



Thunderbirds, Pterosaurs and Tumblers

The Biomechanics of Flight

By Katherine Banks

More than a hundred years after Ludwig Prandtl laid the foundations for the science of aerodynamics, scientists are still struggling to understand very basic aspects of how living organisms accomplish flight.

Part of the lag is a communication problem. Evolutionary biologists are interested in flight because those groups with the ability to fly are among the most successful in evolution - with bats comprising 20% of all mammal species, and insects dividing into more species than all other animals combined (1). Physicists are also interested in animal flight as a quandary in fluid mechanics, while engineers are itching to adopt animal flight strategies to build smaller, more maneuverable, and more robust flying machines. Biomechanics serves as a bridge between these sciences. Research in biomechanics uses a

dizzying array of tools and techniques, from computer simulations to field-work in rainforests to the latest in fluid flow visualization and wind tunnels to examine flight.

The biggest difficulty found in flight biomechanics is due to the diversity of mechanisms animals have developed - causing many researchers to consider problems that normally do not arise at the energy scales typically associated with man-made flying machines. For example, the classic Kutta-Joukowski theorem in aerodynamics can be used to compute the amount of lift a given aerofoil produces, but it only works when the wing has a small angle of attack relative to the air flow. The theorem predicts that if wings are too large, the flow will separate from the boundary, causing vortices that lead to turbulence and stalling (2). Animals,

however, rely on unsteady conditions to achieve flight. They minimize how much energy it takes, often doing things that are more like controlled falling or tumbling nose over tail through the air: the opposite of what a plane regularly does. Animals generate most of the power they need to create thrust and lift by flapping their wings as they lack a motor to do it for them. The computational models of these fliers are therefore much more complicated than those of airplanes, as they require more variables to describe the wings and forbid the assumptions routinely applied to fixed wings. Finally, animals are much better at quick, subtle adjustments in response to changing conditions than man-made aircrafts, and they operate over a much wider range of length and weight scales - a combination which forbids many of the simplifications

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used in classical aerodynamics and electrical control systems.

Size and the Physics of Flight

Flying animals face the same basic problem as aeronautical engineers: how to generate lift and thrust. Animal energetics limit the amount of power an animal can generate with its muscles to something less than what would be required to balance its weight while in the air. There is thus an evolutionary pressure for flying animals to develop large muscles and other adaptations that would help them produce more lift or counteract drag. This is impossible for many animals, and those that weigh more than 20 kilograms rarely develop the ability to fly (1).

Those animals that can fly come in a wide variety of shapes and sizes, but there are some intrinsic limitations on how they are constituted. The methods of biomechanical engineering can be used to generate “power curves”: plots of forward velocity versus muscle force used for a given animal. The shape of those curves can tell us a lot about how the animal’s wings are shaped, how fast they beat, and how wing geometry changes during flight (3). They have been used to study everything from comparative morphology between bird species, to why large birds must generally taxi and then fly over a limited range of speeds, while small birds exhibit a much wider range of flying speeds and modes (4).

In 1968, Colin Pennycuik, a pioneer in the study of animal flight, performed a seminal study explaining how hummingbirds hover. He suggested helicopters, not fixed-wing planes, as the proper model for bird flight (5). Looking at the flat shape of the



▲ **Figure 1.** A gull minimizing drag with its wing shape.

power curve of a pigeon at intermediate speeds—where airplane theory would predict a U-shaped curve—he concluded the curve was consistent with a propeller-based system that separates lift and thrust generation.

By employing comparative and computational approaches, researchers today have been able to determine how viscous the atmosphere a bird is flying through must be before a rowing motion becomes more efficient than a flapping motion (6). Since computers allow researchers to model

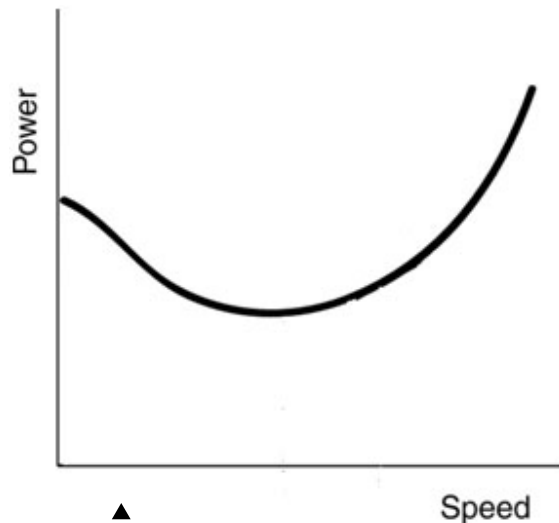
many variations on a design, they have also been able to posit behavioral strategies birds use to minimize drag - such as the characteristic bent wings of descending seagulls, which allow for reduced wing-span and wing area exposed to the air.

