© 2014. Published by The Company of Biologists Ltd | The Journal of Experimental Biology (2014) 217, 2627-2628 doi:10.1242/jeb.104919

SHORT COMMUNICATION

Avian-style respiration allowed gigantism in pterosaurs

Graeme Ruxton*

ABSTRACT

Powered flight has evolved three times in the vertebrates: in the birds, the bats and the extinct pterosaurs. The largest bats ever known are at least an order of magnitude smaller than the largest members of the other two groups. Recently, it was argued that different scaling of wingbeat frequencies to body mass in birds and bats can help explain why the largest birds are larger than the largest bats. Here, I extend this argument in two ways. Firstly, I suggest that different respiratory physiologies are key to understanding the restriction on bat maximum size compared with birds. Secondly, I argue that a respiratory physiology similar to birds would have been a prerequisite for the gigantism seen in pterosaurs.

KEY WORDS: Birds, Bats, Scaling, Allometry, Limits to flight

INTRODUCTION

Powered flight evolved in three lineages of vertebrates: birds, bats and pterosaurs. The largest body sizes seen in these groups are very different. The largest living or extinct bat is around 1.6 kg [a few species of extinct *Pteropus* and the giant golden-crowned flying fox (Neuweiler, 2000; Stier and Mildenstein, 2005)]. In contrast, the largest extant flying birds (Kori bustard *Ardeotis kori*, California condor *Gymnogyps californianus*, mute swan *Cygnus olor*) are nearly an order of magnitude bigger at 12–14 kg (Dunning, 2007), rising to perhaps 70–80 kg for the largest extinct birds [*Argentavis magnificens* (Chatterjee et al., 2007)]. The largest known flying creatures are a group of pterosaurs named azhdarchids, extinct flying reptiles that existed during the age of the dinosaurs and died out at the end of the Cretaceous. Mass estimates for the largest azhdarchids are of the order of 200–250 kg (Witton and Habib, 2010). Recently, Norberg and Norberg (Norberg and Norberg, 2012) argued that different scaling of wingbeat frequencies to body mass in birds and bats can help explain why the largest birds are larger than the largest bats. Here, I extend this argument in two ways. Firstly, I suggest that the difference in respiratory physiology is key to understanding the restriction on bat maximum size compared with birds. Secondly, I argue that a respiratory physiology similar to that of birds would have been a prerequisite for the gigantism seen in pterosaurs.

The findings of Norberg and Norberg

With increasing mass, the aerodynamic lift of fliers increases slower than the force of gravity that must be overcome to keep the animal in the air, so there is an inevitable upper size limit for fliers of a certain type (Alexander, 2006). Norberg and Norberg (Norberg and Norberg, 2012) argue that wingbeat frequency declines with mass in both birds and bats, but wingbeat frequency is higher in birds than in bats of the same size. They also report that downstroke muscle mass is only 9% of body mass on average in bats, compared with 16% in birds. Taken together, these two sets of observations suggest that the power available to birds is greater than that available to bats of a given mass. Norberg and Norberg's calculations suggest that the largest flying birds should be about 12–16 kg, dropping to 1.1–2.3 kg for bats. These estimates are broadly in agreement with the largest extant species, but are less compatible with the 70–80 kg masses estimated for the largest extinct flying birds.

