Avian-style respiration allowed gigantism in pterosaurs

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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 has evolved three times in the vertebrates: in the birds, the bats and the extinct pterosaurs. The largest body sizes seen in these groups are very different. The largest living or extinct bat is around 1.6kg (a few species of extinct *Pteropus* and the giant golden-crowned flying fox: Neuweiler 2000; Stier & 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 greater at 12-14kg (Dunning 2007), rising to perhaps 70-80kg 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 on the order of 200-250 kg (440-550 lbs: Witton & Habib 2010). Recently 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 different respiratory physiologies is key to understanding the restriction on bat maximum size compared to birds. Secondly, I argue that a respiratory physiology similar to birds would have been a prerequisite for the gigantism seen in pterosaurs.

The findings of Norberg & Norberg (2012)

With increasing mass, 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 & 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 weight on average in bats,
compared to 16% in birds. Taken together these two sets of observations suggest that the power
available to birds is greater than to bats of a given mass. Norberg and Norberg’s calculations suggest
that the largest flying birds should be about 12-16kg, dropping to 1.1-2.3kg 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 & Norberg. 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 & 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 bodyweight given over to
downstroke flight muscles can be linked closely to ecology (Bullen & McKenzie 2004).

In bats the respiration rate is synchronised with wing beat frequency. In contrast, in birds matching
of respiratory rates and wingbeat frequencies have 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 birds of an equivalent size. In birds wingbeat 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 & 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; and 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 (Claussens 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 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.

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References


Boca Raton FL: CRC Press.


Chatterjee, S., Templin, R. J. and Campbell, K. E. (2007). The aerodynamics of Argentavis, the world’s largest flying bird from the Miocene of Argentina. PNAS 104, 12398–12403.


