On the Wing: Insects, Pterosaurs, Birds, Bats and the Evolution of Animal Flight

Author: Pennycuick, Colin J.

Source: The Auk, 133(2) : 320-321

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-15-210.1

The Auk
Ornithological Advances
AmericanOrnithology.org

Volume 133, 2016, pp. 320–321
DOI: 10.1642/AUK-15-210.1

BOOK REVIEW

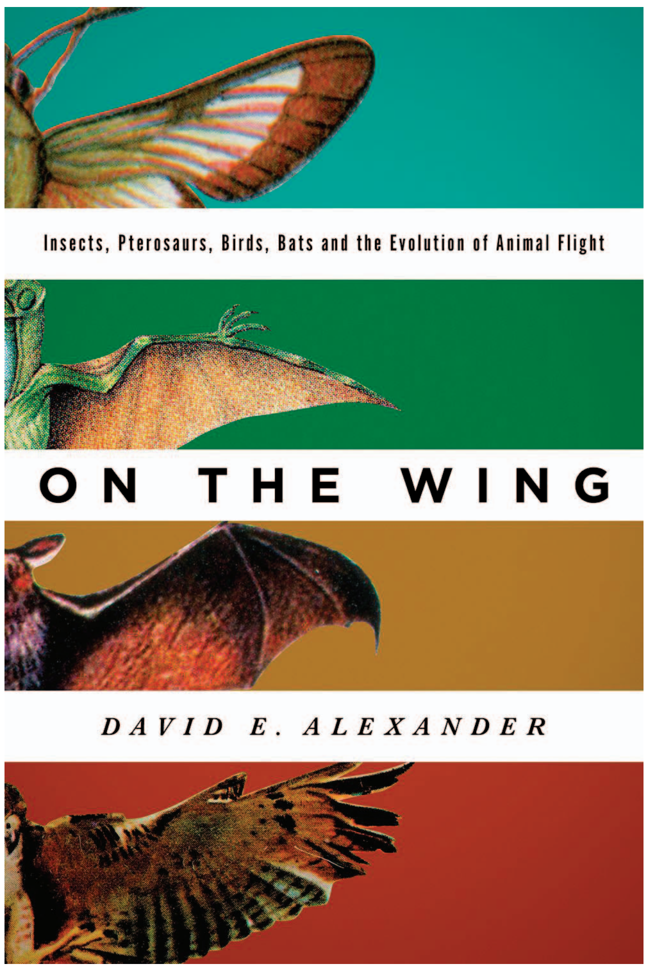
On the Wing: Insects, Pterosaurs, Birds, Bats and the Evolution of Animal Flight

Reviewed by Colin J. Pennycuick

School of Biological Sciences, University of Bristol, Bristol, UK

Published March 30, 2016

On the Wing: Insects, Pterosaurs, Birds, Bats and the Evolution of Animal Flight by David E. Alexander. 2015. Oxford University Press, Oxford, UK. 224 pp. $29.95 (hardcover). ISBN 978-0199996773.



This book is an unusual form of technology. The author reviews the lives of four taxa of animals—the birds, the bats, the pterosaurs, and the insects—which are not related to each other but which typically have wings and can fly. What is it about wings that makes these animals so very different from any others? In his first chapter, Alexander explains that flight allows animals to cover ground faster than walking or running, and that is true also for the bigger species. As to flying slowly, only insects can do that, and it takes a lot of energy. Large or medium-sized birds cannot even think about migrating slowly. A large bird has to go faster than it can run before it can fly. Why is that?

In Chapter 2 Alexander goes through the special properties that wings have, such as generating lift and drag from the fluid passing over them, and the ratio of lift to drag. He defines those variables carefully in Chapter 3, along with some less obvious ones, such as force and power. Having noted that these variables are important to engineers, he does nothing further with them. If the reader wants a lift-to-drag ratio for a bat, he will not find it here. Alexander knows that the lift has to be adjusted in level flight to match the weight, and also that the muscles do work against the drag—and these actions are different from those of locomotion in water or on the ground. He does not say why this makes a bird or bat any more or less efficient than any other animal. The book is full of biological detail, but there is no theory here from which an animal's flight performance could be calculated.

