RECONSTRUCTING THE TAKEOFF MECHANICS OF GIANT PTEROSAURS

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INTRODUCTION

Reconstructing the behavior and mechanical limits of fossil animals is a challenging biomechanical problem. Fossil species are generally analyzed in a comparative context with modern taxa for which we have more complete information. In some cases, the biomechanical limits of fossil species have been estimated from direct analogy to living groups, but this can lead to inappropriate scaling assumptions and erroneous behavioral inferences. Azhdarchid pterosaurs include the largest known flying animals, with the largest species reaching a potential mass of over 250 kg [1]. This greatly exceeds the maximum size observed in all other flying animals. Prior studies [2,3,4] have suggested that giant pterosaurs would have been incapable of takeoff at realistic body masses. These prior studies have all assumed a bird-like, bipedal launch strategy for pterosaurs. Comparative analyses of long bone structural strength, trabecular bracing, and muscle attachment expansion in pterosaurs, birds, and bats demonstrate that prior assumptions of a bipedal takeoff dynamic in pterosaurs were poorly founded. Instead, it is most likely that pterosaurs were quadrupedal launchers. Here, I review my prior results regarding quadrupedal launch [5,6] and present an expanded model that provides estimates of specific launch times and velocities in pterosaurs, and allows for the consideration of water launch in aquatic pterosaurs. The quadrupedal launch model explains the difference in maximum size observed between pterosaurs and birds, and predicts that giant pterosaurs should have been capable of launching from level ground without need for an initial takeoff run.

METHODS

Estimates of bone strength in pterosaur long bones were derived from applying a beam model. Exact sections, as derived from CT imaging, were not available for most of the pterosaur species examined in this study, and an elliptical model was applied where necessary. The taxon *Bennettazhia* was CT scanned at the National Museum of Natural History, and was used to compare the elliptical model to a known, exact section. External measurements of pterosaur long bones were taken at the Smithsonian's National Museum of Natural History (NMNH) in Washington, DC, the American Museum of Natural History in New York City, and the Bavarian State Palaeontological Collection (BSPG) in Munich, Germany. Sections at the midshaft of the humerus and femur of all specimens closely approached a true ellipse. Using a beam model of the femoral and humeral diaphyses, maximum stress in bending is given by My/I (where M is the bending moment, I is the second moment of area about the neutral axis and y is the maximum distance from the neutral axis to the edge of the section. The moment arm for bending was taken to be proportional to element length.

The section modulus, Z, in bending is defined as I/y. If M and T are considered to be proportional to the product of body mass (B) and bone length (L) [7], then structural strength is proportional to Z/(B*L). Relative femoral to humeral structural strength is a ratio of (Zfem/Lfem)/(Zhum/Lhum), and does not require knowledge of animal body mass, which is of great utility in working with fossil taxa. Structural strength in bending was compared for the humerus, femur, and humeral:femoral ratio across 19 pterosaur specimens and 125 specimens of modern birds. The comparative patterns of muscle insertion sites were also examined in four well-preserved pterosaur taxa (*Anurognathus ammoni*, *Anhanguera santanae*, *Pteranodon longcieps*, and *Quetzalcoatlus* sp.)

RESULTS AND DISCUSSION

The ratio of humeral to femoral strength in pterosaurs far exceeds that measured for birds (Figure 1). The only case in which the structural strength ratios for birds and pterosaurs overlap is in the case of *Anurognathus*, a small (approximately 0.22 meter wingspan) species with a suite of unusual characters in the skull, wing, and hind limb.

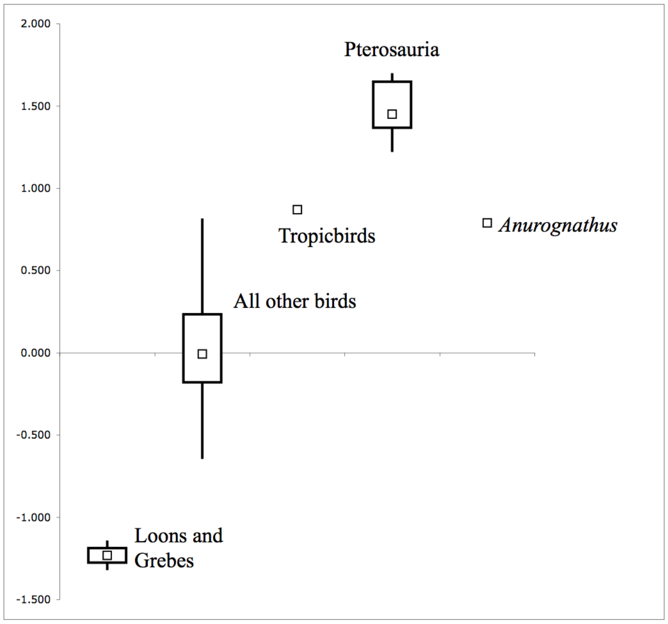

Figure 1: Structural strength ratios between the humerus and femur in birds and pterosaurs. Loons, grebes, and tropicbirds are separated as outliers for comparison, as is *Anurognathus ammonii*, a tiny basal pterosaur from central Europe.

The largest pterosaurs show the greatest disparity in strength between the humerus and femur. This is similar to the situation seen in bats, but differs significantly from the allometric relationship measured for birds. This disparity between birds and pterosaurs suggests that, as in ground-launching bats, pterosaur forelimbs acted as the primary power-generation module for all major motion activities: aerial locomotion, terrestrial locomotion, and launch.

Using known patterns of launch time relative to flapping frequency in modern flying animals, along with estimates of burst muscle capability taken from the closest living relatives of pterosaurs, it is possible to broadly estimate the launch capabilities of giant pterosaurs. For even the largest pterosaurs, a quadrupedal launch model predicts that launch from level ground was possible without special wind conditions. Launch is impossible under a bipedal launch model (femoral failure). This result is robust to uncertainty in body mass and wing proportions. The results for one potential reconstruction are given in Table 1.

CONCLUSIONS

Prior reconstructions of animal launch, particularly for fossil species, have been consistently confounded by a mistaken assumption that launch forces are primarily lift-based in nature. In reality, animal takeoff is ballistic in nature. Prior estimates of pterosaur launch were likely mistaken in assuming a bipedal launch dynamic in the manner of living birds. Structural strength ratios of the limbs indicate that pterosaurs were quadrupedal launchers. Estimates of launch performance using proper ballistic assumptions and a quadrupedal mode of takeoff indicate that giant pterosaurs were fully launch-capable. Pterosaurs were able to achieve greater maximum sizes than birds because they were quadrupedal launchers; this substantially alters the mechanical limits for flight.

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Table 1: Estimated launch parameters for *Quetzalcoatlus northropi*. FMF: Flight muscle fraction.

Body Mass (kg)	Span (m)	FMF	Wing Area (m^2)	Stall Speed (m/s)	Launch time (s)	Flap rate (hrz)	Height gain (m)	Required preload factor
259.00	10.40	0.30	9.01	14.43	0.63	1.19	2.00	2.02