10

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LEONARDO *and the* SCIENCE *of* BIRD FLIGHT

RICHARD O. PRUM

Despite the ubiquity of airplane travel and communication satellites, the vision of a bird in flight still inspires wonder. The efficiency, maneuverability, and sheer exuberance of avian flight strike us as miraculous, or as close to it as we are comfortable admitting. Scientific inquiry can help us understand the inspiration for the awe we experience while watching birds in flight—contradicting the view that scientific and technological progress deadens our experience of the natural world.

An iconic Renaissance genius with diverse accomplishments in art, mathematics, anatomy, physics, and engineering, Leonardo is also the *type specimen*—the exemplar that biologists use to describe a species—of human flight obsession. Nature inspired his intellect, and throughout his life he studied flying creatures, especially birds, all the while recording his thoughts and observations. His principal contribution to the science of flight is the Codex on the Flight of Birds (ca. 1505/1506) in the Biblioteca Reale, Turin, now exhibited for the first time in North America.

Scholars have frequently noted that achieving the dream of human flight strongly motivated Leonardo's intellectual explorations.[1] Most previously published discussions on Leonardo and flight primarily concern his technological ideas and engineering innovations, and present a portrait of Leonardo as Engineer. As an ornithologist and evolutionary biologist, I have been inspired by the Codex to explore another side of the famously multifaceted artist—Leonardo as Biologist, or maybe even Leonardo the Ornithologist. The present essay addresses several new questions: How accurate are Leonardo's observations of birds? How well did Leonardo understand the physical mechanisms of bird flight? What intellectual innovations did Leonardo conceive in his explorations of the biology and biophysics of avian flight?

Because Leonardo moved seamlessly among subjects now confined to various separate disciplines—art, engineering, physics, anatomy, and biology—any modern exploration of his intellectual world likewise requires a stretching of the boundaries we now experience among academic disciplines. For readers better acquainted with the history of art than with the sciences, a brief description of our current understanding of how birds fly is included here. Then we will explore Leonardo's intellectual ideas and innovations on the analysis of bird flight in the Turin Codex and other writings, analyzing the extent to which he appropriately framed the biological questions, the analytical tools he employed, the specific physical mechanisms he described for flight, and the depth of his appreciation for the complexity of avian flight. Last, I will attempt to characterize Leonardo's singular role in the history of science in general and ornithology in particular.

HOW BIRDS FLY

Birds use their wings to create the physical forces that allow them to fly. The description of this process is called *aerodynamics*. To understand how birds create aerodynamic forces, we need to discuss the anatomy of the avian wing. The bird's wing is a vertebrate forelimb. Like the human arm, it has characteristic skeletal elements—a single basal upper arm bone attached to a pair of parallel bones followed by a proliferation of smaller bones in the hand and fingers (fig. 32). In addition to the wing bones having special shapes, and greatly reduced fingers, the bird wing is covered with feathers. Feathers are complex, branched structures that grow out of the skin like hair, scales, or claws.

The tiniest branches of the feather, called barbules, have microscopic hooks and grooves that zipper together like Velcro (fig. 33). This zippering action creates a novel surface of interlacing fibers, like a fabric that weaves itself together, to form the coherent planar surface, or feather vane, that creates the physical forces that allow birds to fly.

A bird's feathers vary in shape, size, and microscopic structure to accomplish the many different tasks in the lives of birds. The large *flight feathers* attached to the trailing edge of the wing are the most important for this discussion. The smaller feathers that cover the wing, called *wing coverts*, also have a critical function in creating the shape or profile of the wing. The complex muscles that drive the wingstroke originate on the bones in the bird's chest, extend out the

