How Does Half a Bird Fly?

The age-old problem of the origin of flight in birds is now being analyzed in terms of sophisticated aerodynamics; an answer is nearer, but is still elusive

Bird flight is an aerodynamically complex and physically demanding process. Therefore, like the origin of flight in insects, which was described in last week's issue (*1*), the transition from a nonflying ancestor to a fully fledged flier presents a challenge to evolutionary biologists. Several research groups have recently developed mathematical models that explore what is probably the most popular idea for the origin of powered flight in vertebrates, namely the arboreal, or trees-down, hypothesis.

According to this notion, the ancestral bird, or Pro-avis as it is usually called, was a glider that extended its range by rudimentary flapping of its airfoils. The locomotory advantages of this mechanism would, through natural selection, eventually lead to fully powered, horizontal flight, or so it goes.

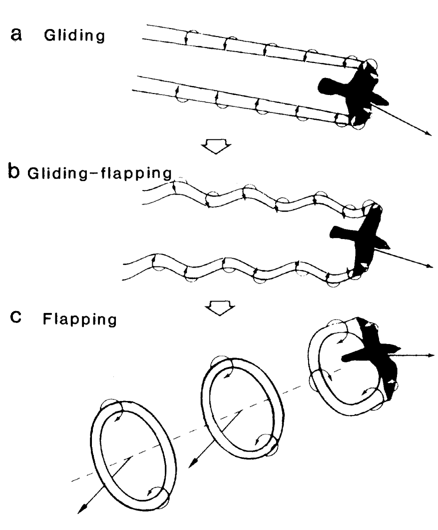
The crucial point here is the transition from glider to flier: is it structurally and aerodynamically feasible? Ulla Norberg, of the University of Göteborg, Sweden, believes that it is, based upon an impressive mathematical analysis of semipowered flight (*2*). However, in a similar analysis, Russell Balda, Gerald Caple, and William Willis, of Northern Arizona University, come to the opposite conclusion (*3*). Each position finds enthusiastic supporters, so the question is clearly not solved. But this age-old problem has reached an important stage, where, at last, the models being produced are accessible to experimental and other tests.

Leaving aside the question of the evolution of feathers, notions about the origin of powered vertebrate flight have principally been two: the arboreal hypothesis already mentioned and the cursorial, or ground-up, hypothesis. This second idea involves a Pro-avis ancestor running bipedally and swiftly along the ground, with its feather-covered forelimbs eventually taking on the role of wings. Ideas for the initial role of the forelimbs have differed over time, with an early suggestion that they might enable the animal to increase its ground speed being replaced in 1974 by John Ostrom's famous insect-net idea. Ostrom, who is at Yale University, recently declared that the idea, though wrong, had served its purpose, which was to focus attention on cursorial adaptations. This is where the Arizona team stepped into the debate.

A little over 2 years ago Balda and his colleagues described the hypothetical advantages conferred by protowings on a small, insectivorous, cursorial, dinosaur-type of animal (*4*). Even a very small amount of aerodynamic lift produced by diminutive but mobile airfoils would, they argued, bestow great maneuverability and stability on a running, jumping insectivore. Such an animal would be able to double its foraging area at little energy cost. They proposed that a fully powered flier could be derived from such an animal, because it is already equipped with strong hind legs and potentially powerful pectoral muscles. Natural selection would simply have to work on the energetic advantages of increased foraging area.

Balda and his colleagues noted at the time their belief that the arboreal hypothesis runs into trouble, because a glider that flaps its airfoil incurs considerable aerodynamic disadvantages as well as advantages. This represented an adaptive barrier across which the animal would be unable to pass, they said.

Norberg and others, notably Jeremy Rayner of Bristol University, England, took up this challenge, the results of which they presented at the *Archaeopteryx* conference, which was held in Eichstatt, Germany, last year. Norberg's presentation, now more fully developed in the *American Naturalist*, looks formidable, buttressed as it is by elegant mathematics. The principal thrust of the argument is that between the complete glider and the fully developed flier is an aerodynamically feasible, flapping glider.



Flying vortices

The vortex tubes generated at the wing tips of a pure glider (a) contrast with the power-giving rings of the flapping flier (c). The gliding flapper has something of an intermediate form (b).

Gliding is clearly a useful adaptation, as is evidenced by its parallel evolution in amphibians, reptiles, and mammals. The glider simply has to balance lift and drag to achieve a relatively shallow glide path, thus traversing considerable distances at minimum energy cost. Indeed, a combination of gliding down and climbing up is an exceedingly energy efficient way of foraging from tree to tree, and modern birds do it when they can. And many modern birds alternate a pure downward glide path with bursts of upward flight, producing an undulating flight pattern that is 10 to 20 percent cheaper to fuel than is horizontal flight.

Now a wing that works in powered flight is longer and narrower than its equivalent in a glider: it is said to have a higher aspect ratio. At least one reason for this difference is that the thrust produced in powered flight derives from the outer one-third of the wing. The evolutionary transition from a pure glider to a powered flier would therefore involve a significant change in wing morphology, a change that Caple and his colleagues find difficult to accept as being feasible, while Norberg does not.

Norberg inserted the dimensions of an *Archaeopteryx*-sized bird into her quasi-stationary aerodynamic model in order to determine the animal's flight characteristics. The model computes several flight variables, such as glide speed and angle, angle and amplitude of wingbeat, and wingbeat speed, from which can be derived the wingbeat frequency required to extend the normal glide length. With a glide speed of 7 m per second and a vertical wing motion, such a protobird would need to flap 6.6 times a second, a figure that could be reduced to 6 times a second if the downstroke of the wing is slightly forward rather than straight down.

