Penguins continue diving long after muscles run out of oxygen

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Breathing heavily at the edge of an ice hole, an Antarctic emperor penguin prepares to dive. Taking a last gulp of air, the bird descends and may not emerge again for another 20 minutes. The penguin initially carries sufficient oxygen in three stores – the blood, lungs and myoglobin in muscle – to sustain aerobic metabolism. However, around 5.6 minutes after leaving the surface, lactate begins appearing in the penguin's blood and the bird crosses the so-called 'aerobic dive limit', switching to anaerobic metabolism in some tissues. So what triggers this transition?

Cassondra Williams from the Scripps Institution of Oceanography

explains that the animals were thought to cross the aerobic dive limit when one of their three oxygen stores became exhausted. However, when Paul Ponganis measured oxygen levels in the blood and lungs of penguins after long dives, the animals had oxygen to spare. That only left the muscle as the potential trigger. Williams explains that diving animals were thought to isolate their muscle from the circulatory system, leaving oxygen stored in the tissue as its only source of aerobic metabolism while submerged and forcing it to switch to anaerobic respiration once the supply was exhausted. So, she and Ponganis teamed up with Jessica Meir to travel to Antarctica to measure muscle oxygen levels in diving emperor penguin muscles and they publish their discovery that depleted muscle oxygen supplies trigger the aerobic dive limit in The *Journal of Experimental Biology*.

However, before their departure, Williams had to design a near-infrared spectrophotometer to record the penguins' muscle oxygen stores as they dived in the wild. After two trying years of technical development and testing, Williams was able to travel south with her colleagues to surgically implant the spectrophotometers in the pectoralis muscles of emperor penguins. They also attached time–depth recorders to the animals' backs to track their dive profiles. Finally, the team ensured that the animals would return with their precious equipment by drilling an isolated hole in the sea ice – to which the penguins were guaranteed to return – before releasing the implanted animals to go foraging for a day or two.

After successfully retrieving all of the spectrophotometers and dive recorders and returning the penguins to their colony, Williams began analysing the data and found that the penguins had been actively foraging beneath the ice. Of the 50 dives that Williams successfully recorded, 31 exceeded the emperor penguin's calculated dive limit.

Next, Williams plotted the muscle oxygen profiles over the course of

each dive and identified two distinct patterns. In the first, the oxygen levels fell continually, approaching zero around the point when the birds crossed the aerobic dive limit. Williams says, 'This profile certainly supports the hypothesis that muscle oxygen depletion is the trigger of the aerobic dive limit.'

However, when the team saw the second pattern, they were surprised that, after initially falling, the oxygen levels plateaued for several minutes before falling again to almost zero. They realised that blood must be flowing into the muscle to replenish the oxygen supply during the middle phase of the dive, delaying the onset of the aerobic dive limit.

Finally, having confirmed that the dive muscles are the source of the aerobic dive limit, Williams calculated the muscle oxygen consumption rate for dives with the first oxygen depletion pattern and was amazed to see that it was only 12.4ml of oxygen per kg of muscle per minute: 1/10th the value calculated for penguins swimming in an artificial flume and only 2□□ times their resting metabolic rate. 'I think this metabolic rate is impressive. You can see how hard they are working underwater but they are efficient swimmers and very hydrodynamic,' says Williams.

More information: Williams, C. L., Meir, J. U. and Ponganis, P. J. (2011). What triggers the aerobic dive limit? Patterns of muscle oxygen depletion during dives of emperor penguins. J. Exp. Biol. 214, 1802-1812. jeb.biologists.org/content/214/11/1802.abstract

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