How Did Vertebrates Take to the Air?

Aerodynamic analysis has produced novel support for the cursorial, as opposed to the arboreal, theory of the origin of birds

The origin of powered flight in vertebrates is one of the greatest challenges to evolutionary biology. That challenge has been taken up by the somewhat unlikely team of a chemist, a physicist, and a biologist at Northern Arizona University, Flagstaff. "We wanted to apply aerodynamic principles to the origin of flight," says Gerald Caple, the chemist in the team and the initiator of the project. "This hasn't been done to any great extent before."

The upshot of this neglected but highly pertinent approach is an evolutionary model that progresses rapidly and smoothly through a series of forms intermediate between a ground-running biped to a fully powered flier. Unlike other major hypotheses on the origin of flight, the intermediate forms in the Flagstaff model are all functionally adapted: there is no requirement for a leap of faith at any point.

Ever since the beginning of the century there have been two schools of thought on the origin of bird flight. One, the arboreal theory, proposed the transition of a tree-living animal through a gliding stage to powered flight. The second, the cursorial theory, sees the development of flight in a bipedal, running animal that uses its forelimbs (protowings) to produce thrust and thus greater speed. Of the two, the arboreal theory is intuitively the most appealing, partly because the gravity effect helps rather than hinders.

Both theories are, however, marred by functional gaps. In the trees-downward idea, there is no good explanation of the functional transition between an airfoil designed for gliding and a wing that must be powered for flight. The ground-upward notion does not readily explain how a rudimentary wing that helps increase running speed during predation or escape might be transformed into a full wing capable of the powerful and complicated flight stroke.

Early in 1979, John Ostrom of Yale University published an essay in *American Scientist* on the current status of the two theories on the origin of bird flight. Ostrom, who is the most prominent proponent of the cursorial theory, took the opportunity to describe his insect-net theory. He recognized that the skeleton of *Archaeopteryx*, the earliest birdlike creature in the fossil record, was much like that of a small, running, insectivorous dinosaur. *Archaeopteryx*, he speculated, might have increased its predatory efficiency by beating its prey out of the air, using its wings as it ran along the ground. The main objective of the essay, Ostrom now says, was "to stop people accepting that the arboreal theory was gospel, and to show that there were good reasons for considering the cursorial theory."

Unknown to Ostrom, the essay was on target. Caple read it, enlisted the interest of Russell Balda, an ornithologist at Flagstaff, and within a week had a crude model for proavis. Realizing they needed an expert on aerodynamics, Caple and Balda recruited physicist William Willis, a former fighter pilot. "All previous models had emphasized either thrust or lift," says Caple. "We started from the premise that control of body position and of movement was critical." Control—in running, in jumping, and in flight—is a persistent theme of the Flagstaff model. "It is reasonable to assume that an animal with lift and thrust but not in control of its body could not successfully evolve flight," write Caple, Balda, and Willis.*

John Ostrom

Archaeopteryx

With a skeleton like that of a small, running dinosaur, this 140-million-year-old fossil supports the cursorial theory of flight.

Using anatomical inference based on *Archaeopteryx*, Caple and his colleagues assume its nonflying ancestor to have been a small, ground-running, insectivorous dinosaur, such as a small theropod. For purposes of calculations they refer to a 100-gram cylinder 15 centimeters long and 3 centimeters in diameter; forearms (of varying lengths) project from the "body" just in front of the center of mass.

The first question to be addressed using this preflight model is, what advantages are there to jumping? Assuming a conservative running speed of 3 meters per second, the animal would be able to forage for insects within the space of a cylinder that was 3 meters long and 15 centimeters in diameter when it runs for 1 second. If the animal jumps to a height of 30 centimeters at any point in its run it doubles its potential foraging volume. The Flagstaff team calculates the cost of running for 1 second to be 1.6 calories and the cost of jumping less than 0.4 calorie, giving a total of 2.0 calories. The energetic cost of achieving a doubled foraging volume by running is 2.3 calories. As the potential reward is great–insects have a calorific value of several thousand calories per gram—the cost-benefit ratio of jumping is likely to be favorable.

Jumping at speed, however, has its problems. An assymetric takeoff, through a one-footed jump or a two-footed jump on an uneven surface for instance, will impart a degree of angular momentum about the roll axis. With roll uncorrected, the animal might land on its back. Caple and his colleagues present in detail the extent of control possible over destabilizing movements by simple extension and movement of the forelimbs. They show that forelimbs that contain 7.5 percent of body mass and can extend to 4.5 times the body radius impart substantial control over roll but somewhat less in the pitch and yaw axes because of the greater moment of inertia about these

*Am. Nat. 121, 455 (1983).

axes. A concentration of mass at the limbs' extremities enhances control.

In addition to imparting some stability to the jumping animal, the slight maneuverability allowed by movements of these no-lift forelimbs will also extend the foraging volume, albeit to a relatively small degree. The movement of a tail up or down would allow a similar movement of the head, while the center of mass continues on its ballistic path. The further the animal can move its head, the further it can extend its foraging space.

At this point the Flagstaff team introduces the facility for lift, by simple flattening of the forelimb or by extension of scales or feathers, for instance. In the arboreal theory lift has been seen as enhancing the glide path, whereas in the traditional cursorial theory it was a means of increasing running speed. (In Ostrom's version of the cursorial theory the lift structures were the insect nets.) By contrast with these models, say Caple, Balda, and Willis, "our studies indicate that small increments of lift will dramatically increase the control of body orientation and thus enhance foraging and landing efficiency of a jumper."