Mechanisms underlying these scaling relationships and extension to pterosaurs

Here, I suggest that the highly efficient avian respiratory system may be key to the differences between birds and bats discussed by Norberg and Norberg (Norberg and Norberg, 2012). A bird and bat of the same size need to generate similar amounts of energy by beating their wings to counteract the force of gravity acting on the organism; thus (for sustained flight, and assuming similar aerodynamic and aerobic muscle efficiencies), they need to consume oxygen at similar rates. The avian unidirectional-flow respiratory system is more efficient at any given size than the mammalian tidal system (Proctor and Lynch, 1998). Improved efficiency comes from a number of factors (Maina, 2002). Firstly, the lungs can be essentially fully expanded all the time in birds, whereas cycles of expansion and contraction are required in mammals, and only when the lung is near full expansion (and alveoli are open) is effective gas exchange possible (Sherwood et al., 2005). Secondly, in the avian system there is little or no recirculation of air that has already passed through the lungs, whereas re-breathing of stale air is much more prevalent in mammals. Because of this efficiency difference, bats have considerably larger lungs (and associated organs) than birds of the same size (Maina, 2000). The body cavities of birds and bats of a similar size should be broadly equivalent (with their cross-section being constrained by the need for drag reduction). This is supported by strong convergence in body plan and allometric scaling of birds and bats with similar ecologies (Norberg, 1981). The greater volume of the mammalian respiratory system requires that less space in the body cavity be given up to other systems, and this may explain the lower downstroke muscle mass in bats than in birds. That is, muscle mass may be subject to greater constraint to allow the bat to accommodate its more voluminous respiratory system. There is evidence that downstroke muscle mass is under strong selection in bats: interspecific comparison shows that the fraction of body mass given over to downstroke flight muscles can be linked closely to ecology (Bullen and McKenzie, 2004).

In bats, the respiration rate is synchronised with wing beat frequency. In contrast, in birds, matching of respiratory rates and wingbeat frequencies has been observed only in a small minority of species; and in general there is little observed effect of wing movements on pulmonary air flow or volume (Maina, 2000; and references therein). This difference between birds and bats can be directly linked to their different respiratory physiologies (Bernstein, 1987). This likely explains why wingbeat frequency is lower in bats than in birds of an equivalent size. In birds, wingbeat

School of Biology, University of St Andrews, St Andrews KY16 9TH, UK.

*Author for correspondence (gr41@st-andrew.ac.uk)

Received 3 March 2014; Accepted 5 May 2014

The Journal of Experimental Biology

frequency varies between species, and this variation is likely driven by locomotive selection pressures. Bats will face the added constraint that rapid wingbeats would mean rapid ventilation of the lungs and potentially insufficient time per breath for effective gas exchange to occur in the lungs. That bats are highly selected for respiratory gas exchange can be seen in recently discovered evidence that the wing membrane functions in gas exchange (Makanya and Mortola, 2007). Despite this, bats still have the largest relative lung volume of all the mammals (Canals et al., 2005). Thus, it seems that the differences between birds and bats in attributes related to lift generation can be directly related to respiratory differences; hence, I speculate that the efficient unidirectional respiratory system of the birds was a key facilitator in allowing them to reach large sizes not exploited by bats.

There now seems to be evidence from a number of different lines of reasoning that pterosaurs had a flow-through pulmonary ventilation system analogous to that of birds, but quite different from the tidal system of mammals (Claessens et al., 2009; Butler et al., 2009; Schachner et al., 2014). Claussens et al. argued that this adaptation allowed gigantism to occur in the pterosaurs. Specifically, they argue that ‘density reduction via the replacement of bone and bone marrow by air-filled pneumatic diverticula likely played a critical role in circumventing the limits imposed by allometric increases in body mass, enabling the evolution of large and even giant size in several clades’. However, this argument may not be as compelling as it first appears. Recent research has shown that although bird bones are typically hollow, the bone material is denser than in non-flying animals; and so overall the skeletons of birds contribute the same fraction of total body mass as do the skeletons of terrestrial animals (Dumont, 2010). Further, hollow cross-sections are typical of the large long-bones of bats (Swartz et al., 1992). Here, I argue that a flow-through respiratory anatomy was key to allowing gigantism in pterosaurs but through entirely different mechanisms to that previously suggested. Specifically, a bird-like respiratory system allows wingbeat frequency to be driven solely by aerodynamic and muscle functioning needs and not the needs of respiration (allowing more rapid flapping), and reduced size of the respiratory organs allows more space in the body cavity for flight muscle (allowing more powerful strokes). Both these mechanisms would have enhanced the ability of pterosaurs to generate lift. Thus, I speculate that avian-style respiratory physiology was key to the facilitation of very large size in some flying pterosaur species. This line of reasoning suggests that such a respiratory physiology facilitated gigantism through an enhanced ability to generate lift at least as much as (and perhaps more than) through a reduction in body mass.

