

Scaling of soaring seabirds and its implication for the maximum size of flying pterosaurs

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The flight ability of animals is restricted by the scaling effects imposed by physical and physiological factors. In comparisons of the power available from muscle and the mechanical power required to fly, theoretical studies have predicted that the margin between the powers should decrease with body size and that flying animals have a maximum body size¹⁻⁷. However, predicting an absolute value of this upper limit has been difficult because wing morphology and flight styles vary among species. Albatrosses and petrels have long, narrow, aerodynamically efficient wings and are considered to be soaring birds. Here, using animal-borne accelerometers, we show that scaling analyses of wing-flapping frequencies in these seabirds indicate that the maximum size limit for soaring animals is a body mass of 41 kg and a wingspan of 5.1 m. Soaring seabirds were observed to have two modes of flapping frequencies: vigorous flapping during takeoff and sporadic flapping during cruising flight. In these species, high and low flapping frequencies were found to scale with body mass ($mass^{-0.30}$ and $mass^{-0.18}$) in a manner similar to the predictions from biomechanical flight models ($mass^{-1/3}$ and $mass^{-1/6}$)^{2, 4, 6, 8-10}. The

scaling relationships predicted that animals larger than the limit will not be able to flap fast enough to stay aloft under unfavourable wind conditions. Our result therefore casts doubt on the flying ability of large, extinct pterosaurs. The largest extant soarer, the wandering albatross, weighs about 10 kg, which might be a pragmatic limit to maintain a safety margin for sustainable flight and to survive in a variable environment.

Albatrosses fly thousands of kilometres in a few days to forage¹¹ and always return to their nesting grounds during breeding. When albatrosses are viewed from the deck of a ship, they seem to transit effortlessly with the ship for a prolonged period with no significant flapping of their wings. A combination of the high-aspect ratio of their wings and the anatomical capability to lock their wings in a stretched position¹² permits albatrosses to travel with the lowest energy expenditure among seabirds¹³. While albatrosses are highly specialised for soaring, this does not exactly mean that their flight consists only of gliding; rather, they have been observed to flap their wings under calm wind conditions¹². According to records of heart beat rates, the flight cost of wandering albatrosses is the highest during takeoff and is higher during flight in headwinds than when the wind is behind them¹⁴. One possible explanation is that for albatrosses, both takeoff and flying in headwinds require relatively more flapping.

Precise kinematic descriptions of wing flapping by free-flying birds are still rare in the literature¹⁵. In particular, measuring the quantitative characteristics of an entire flight, from takeoff to landing, under natural conditions has been virtually impossible. However, due to recent innovations in measuring technology, small accelerometers have been developed for the study of flight kinematics in the field. Using these animal-borne accelerometers, we continuously monitored the flight performance of albatrosses and petrels during their long-distance foraging trips at sea. Based on these data, scaling analyses were conducted for five procellariiform species, including streaked shearwater

Calonectris leucomelas (mean body mass = 0.6 kg, $n = 7$), white-chinned petrel *Procellaria aequinoctialis* (1.3 kg, $n = 5$), sooty albatross *Phoebetria fusca* (2.3 kg, $n = 2$), black-browed albatross *Thalassarche melanophrys* (3.4 kg, $n = 4$) and wandering albatross *Diomedea exulans* (9.4 kg, $n = 8$), the largest soaring bird.

Figure 1A provides an example of the acceleration records for a streaked shearwater during takeoff from the water surface and subsequent flight. A spectrogram calculated from the time series data of acceleration indicated that the shearwater flapped with a high frequency (7.5 Hz) at the beginning and then sporadically, with a lower constant frequency (4.2 Hz), throughout cruising flight. Unsupervised cluster analysis *k*-means methods were used to obtain ten discrete spectra from the entire data of this individual (Fig. 1B). Two frequencies, 7.5 and 4.2 Hz, corresponded with continuous flapping during takeoff and sporadic flapping during cruising flight, respectively. Since their introduction by David Attenborough in his book¹⁶ and in his documentary film (http://jp.youtube.com/watch?v=Cjmtt_B_i4A), streaked shearwaters have become famous as a seabird that climbs trees. Some ornithologists consider that tree-climbing is essential for takeoff to compensate for streaked shearwaters' limited capacity of flapping. However, these birds actually have enough capacity for taking off from the ground by jumping into the air accompanied by vigorous wing flapping (see Supplementary Movie1). Streaked shearwaters are a pelagic seabird that relies on marine food resources. During their foraging trips at sea, they sometimes land on the sea surface and capture prey by surface-seizing or shallow dives. The ability to achieve multiple takeoffs by wing flapping is therefore critical for the survival of streaked shearwaters.