The benefits to predation efficiency are unexpectedly great, explain Caple and his colleagues: "Relatively small combinations of pitch and roll will result in a large increase in foraging volume because the cross-sectional area depends on the square of its radius." For instance, a change of only 8 degrees in the longitudinal axis of the jumper's body effectively quadruples its foraging volume. An animal would have to be able to generate lift equivalent to only 5 percent of its body weight in order to complete such a maneuver within one-tenth of a second. Even 1 percent lift confers considerable control over body orientation.

So, with the commitment of as little as 4 percent of its body surface area to generating lift, a jumping animal can acquire a surprising degree of "inflight" control, which brings a substantial extension of its predatory space. Such outstanding benefits would be sharply available to natural selection.

The Flagstaff researchers note that the motions of the forelimbs in controlling roll and pitch resemble a rudimentary flight stroke, which is rather like a lazy figure of eight. With lift capabilities in the range 1 to 5 percent, however, the animal is barely able to extend its jump path, let alone fly. But by this time the animal would be subject to a positive feedback system that, the Flagstaff team believes, would propel the animal rapidly along an evolutionary path toward fully powered flight.

With the development of lift in the forelimbs and the tail, the animal becomes more stable while running, and can therefore run faster. As lift is proportional to the square of the airspeed over the lifting surfaces, faster running means greater lift: doubling the running speed quadruples lift. Forward movement of the forelimbs, as in control of pitch for instance, would also increase airspeed across the lifting surfaces, further enhancing the lift force.

The combination of two squared functions—lift as a function of velocity squared, and foraging volume as a function of radius squared—constitutes the positive feedback system, argue Caple, Balda, and Willis. "This positive feedback mechanism could account for the very rapid evolution from a running animal to an animal capable of powered flight."

One of the most difficult maneuvers birds must complete is that of landing on a branch. The margin for error for a bipedal animal is small and the forces needed to correct such errors very large. The Flagstaff workers calculate that only an animal that has already developed fully powered flight would be capable of such a precarious landing. If birds evolved from arboreal animals, as the arboreal theory suggests, they might be expected to fly from branch to branch, even at an early stage. But the Flagstaff researchers are forced to conclude that frequent landing in trees might be one of the last adaptations made by birds. For this and other reasons they find the arboreal theory untenable.

Walter Bock, professor of evolutionary biology at Columbia University, New York, is the most prominent proponent of the arboreal theory. He counters this conclusion by suggesting that arboreal animals in the early stages of the evolution of flight might have retained the ability to climb trees while flight would mainly be from branches to the relatively undemanding landing platform of terra firma. He champions the superiority of the arboreal theory because, he says, "in evolution you look for living intermediates. The many forms of gliding animals are good intermediates for the arboreal theory. There are none for the cursorial theory."

Caple and his colleagues address in a preliminary way in the *American Naturalist* paper the question of transition from a glider to a powered flier. The changes required for the transition are great, they say, "and in some cases the physical adaptations for powered flight are in opposition to those necessary for gliding." The airfoil for a gliding animal, for instance, is usually a soft membrane stretched between the fore- and hindlimbs and attached along the length of the body. The lifting surfaces of a flier, by contrast, are far away from the length of the body, such as the wings and the tail.

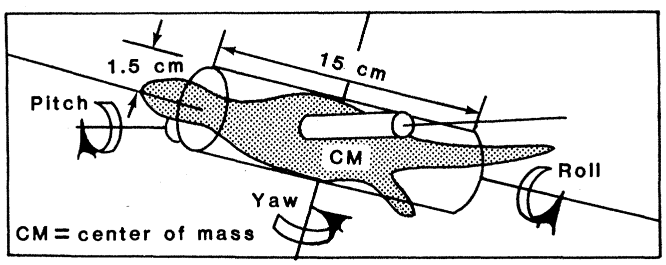
The arboreal theory has always assumed that rudimentary flapping of the lifting surfaces employed in gliding would be a transitional state towards powered flight. But, say the Flagstaff workers, aerodynamic calculations show that such flapping would dramatically reduce lift, not increase it. The development of powerful flight muscles from a rudimentary state through an adaptive vacuum would also be a problem.

Bock notes the suggestion that the flapping of a gliding airfoil would reduce lift but witholds judgment because Caple and his colleagues have yet to publish any data on the subject. If their data do show this effect, and if they are confirmed independently, this would be a serious problem for the arboreal theory, acknowledges Bock. The Flagstaff workers are currently preparing a paper on the subject.

Ostrom, need it be said, is delighted with the conclusions of Caple and coworkers. "They have added a more logical and acceptable aspect to the cursorial theory. The notion of a bipedal precursor to flight has been difficult to accept by critics, but Caple's arguments must be seen as persuasive." Ostrom agrees that the critical question now is to determine whether or not it is feasible in aerodynamic terms to go from a glider to a powered flier.

"Yes," says Ostrom. "The insect net idea is dead. It did its job."

—Roger Lewin



Model flier

The Flagstaff team used a 15 × 3 centimeters, 100-gram cylinder as its "model" in aerodynamic calculations of the consequences of running and jumping with varying degrees of lift.