Of course, behavior

can only compensate for so much - truly ungainly animals would not be able to fly, and simulations of bird shape can tell researchers what limits on shape exist for flying animals.

Flying in Micro

When it comes to insects, much of the theory applied to larger animals no longer applies. For example, an analysis of four species of fruit flies with similar shapes, but different masses, found that the smaller flies expended less energy, as measured by carbon dioxide output, than the larger ones while hovering - the opposite of what happens in birds (7). Insects, for the most part, are slaves to the viscous forces battering their thin, membranous wings. The problem is no longer the use of muscles



▲ **Figure 2.** An example of the expected U-shape of a power curve.

to generate thrust but in wing geometry.

For that reason, research on insect flight is focused on optimization and control problems: how to produce the most force with the least power - considering power production is so costly for small insects (8). In her lab at Cornell, Jane Wang studies simulations of falling paper and insect flight. Her team has found many similarities between the two motions (9). Both systems are analyzed with a method that emphasizes the rapidly changing

shape of the boundary layer - a rare feature in manufactured systems.

Wang’s lab is also working on a fundamental problem in insect flight: given that insects must beat their wings hundreds of times a second to generate enough lift, how can they possibly alter the wing motions to execute turns and other

adjustments? To answer this question, her lab has developed novel methods for analyzing the kinematic data from high-speed videos of flies. They employ principal component analysis, shape analysis, and computational geometry to extract accurate position data from the fly’s fast but subtle motions (10). They have concluded that fly wings can

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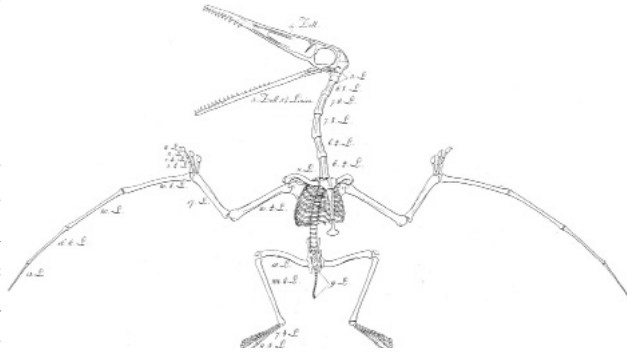
be modeled as torsional springs that passively resist the tendency for the wing to flip. That resistance causes an asymmetry in wing orientation that lets the fly turn using no further active wing movement (11). They have also used this model to demonstrate that flapping wing flight can require less energy than fixed-wing flight - suggesting that maneuverability and energy efficiency need not be competing goals (12).

Out of the Lab, Into the Field

While fluid mechanics like Wang are measuring wing motions in the lab, biologists are using new types of data available to them to expand the range of flight biomechanics studies done in the field. Wind tunnels used to be the primary way of collecting physiological and kinematic data from a flying animal. Quantities like metabolic rate were first determined very indirectly by measuring the mass a bird lost during a long flight and assuming most of that was fat loss. These days, there are sensors, satellite transmitters and data loggers, that are small enough to attach to a bird without significantly changing its movement and are quick enough to constantly send physiological and motion data to the lab (13). This provides unprecedented access to atmospheric, physiological, and behavioral data of flying animals in the wild.

Biologists can also use paleontological field data to figure out whether an extinct species might have flown. A team led by Sankar Chatterjee, from Texas Tech University, made a com-

puter simulation from a fossil of *Argentavis*, the largest flying bird ever to have existed. The team used bone density and other structural measurements to confirm that the heavy bird was indeed a flier. (14) They suggested several possible ways the bird could have obtained the extra energy it would need to support its weight while flying—the options range from leaping



▲ **Figure 3.** Samuel von Sömmering's 1812 reconstruction of *Pterodactylus antiquus*, a Pterosaur from the Jurassic Period. Scientists have managed more accurate ones since.

off a perch to taking a running start off an incline and using energy from thermal columns. Another group of biologists has determined the gliding mechanism of a newly discovered flying lizard by noting that a thickened rib implies heavily muscled wings (15). Still others continue to study the pterosaurs, the earliest vertebrates to develop flapping flight, for evidence of the mechanism behind its efficient and controlled flight abilities (16).

Going Forward

Engineers and doctors are already applying the fundamental biology and physics of animal flight to man-made appliances. Here at Harvard, Professor Robert Wood runs a Microbotics Laboratory that is building micro-sized robotic flies, with military applications. His work illuminates

more of the fundamental science - by trying to reconstruct fly flight, he has learned more about the passive control of maneuvers that Jane Wang noted (17). At the same time, in constructing these robots, Wood and his team have developed new techniques to create artificial insect-like wings (18). With the recent explosion of interest and computing power, there is surely much more to come. **H**

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