Data obtained from the largest soaring bird, the wandering albatross, indicate a similar pattern (Fig. 1C). Wandering albatrosses usually run on the ground or the sea surface during takeoff (see Supplementary Movie2). Our data indicated that they flap at

relatively higher frequencies during takeoff than during cruising flight (Fig. 1C). The differences between the high and low flapping frequencies of wandering albatrosses were not as marked as those of streaked shearwaters (Fig. 1B, D). All individuals in the five species of Procellariiformes had ‘top’ and ‘low’ gears for wing flapping. The time percentage of flapping varied among individuals within each species (Fig. 2A), possibly due to variable wind conditions, as reported in previous observations^{12, 14}. The larger species had lower time percentages of slow flapping (Fig. 2A), which indicated a less-frequent use of flapping. Based on our observations, wandering albatrosses spend only 1.2–14.5% of time in slow flapping and 0.1–0.4 % in quick flapping, i.e., not zero (Fig. 2A). Both high and low flapping frequencies decrease, albeit with different slopes, according to the size of the bird (Fig. 2B). The lower and higher stroke frequencies were proportional to $mass^{-0.18}$ and $mass^{-0.30}$, respectively (major axis estimation, see Methods).

Takeoff is the most crucial task for flying birds and requires more active flapping than level flight because the flight speed is zero at the beginning and the birds must raise their body mainly by muscular effort. Birds can thus be expected to flap their wings at the maximum power of their muscles when taking off. The upper limit of the flapping frequency would be proportional to $mass^{-1/3}$ for geometrically similar birds^{4, 6, 8, 9}. Indeed, the observed scaling exponent (–0.30) was near the predicted value (–1/3).

In level flight, a bird must flap its wings to generate lift, and an optimum wing-flapping frequency exists at which lift and gravity forces on the bird are in equilibrium and mechanical power is minimum for sustainable flight performance⁶. Procellariiformes may be able to keep themselves airborne indefinitely without flapping their wings, if the surrounding air is moving¹, but when flight is not aided by the winds, the birds have to flap to avoid being pulled down by drag and gravity. The slow sporadic flapping of Procellariiformes during cruising flight is required to accelerate the

birds' flight speed when wind conditions are unfavourable. The thrust (lift) produced by the wing flapping is, $\frac{1}{2}\rho C_L S U^2$, where ρ is the density of the air (kg m^{-3}), C_L is the lift coefficient, S is the area of the wing (m^2), U is the speed of the wing (m s^{-1}). The wing speed U is proportional to the products of frequency f ($\text{Hz} = \text{s}^{-1}$) and the amplitude A (m) of wing flapping: $U \propto fA$. Assuming geometric and dynamic similarities ($C_L = \text{const.}$, $m \propto L^3$, $S \propto L^2$ and $A \propto L$, where m is the mass and L is the representative length of the body), the thrust would be proportional to $f^2 L^4$. The amount of resistance that confronts a bird seeking to change its flight velocity can be quantified as a function of mass ($\propto L^3$). In other words, large body mass is accelerated only with difficulty because of the large inertia. This situation can be expressed as $f^2 L^4 \propto L^3$. We thus obtain the following relationship of the minimum flapping frequency with body mass for geometrically similar birds:

$$f \propto m^{-1/6}. \quad (1)$$

This relationship is the same for continuously flapping birds^{4, 6, 9, 10} and close to the obtained result of lower flapping frequencies proportional to $m^{-0.18}$ (Fig. 2B). The present study compares phylogenetically but not geometrically similar species ($\text{wingspan} \propto m^{0.37}$, $\text{wingarea} \propto m^{0.58}$, see Methods), with larger species having relatively longer and smaller wings. This might partially explain the discrepancy between observed and expected scaling of flapping frequency versus body mass.

In the Freq-Mass diagram (Fig. 2B), the two lines of the higher and lower flapping frequencies would, if extended, intersect at a body mass of 41 kg (5.1-m wingspan). Thus, albatross-like animals weighing close to 41 kg would lack any power margin to fly under unfavourable winds. Furthermore, an animal heavier than 41 kg would not be able to flap fast enough to accelerate its flight speed. These deductions lead to an interesting implication regarding the maximum size of soaring animals, including

extinct pterosaurs. Pterosaurs existed from the late Triassic to the end of the Cretaceous (220–65 million years ago)¹⁷. According to fossil-based estimates, their body mass ranged from 0.015 kg (0.4-m wingspan) to 70 kg (10.4-m wingspan) and they are thought to have had large narrow wings similar to those of albatrosses¹⁷. The morphology and flight ability of pterosaurs are widely debated^{5, 7, 18-20}. Giant pterosaurs such as *Pteranodon* (16.6 kg, 6.95-m wingspan) and *Quetzalcoatlus* (70 kg, 10.4-m wingspan) are generally believed to have conducted soaring flight like that in extant albatrosses^{17, 21}. Other mass estimates of *Quetzalcoatlus* have ranged from 85 to 250 kg²². Based on our morphologic measurements of Procellariiformes ($mass = 0.53 wingspan^{2.7}$), for *Pteranodon* a body mass of 95 kg corresponds to wingspan of 6.95 m while for *Quetzalcoatlus* a body mass of 295 kg corresponds to a wingspan of 10.4 m. If those large pterosaurs had extremely slender bodies, more so than albatrosses and petrels, the maximum power of their muscles would have been less and their flapping capacity accordingly diminished. Previous work on the flight performance of pterosaurs has often been based on the dogmatic assumption that pterosaurs were predominantly aerial piscivores living in coastal areas²².

