geese is only one third of that of their sister group, the gamebirds.

Having a slow rate of evolution is bad news in a rapidly changing world. However, it is encouraging to learn that the rate of penguin evolution has increased during the past 1–2 million years, coincident with the onset of glacial–interglacial cycles. And the rate of evolution has been fastest in high polar species, which would have been subject to the most extreme impacts of climate change. This finding suggests that penguins retain the ability to evolve more rapidly when faced with changing conditions, but it remains to be seen whether this will be sufficient to enable them to survive the looming global climate crisis.

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