Acknowledgements
I thank two reviewers for valuable comments on an earlier version.

Competing interests
The author declares no competing financial interests.

Funding
This research received no specific grant from any funding agency in the public, commercial or not-for-profit sectors.

References

Alexander, R. M. (2006). *Principles of Animal Locomotion.* Princeton, NJ: Princeton University Press.
Bernstein, M. H. (1987). Respiration in flying birds. In *Bird Respiration II* (ed. T. J. Seller), pp 43-73. Boca Raton, FL: CRC Press.
Bullen, R. D. and McKenzie, N. L. (2004). Bat flight-muscle mass: implications for foraging strategy. *Aust. J. Zool.* **52**, 605-622.
Butler, R. J., Barrett, P. M. and Gower, D. J. (2009). Postcranial skeletal pneumaticity and air-sacs in the earliest pterosaurs. *Biol. Lett.* **5**, 557-560.
Canals, M., Atala, C., Grossi, B. and Iriate-Diaz, J. (2005). Relative size of hearts and lungs of small bats. *Acta Chiropterologica* **7**, 65-72.
Chatterjee, S., Templin, R. J. and Campbell, K. E., Jr (2007). The aerodynamics of *Argentavis*, the world’s largest flying bird from the Miocene of Argentina. *Proc. Natl. Acad. Sci. USA* **104**, 12398-12403.
Claessens, L. P., O’Connor, P. M. and Unwin, D. M. (2009). Respiratory evolution facilitated the origin of pterosaur flight and aerial gigantism. *PLoS ONE* **4**, e4497.
Dumont, E. R. (2010). Bone density and the lightweight skeletons of birds. *Proc. Biol. Sci.* **277**, 2193-2198.
Dunning, J. B., Jr (2007). *CRC Handbook of Avian Body Masses*, 2nd edn. Boca Raton, FL: CRC Press.
Maina, J. N. (2000). What it takes to fly: the structural and functional respiratory refinements in birds and bats. *J. Exp. Biol.* **203**, 3045-3064.
Maina, J. N. (2002). Structure, function and evolution of the gas exchangers: comparative perspectives. *J. Anat.* **201**, 281-304.
Makanya, A. N. and Mortola, J. P. (2007). The structural design of the bat wing web and its possible role in gas exchange. *J. Anat.* **211**, 687-697.
Neuweiler, G. (2000). *The Biology of Bats*. New York, NY: Oxford University Press.
Norberg, U. M. (1981). Allometry of bat wings and legs and comparison with bird wings. *Philos. Trans. R. Soc. B* **292**, 359-398.
Norberg, U. M. and Norberg, R. A. (2012). Scaling of wingbeat frequency with body mass in bats and limits to maximum bat size. *J. Exp. Biol.* **215**, 711-722.
Proctor, N. S. and Lynch, P. J. (1998). *Manual of Ornithology: Avian Structure & Function.* Yale, CN: Yale University Press.
Schachner, E. R., Cieri, R. L., Butler, J. P. and Farmer, C. G. (2014). Unidirectional pulmonary airflow patterns in the savannah monitor lizard. *Nature* **506**, 367-370.
Sherwood, L., Klandorf, H. and Yancey, P. H. (2005). *Animal Physiology: From Genes to Organisms*. Singapore: Brooks/Cole.
Stier, S. and Mildenstein, T. L. (2005). Dietary habitat of the world’s largest bats: the Philippine flying foxes, *Acerodon jubatus* and *Pteropus vampyrus lanensis*. *J. Mammal.* **86**, 719-728.
Swartz, S. M., Bennett, M. B. and Carrier, D. R. (1992). Wing bone stresses in free flying bats and the evolution of skeletal design for flight. *Nature* **359**, 726-729.
Witton, M. P. and Habib, M. B. (2010). On the size and flight diversity of giant pterosaurs, the use of birds as pterosaur analogues and comments on pterosaur flightlessness. *PLoS ONE* **5**, e13982.