

1 Avian-style respiration allowed gigantism in pterosaurs

2

3 Graeme Ruxton

4 School of Biology

5 University of St Andrews

6 St Andrews KY16 9TH

7 UK

8

9 **Abstract**

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

18

19 **Key words:** birds, bats, scaling, allometry, limits to flight

20

21

22 Introduction

23 Powered flight has evolved three times in the vertebrates: in the birds, the bats and the extinct
24 pterosaurs. The largest body sizes seen in these groups are very different. The largest living or
25 extinct bat is around 1.6kg (a few species of extinct *Pteropus* and the giant golden-crowned flying
26 fox: Neuweiler 2000; Stier & Mildenstein 2005). In contrast the largest extant flying birds (Kori
27 Bustard *Ardeotis kori*, California Condor *Gymnogyps californianus*, Mute Swan *Cygnus olor*) are
28 nearly an order of magnitude greater at 12-14kg (Dunning 2007), rising to perhaps 70-80kg for the
29 largest extinct birds (*Argentavis magnificens*: Chatterjee et al. 2007). The largest known flying
30 creatures are a group of pterosaurs named *azhdarchids*, extinct flying reptiles that existed during the
31 age of the dinosaurs and died out at the end of the Cretaceous. Mass estimates for the largest
32 *azhdarchids* are on the order of 200-250 kg (440-550 lbs: Witton & Habib 2010). Recently Norberg
33 and Norberg (2012) argued that different scaling of wingbeat frequencies to body mass in birds and
34 bats can help explain why the largest birds are larger than the largest bats. Here I extend this
35 argument in two ways. Firstly, I suggest that different respiratory physiologies is key to
36 understanding the restriction on bat maximum size compared to birds. Secondly, I argue that a
37 respiratory physiology similar to birds would have been a prerequisite for the gigantism seen in
38 pterosaurs.

39

40 The findings of Norberg & Norberg (2012)

41 With increasing mass, aerodynamic lift of fliers increases slower than the force of gravity that must
42 be overcome to keep the animal in the air, so there is an inevitable upper size limit for fliers of a
43 certain type (Alexander 2006). Norberg & Norberg (2012) argue that wingbeat frequency declines
44 with mass in both birds and bats, but wingbeat frequency is higher in birds than in bats of the same
45 size. They also report that downstroke muscle mass is only 9% of body weight on average in bats,

46 compared to 16% in birds. Taken together these two sets of observations suggest that the power
47 available to birds is greater than to bats of a given mass. Norberg and Norberg's calculations suggest
48 that the largest flying birds should be about 12-16kg, dropping to 1.1-2.3kg for bats. These
49 estimates are broadly in agreement with the largest extant species, but are less compatible with the
50 70-80 kg masses estimated for the largest extinct flying birds.

51

52 **Mechanisms underlying these scaling relationships and extension to pterosaurs**

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

71 muscle mass may be subject to greater constraint to allow the bat to accommodate its more
 72 voluminous respiratory system. There is evidence that downstroke muscle mass is under strong
 73 selection in bats: interspecific comparison shows that the fraction of bodyweight given over to
 74 downstroke flight muscles can be linked closely to ecology (Bullen & McKenzie 2004).

75 In bats the respiration rate is synchronised with wing beat frequency. In contrast, in birds matching
 76 of respiratory rates and wingbeat frequencies have been observed only in a small minority of
 77 species; and in general there is little observed effect of wing movements on pulmonary air flow or
 78 volume (Maina 2000 and references therein). This difference between birds and bats can be directly
 79 linked to their different respiratory physiologies (Bernstein 1987). This likely explains why wingbeat
 80 frequency is lower in bats than birds of an equivalent size. In birds wingbeat frequency varies
 81 between species, and this variation is likely driven by locomotive selection pressures. Bats will face
 82 the added constraint that rapid wingbeats would mean rapid ventilation of the lungs and potentially
 83 insufficient time per breath for effective gas exchange to occur in the lungs. That bats are highly
 84 selected for respiratory gas exchange can be seen in recently discovered evidence that the wing
 85 membrane functions in gas exchange (Makanya & Mortola 2007). Despite this, bats still have the
 86 largest relative lung volume of all the mammals (Canals et al. 2005). Thus, it seems that the
 87 differences between birds and bats in attributes related to lift generation can be directly related to
 88 respiratory differences; and hence I speculate that the efficient unidirectional respiratory system of
 89 the birds was a key facilitator in allowing them to reach large sizes not exploited by bats.