Our study of living Procellariiformes as model animals infers that pterosaurs larger than 41 kg (or 5.1-m wingspan) could not have attained sustainable flight. Some studies have proposed that large pterosaurs such as *Pteranodon* and *Quetzalcoatlus* used slope soaring, thermal soaring and possibly dynamic soaring¹⁷. However, our results indicate that this would only have been possible under very specific—but highly unlikely—environmental conditions such as constant strong winds or thermals. As demonstrated for albatrosses, which are mostly restricted to the Southern Ocean’s “*roaring forties*”, where powerful winds blow consistently, sustained flapping is necessary at certain stages of flight. Stronger and more constant wind conditions are essential for the sustainable flight of large pterosaurs. If other environmental factors (strength of gravity and density of the air) have changed over geological time, this might explain the brief

appearance of large pterosaurs in the fossil record⁵. Alternatively, the results of the present study lend support to a recent reappraisal suggesting that large pterosaurs were terrestrial stalkers, finding much of their food via terrestrial, ground-level foraging²². Extant Procellariiformes employ the novel method of soaring to minimise the energetic costs of transit but they do not rely exclusively on soaring because the winds do not always allow it. Instead, these birds must have enough flapping ability to be able to take off from the sea surface and to attain sustainable flight under unfavourable winds.

Methods

Field experiments were conducted during breeding periods at Possession Island, Crozet Archipelago (wandering albatross, white-chinned petrels, sooty albatross in 2006/07); Kerguelen Islands (black-browed albatross in 2005/06), in the South Indian Ocean with permission from the ethics committee of the Institut Polaire Paul Emile Victor. Field studies in Japan were conducted on Sangan Island, Japan (streaked shearwater in 2006) with permission from the Ministry of the Environment and the Agency for Cultural Affairs, government of Japan, and the Ethics Committee of University of Tokyo. Acceleration data loggers (D2GT, Little Leonardo Ltd., Tokyo, Japan) were used to detect the flapping movements of birds. The D2GT was 15 mm in diameter and 53 mm in length, with a mass of 18 g in the air; it recorded depth (1 Hz), two-dimensional acceleration (32 Hz) and temperature (1 Hz). The accelerometers were attached with waterproof tape to the feathers on the back or belly of the birds when departing for foraging trips and were retrieved when the birds returned to their nests. Loggers were positioned to detect longitudinal and dorsoventral accelerations. The raw values recorded by the accelerometers were converted into acceleration (m s^{-2}) as described previously²³.

Data analysis. To investigate modulation of the wing-flapping frequency throughout flying periods, a spectrogram of the dorsoventral acceleration was calculated by continuous wavelet transformation with the Morlet wavelet function²⁴, $\psi(\eta) = \pi^{-1/4} e^{i\omega_0\eta} e^{-\eta^2/2}$, where ω_0 is the nondimensional frequency, here taken to be 10. The newly developed software “Ethographer”, which works on the Igor Pro (WaveMetrics, Inc., Lake Oswego, OR, USA) platform, readily allowed discrete stroke frequencies to be obtained from the spectrogram for each bird by unsupervised cluster analysis, *k*-means methods. The main focus in the scaling analyses of the present study was on the slope of regression. Major axis (MA) estimations for the scaling relationships were performed in R ²⁵. Morphological measurements were conducted in the field. As in a previous study¹², wingspan and wing area of the instrumented birds were measured including the torso segment between the wings. Scaling relationships were obtained as follows:

$$\text{wingspan} = 1.3 \text{ mass}^{0.37},$$

$$\text{wingarea} = 0.15 \text{ mass}^{0.58}.$$

The scaling relationships were significantly different from one-third and two-thirds powers, as would be predicted based on geometric similarity ($n = 22$, $\alpha = 0.05$).

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Figure legends

Fig. 1 Spectrogram calculated from dorsoventral acceleration (black line) of a streaked shearwater (A) and a wandering albatross (C) during takeoff from the sea surface (black horizontal bars) and subsequent flight (grey horizontal bars). Ten discrete spectra were obtained from the entire data of the streaked shearwater (B) and the wandering albatross (D). Arrows indicate the frequencies used for takeoff (red) and sporadic flapping (blue).

Fig. 2 (A) The relationship between body mass and time percentage of slow (blue plots) and quick (red plots) flapping in a foraging trip of all individuals from the five species of albatrosses and petrels. (B) The relationship between body mass and wing-flapping frequencies. Regression lines were calculated for high (red plots) and low (blue plots) frequencies using MA estimation²⁵. Dashed lines were extrapolated for larger animals. The two lines intersect at a body mass of 41 kg (5.1-m wingspan), as indicated by the arrow.

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