Starting with gliding animals, there are many interesting details about the flight of rib-winged dragon lizards, followed by a chapter each on insects, birds, bats, and pterosaurs. In addition to having wings, these power-flying animals also have flight muscles that flap the wings up and down. Insects have the small-scale world to themselves, from about 5 g body mass downward, and that is because they have their own type of flight muscle, whose contraction frequency is not limited by the mechanics of the wings that they flap. Insect flight muscles produce rather little power but work well at frequencies higher than those of vertebrates, into the lower kHz range. Flapping wings is not the only way to make muscles work on the surrounding air, but it is the way that all living groups do it, and it is well suited to the mechanical properties of muscles. Among the vertebrate fliers, birds are by far the best, because their legs are not part of the wing structure but are free for running, swimming, and other activities. A bird with wings folded can run and jump like any small, nimble, bipedal animal, whereas bats, when not flying, can only hang down from their feet, wrapping their wings around them. To find out how much work the flight muscles have to do, we need some physics, which applies to any kind of flying animal or machine. Vertebrates can flap their wings at frequencies from about 15 or 20 Hz downward, which means that hardly any have a body mass below about 5 g. The small and medium-sized species easily meet the need for power, but as you increase the size the work gets harder, until eventually you get near the limit of 41 J kg^{-1} of muscle, which is the maximum that any muscle today can produce. Birds become impractical above about 16 kg, when the wingbeat frequency is down to 2–3 Hz, as they then cannot get enough work out of each wingbeat to keep going.

There is no such activity as "low-powered flight," and the low wingbeat frequency at large sizes also means that big birds need large lungs for continuous flight. Big swans fly with little power margin, and that is no doubt one reason why bats, with their mammalian lungs, top out at a smaller size than the larger birds. Swans need a lot of space to take off and are forever crashing into wires. Pterosaurs got to bigger sizes than birds but could not walk or stand on their back legs. If Alexander thinks their wing shape could be controlled by very thin surface wrinkles, he should build a model and show us how it works. Those wrinkles are not "stiffening fibres," whatever the original paleontologists may have said. They are seen only in dead, contracted wings and are surface wrinkles caused by the contraction of elastic tissue in the relaxed underlying membrane. Seen in that way, pterosaurs look no better than bats, able to modify their wing shape in flight, but not to move on the ground like unimpeded normal animals. Despite that, they competed with birds from the late Jurassic (or before) until the extinction of the dinosaurs at the end of the Cretaceous.

Those very big pterosaurs are also the last ones known; they existed for a short time at the very end of the Cretaceous. Before that, the biggest pterosaurs had been gradually getting bigger than today's biggest birds, for 50 million years or more. What was going on in those times? Was there a change in Earth's surface gravity that made flight easier for very big forms but harder for smaller ones? That is possible but needs some unrestrained paleontological thinking to look into it. As to pterosaurs, some of them were *much* bigger than any modern birds (12 m span) and they do not look right or possible in today's world.

The book does not go into the original *Archaeopteryx* "feather" but recognizes that early birds could fly from features seen in that feather. The later Chinese fossils of the Lower Cretaceous, with "feather-like" wing coverings, are described with detailed taxonomic diagrams, but the question as to whether any one of them could fly is not considered. That depends on whether the supposed "feathers" were made of keratin and capable of carrying aerodynamic loads. More likely the "feathers" were outer coverings, unable to bear such loads, and the difference determines whether those structures were early wings or merely superficial external decoration. These fossils are too late to have anything to do with the origin of flight, as the basic steps were taken by *Archaeopteryx* back in the Jurassic period.

The last two chapters of the book cover related problems, such as the loss of flight in some birds, but mainly the book is about the morphology of flying animals, with taxonomic diagrams. Somewhere it says that Alexander is an "aeromodeller," and so he may be, but I do not think he has held a throttle in his hand, accelerated to the highest speed he can get, and tried to coax a reluctant, overloaded aircraft into the air and away from the ground. The horrors of getting that wrong are never far away, and we have to look at the physics of flight to see why all takeoffs are like that, for animals and aircraft alike. Takeoff is the entry to another world, where the rules are very different than in our familiar world on the ground. Those rules are defined by physics, not by biology. We are no longer Victorian biologists, and if we want to fly we can learn to do so and find out what the rules are.

Book Review Editor: Jay Mager, j-mager@onu.edu