90 There now seems to be evidence from a number of different lines of reasoning that pterosaurs had a
 91 flow-through pulmonary ventilation system analogous to that of birds, but quite different from the
 92 tidal system of mammals (Claussens et al 2009; Butler et al. 2009; Schachner et al. 2014). Claussens
 93 et al. argued that this adaptation allowed gigantism to occur in the pterosaurs. Specifically they
 94 argue that “density reduction via the replacement of bone and bone marrow by air filled pneumatic
 95 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 driven solely by aerodynamic and muscle functioning needs and not be 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 enhanced ability to generate lift and least as much as (and perhaps more than) through reduction in body weight.

Acknowledgement

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

References

- Alexander, R. M.** (2006) *Principles of Animal Locomotion*. Princeton: 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.

- 119 **Bullen, R. D. and McKenzie, N.L.** (2004) Bat flight-muscle mass: implications for foraging strategy.
 120 *Aust. J. Zool.* **52**, 605-622
- 121 **Butler, R. J., Barrett, P.M. and Gower, D. J.** (2009) Postcranial skeletal pneumaticity and air sacs in
 122 the earliest pterosaurs. *Biol. Lett.* **5**, 557-560
- 123 **Canals, M., Atala, C., Grossi, B. and Iriate-Diaz, J.** (2005) Relative size of hearts and lungs of small
 124 bats. *Acta Chiropterologica* **7**, 65-72
- 125 **Chatterjee, S., Templin, R. J. and Campbell, K. E.** (2007). The aerodynamics of Argentavis, the
 126 world's largest flying bird from the Miocene of Argentina. *PNAS* **104**, 12398–12403.
- 127 **Claessens, P. P. A. M., O'Connor, P. M. and Unwin, D. W.** (2009) Respiratory evolution facilitated
 128 the origin of pterosaur flight and aerial gigantism. *Plos One* **4**, e4497
- 129 **Dumont, E. R.** (2010) Bone density and the lightweight skeletons of birds. *Proc. R. Soc. Lond. B* **277**,
 130 2193-2198
- 131 **Dunning, J. B. Jr.** (2007) *CRC Handbook of avian body masses* (2nd ed.) Boca Raton FL: CRC press
- 132 **Maina, J.N.** (2000) What it takes to fly: the structural and functional respiratory refinements in birds
 133 and bats. *J. Exp. Biol.* **203**, 3045-3064
- 134 **Maina, J. N.** (2002) Structure, function and evolution of the gas exchangers: comparative
 135 perspectives. *J. Anatomy* **201**, 281-304.
- 136 **Makanya, A.N. and Mortola, J.P.** (2007) The structural design of the bat wing web and its possible
 137 role in gas exchange. *J. Anatomy* **211**, 687-697
- 138 **Neuweiler, G.** (2000). *The Biology of Bats*. New York: Oxford University Press.
- 139 **Norberg, U. M.** (1981) Allometry of bat wings and legs and comparison with bird wings. *Phil. Trans.*
 140 *R. Soc. Lond. B* **292**, 359-399

- 141 **Norberg, U. L. M. and Norberg, R. A.** (2012) Scaling of wingbeat frequency with body mass and
 142 limits to maximum bat size. *J. Exp. Biol.* **215**, 711-722
- 143 **Proctor, N. S. & Lynch, P. J.** (1998) *Manual of Ornithology: Avian Structure & Function*. Yale: Yale
 144 University Press
- 145 **Schachner, E. R., Cieri, R. L., Butler, J. P. and Farmer, C.G.** (2014) Unidirectional pulmonary airflow
 146 pattern in the savannah monitor lizard. *Nature* **506**, 367-371
- 147 **Sherwood, L., Klandorf, H. and Yancey, P.H.** (2005) *Animal Physiology: From Genes to Organisms*.
 148 Singapore: Brooks/Cole.
- 149 **Stier, S. and Mildenstein, T. L.** (2005) Dietary habitat of the world's largest bats: the Philippine flying
 150 foxes, *Acerodon jubatus* and *Pteropus vampyrus lanensis*. *J. Mammology* **86**, 719–728
- 151 **Swartz, S. M., Bennet M. B. and Carrier, D. R.** (1992) Wing bone stresses in free flying bats and the
 152 evolution of skeleton design for flight. *Nature* **359**, 726-729
- 153 **Witton, M. P. and Habib M. B.** (2010). "On the Size and Flight Diversity of Giant Pterosaurs, the Use
 154 of Birds as Pterosaur Analogues and Comments on Pterosaur Flightlessness." *PLoS ONE* **5**, e13982
- 155
- 156
- 157
- 158
- 159