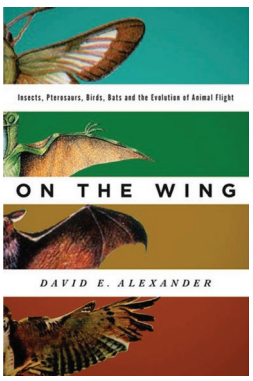
BioScience Advance Access published May 2, 2016

Unifying Themes of Flight Evolution?

On the Wing: Insects, Pterosaurs, Birds, Bats and the Evolution of Animal Flight. David E. Alexander. Oxford University Press, 2015. 210 pp., illus. $29.95 (ISBN: 9780199996773 cloth).

When it comes to moving around our planet, humans make for decent runners and swimmers. Our ability to fly without engineered assistance is markedly less impressive. This is perhaps why flying animals have historically elicited a nearly universal sense of wonder from children and adults, myself included. We see flight as so difficult and divergent from our own experiences that it arouses our curiosity. The story of the evolution of flying animals became one of Darwin's greatest challenges, and despite a century and a half of study, it remains one of the more contentious areas of evolutionary biology. The last 20 years have been no different. New fossils, especially those coming out of Liaoning Province in China; new genomics techniques; and new behavioral and biomechanical findings have at once advanced and complicated the story. In *On the Wing*, David Alexander distills the relevant findings, which span several fields of study and four disparate animal groups (the subtitular insects, pterosaurs, birds, and bats). An associate scientist studying biomechanics at the University of Kansas, Alexander's goal in writing was clearly not an in-depth review but an accessible introduction. In the early chapters, the reader learns just enough relevant natural history, evolutionary theory, and biomechanics to grasp the historical and current hypotheses on flight origins in each animal group covered in subsequent chapters. Unlike related books, the reader will not find detailed stories of fossil expeditions or of the years of laboratory and fieldwork leading to the development of new hypotheses. Short of several supportive and well-told anecdotes and valuable supplemental information provided in boxes, Alexander's focus is substance.

For 150 years or more, hypotheses on the evolutionary origins of flight, especially in birds, fell into one of two camps: down or up. We humans like our categories crisp and uncomplicated. We knew that animals evolved from swimming to walking on land, and to get from walking to flying was no easy feat. Some argued that the ancestors of flying animals were climbers that leaped from their elevated perches using whatever aerodynamically functional anatomy was at their disposal to slow and guide their descent. Larger or more functional structures, be it webbed hands, feathers, or even gills, had a survival or energetic advantage over smaller structures. And as guided falling stretched to gliding, Alexander argues, animals were gaining the internal neuroanatomy and other systems needed to fly. This is the arboreal or trees-down argument, and it is the position that Alexander stakes throughout *On the Wing*.



Hypotheses falling in the up direction—cursorial or ground-up hypotheses—receive fair treatment from Alexander, especially those proposed in the past 20 years. In such scenarios, preflight animals ran or jumped from the ground and used their incipient aerodynamic anatomy to run faster, jump higher, flap–run up steep obstacles, or control themselves once in the air. Again, individuals with more effective or larger aerodynamic structures had an advantage and were favored by natural selection. Alexander tells us that such hypotheses should be discounted in pterosaurs and bats because the wings in those groups include the hindlimb, which would make running difficult, a strong anatomical and biomechanical argument. But we also learn that we lack fossils for early versions of bats and pterosaurs, so estimating behavior in those groups is particularly difficult.

Alexander makes a far less convincing argument for the case of birds and insects passing through gliding stages on their way to flapping flight. But here, certainly, my own biases as an invested researcher must come into play. First, Alexander uses directed aerial descent—an amazing behavior in which some tropical tree-dwelling insects, ants especially, use whatever nonwings they have to direct their fall back to their home tree trunk (Yanoviak et al. 2005)—as support for gliding origins in all four flying clades. This argument should raise concern, because so much of flight anatomy and physiology differs among insects, birds, bats, and pterosaurs. Second, Alexander explains the origin of flapping, especially the avian "flight stroke," as starting with practically accidental adjustments to limb position in gliding animals—or analogous to the symmetric bounding gait his cat uses when climbing a tree. However, the story is undoubtedly more complex than that. Finally, while he critiques my own work on modern bird chicks because the birds have derived neurological systems capable of flight as adults, he fails to tell the reader that the nonwinged ants that perform directed aerial descent have winged brethren and therefore potentially sophisticated

sensory and motor systems also. In sticking to the century-old tree-down argument as omnipotent, Alexander misses the opportunity to point out the complexity of form–function relationships and that incipient wings were probably used for multiple aerodynamic and other functions in every clade, just as modern wings have many functions in today's birds, insects, and bats. It is time to break out of the up-or-down dichotomy.

I do not, however, find those faults to completely discount the book. Alexander's writing is clear and concise, approachable and accessible. In addition to the larger topics, he covers taxonomic terminology, various fossils of each group and where they fit into old and new phylogenies, the evolution of flightlessness, the difference between homology and homoplasy, and even how penguins got their name. *On the Wing* would be an excellent introduction to the field for amateur birders and entomologists—or just the flight curious. Furthermore, while reading, I found myself designing an undergraduate seminar course, using the book as a foundation and introduction to supplemental primary research. Alexander gives each topic just enough space to help the reader understand the next, but he leaves enough untold to entice the reader to want to know a bit more of each part of the story. After all, a full treatment of every related topic would take many volumes. And although I disagree that the evidence supports the gliding precursor as a unifying theme to animal flight, I appreciate that Alexander uses a subtle caveat in his final chapter, which is titled "Unifying themes?"

Reference cited

Yanoviak SP, Dudley R, Kaspari M. 2005. Directed aerial descent in canopy ants. Nature 433: 624–626.

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doi:10.1093/biosci/biw055