Barreiros, J Biodivers Manage Forestry 2017, 6:1
DOI: 10.4172/2327-4417.1000172

Journal of Biodiversity Management & Forestry

Letter To Editor

A SCITECHNOL JOURNAL

Why Flightless Birds are 'Condemned' to Lay Eggs

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Abstract

Birds evolved very fast and are the only vertebrate group that never turned to ovoviviparity. While this is explainable as an evolutionary pressure for feathered flight and reduced size, their fast evolution apparently caused the disappearance of a significant proportion of genes. However posterior evolutionary trends of Aves to become flightless and with increased body sizes were not accompanied by an 'expected' turn to ovoviviparity, something known for a number of reptile taxa (e.g. some constrictor serpents). This impossibility is particularly noted in marine flightless birds from which penguins are certainly the best extant example having to endure seasonal extreme energy losses when coming ashore to lay eggs. This same limitation was most certainly the major cause for the extinction of the largest marine bird in the Northern Hemisphere – The Great Auk *Pinguinus impennis*. Here we discuss why ovoviviparism is probably an impossibility for birds while proposing lines of research that could prove, or disprove, our hypothetical and speculative view.

Keywords: Ovoviviparity; Aves; Evolutionary constraint; Feathered flight

Avian evolution is a fascinating subject that was recently extensively discussed in Science's Special Section "A Flock of Genomes" (12 December 2014 issue 346). One of the many key points in this special section is pointed out when referring that avian genomes consistently contain fewer genes and the ancestral avian lineage has distinctly lost a large number of genes by means of large segmental deletions after their divergence from other extant reptiles [1]. Is it in here the cause for birds had never ever turned to ovoviviparity? If so, then how may the study of bird's genomes give an answer to this 'riddle'? The section "A Flock of Genomes" does not offer a response to this question although it gives us important clues on how to investigate it.

It is known that a sustained size reduction was essential for the origin of birds and flight [2]. However, it is precisely that selection and the mechanical characteristics of feathered flight that probably caused the evolutionary impossibility of a modern bird – especially large, heavy bodied flightless species - turning to ovoviviparity. In fact, the evolutionary trend to miniaturization did happen at a rate of ca. 150 times faster than normal [3]. According to Benton [2] a move to tree dwelling is a crucial driver to the above changes although this does not explain how large sized birds, even before the K-T boundary event, adopted the opposite trend of becoming heavier and flightless (e.g. Cretaceous *Hesperornis*). All amniotes produce eggs but birds just had to 'get rid of them' very quickly in order to keep their low weight for flight. In fact, this evolutionary pressure for reduced weight might have 'erased' the genes that would allow birds to develop an alternate way of reproducing by turning to ovoviviparity. As explained almost all birds develop only a single functional ovary on the left side as a result of the evolutionary loss of the right ovary during the transition from nonavian theropods to birds [1]. It has been hypothesized that this loss represents an adaptation to reduce weight during flight [4]. Together with their very fast evolution, the disappearance of two genes related with ovary development is the probable key to the impossibility of ovoviviparism in birds [2].

While there is no evidence that non-avian dinosaurs and Pterosaurs, small or big, turned to ovoviviparity, it is certainly more probable than not that giant marine reptiles such as Pliosaurs, Plesiosaurs and Mosasaurs were ovoviviparous as Ichthyosaurs certainly were.

Penguins have to endure enormous energy consuming efforts to lay eggs and for parental care. Being exclusively marine, ovoviviparity should have been the 'logical' evolutionary step for a high metabolic animal that does need to lay eggs on land. Of course, marine turtles also have to lay eggs on beaches but their lower metabolic rates are certainly more compatible with the effort and only females do it. Besides, turtles, while not having parental care, only come ashore a few times while both members of a penguin breeding pair do have to endure this effort several times. Therefore, the genes that would allow a transition to ovoviviparity have most probably disappeared.

We can speculate that one of the most iconic recent Aves extinction, the Great Auk *Pinguinus impennis*, the only flightless marine bird in the Northern Hemisphere together with the lesser known and also extinct Spectacled Cormorant *Phalacrocorax perspicilliatus*, could still be amongst the extant species if ovoviviparity had developed since, especially the former, was probably hunted to extinction only because of their need to aggregate in breeding colonies where they became an easy target [5].

Modern birds are now better known but this key evolutionary aspect should and can be thoroughly studied in order to explain why ovoviviparity is absent or even 'impossible'. If possible, a new window for understanding Aves evolution would become an important step of vertebrate evolution studies.

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Received: January 27, 2016 **Accepted:** February 02, 2017 **Published:** February 09, 2017

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Top

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