This beat frequency is close to that of a modern bird of the same size, a fact that caused Norberg some concern. It would be unreasonable, she inferred, to expect the protoflier instantly to achieve a beat frequency of such a high rate. By changing the characteristics of the wingbeat to a fast downward stroke followed by a slow return, it is possible, calculates Norberg, to achieve the required thrust and lift with a very low wingbeat frequency. For instance, with a downstroke taking just one-tenth the time of the upstroke, and depending on other parameters, the wingbeat rate could be as low as 2 per second.

Therefore, the transitional form, according to this model, is a glider that can increase its glide-path length by a low frequency, asymmetric (fast down, slow up) and deep wingbeat. This manner of progression would convert the pair of vortex tubes that are generated at the wing tips of a pure glider to an undulating form, as shown in the diagram. It is but a short step to the generation of the trail of vortex rings that power flapping flight: a rather more vigorous wingbeat pattern is all that is required, says Norberg.

The Arizona team's objections to Norberg's conclusions are several, and include both biological and physical questions. Central among these are the energetic and aerodynamic penalties incurred by a glider that moves toward semi-powered flight. They say that their aerodynamic calculations show that, for such a putative transitional form, benefits from extra lift and thrust are accrued only when the characteristics of fully powered flight are approached. Furthermore, a glider is muscularly ill-equipped to make this rapid transition. In other words, there is an adaptive chasm to be bridged between glider and flier. By contrast, a cursorial runner and jumper would already be on something of a functional trajectory toward powered flight, they argue.

Flight characteristics of modern birds are also adduced to argue against Norberg's proposal. For instance, the fast-down/slow-up wingbeat suggested by Norberg for the Pro-avis form is rare or absent in modern animals. And, asks Caple, if the slow flap so easily and efficiently extends the glide-path length, why don't modern birds do this in their undulating flap/glide pattern? Such observations can, of course, only be suggestive, never conclusive.

The mathematical schemes developed by the Swedish and Arizona teams can be tested experimentally, using both modern birds and models. It therefore remains to be seen which of the models is correct and, if correct, whether it is relevant. —ROGER LEWIN

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Signs of an Eastern Quake?

Geophysicists who have been analyzing old surveying records believe that they may have found a way of pinpointing the sites of possible future earthquakes in the eastern United States. With little else to go on, researchers could in the past only assume that the next large earthquakes would strike where past ones have, although many hundreds or thousands of years pass between recurrences. Mark Zoback of Stanford University and William Prescott and Scot Krueger of the U.S. Geological Survey in Menlo Park have found evidence suggesting that during the past 100 years stress has been concentrating in the upper crust just north of New York City (*1*). Such stress accumulation, if maintained for several hundred years and then released suddenly, would generate a major earthquake.

The Stanford-USGS group looked for signs of stress accumulation by analyzing a few of the 10 million measurements used to locate the quarter million markers that guide local engineering and property surveys. In fact, the group could only use the occasional serendipitous redetermination of angles between markers to detect a change in the angles and thus a deformation of the crust due to a stress accumulation. Five suitable fragments of the network near the Middle Atlantic coast were analyzed for changes occurring between 1872 and 1973.

Only along 60 kilometers of the eastern shore of the Hudson River and in western Long Island did significant changes appear, but they were considerable. The surface along the Hudson seemed to have deformed nearly as rapidly as is happening on most parts of the San Andreas fault, where the motion of the Pacific plate past the North American plate builds up enough stress to rupture the fault every 150 years or so. The western Long Island area seemed to be accumulating stress several times faster than that.

Richard Snay of the National Geodetic Survey has brought down these uncomfortably high rates by using an analysis approach that, although less rigorous, allows the inclusion of two to three times as many angles (*2*). Along the Hudson, Snay's technique revealed a slightly lower rate of deformation than Zoback and his colleagues found, but it is still significant. In western Long Island, Snay determined the same high rate of deformation, but he found that the rate varied from one part of the area to another. From that he concludes that it is not broad surface deformation but disturbance of individual markers that caused the angles to change.

Although there is no plate boundary in the East, the group concludes that things work in the East much as they do along the San Andreas. The source of stress is different in the East—the drag of the moving North American plate, perhaps—but where stress is concentrated in the upper crust is probably determined in the lower crust, they conclude, as happens in the case of the San Andreas. A popular theory has held that stress that is too low to break normal crust would rupture a zone of weakness, such as the scar left by an old rift, in the brittle upper 20 kilometers of the crust.

The Stanford-USGS group argues that in the upper crust one rock is as strong as the next, so that geologic evidence of a past disruption of the surface would often be irrelevant. Instead, one should look for geodetic evidence, as they have, that rock below 20 kilometers is deforming ductilely, behavior midway between the elastic distortion of the upper crust and the flow of the deeper mantle. Such localized ductile deformation, whose ultimate cause remains obscure, would then concentrate stress in the brittle crust above it to produce the observed deformation.

"Right now," says Zoback, "we just don't have any constraints on" the timing or size of a future earthquake, if one occurs at all. The Hudson area does lie at the northern end of a zone of low-level seismic activity. And larger earthquakes have struck before—an 1884 shock probably located at the mouth of the Hudson was felt from Maryland to New Hampshire. The next step will be to use the satellite-based global positioning system to check recent deformation.—RICHARD A. KERR

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