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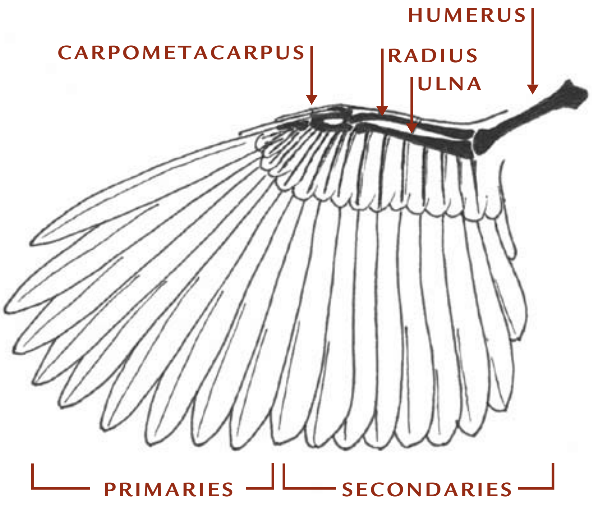

FIGURE 32 Bones and feathers of a bird's wing

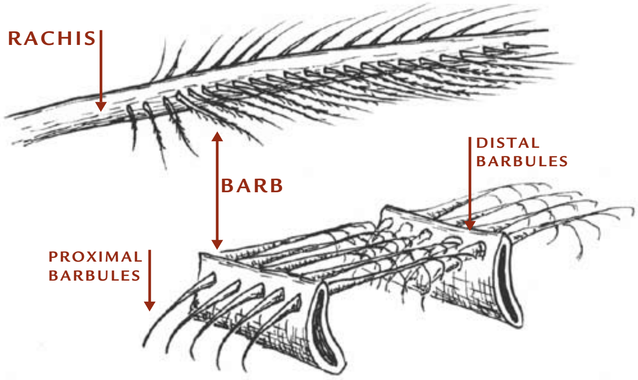

FIGURE 33 Structure of a vaned feather. The hooks and grooves of the smallest branches, called barbules, interlock to create the coherent surface of a planar feather vane

wing, and insert on the outer bones of the wing through fine ligaments. Fine control of the timing and strength of the firing of these muscles provide incredibly delicate and flexible control of the wing movements during flight.

To describe the aerodynamics of a flying bird, we need to account for four idealized physical forces (fig. 34). Two outside forces act on the bird. *Weight* is the downward force created by the mass of the bird in the earth's gravity. We are all too familiar with the force of weight. The second, *drag*, is the frictional force created by the movement of air over the plumage. Drag is the force of resistance that acts to impede the forward motion of the bird through the air. (Humans experience drag while riding in a motorcycle or a convertible with the top down, or swimming.) The bird itself creates two other forces with its wings: *lift*, the vertical, aerodynamic force that keeps the bird aloft, and *thrust*, which propels the bird forward in the air.

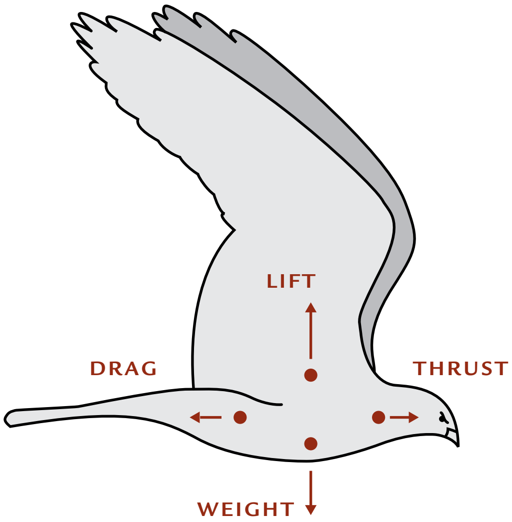

FIGURE 34 The centers and directions of the four forces acting on a flying bird—weight, drag, lift, and thrust

How do birds exploit these forces to fly? In brief, birds fly when the forces they create—lift and thrust—are greater than the forces acting upon them—weight and drag. But how do birds create lift and thrust? Clearly, that is what all that flapping is about!

To answer these questions, we need to look at the shape of a bird's wing. In cross-section, the top surface of a bird's wing is more curved than the bottom surface (fig. 35a), a consequence of both the distribution of wing mass and the covering of covert feathers. Imagine air flowing across the top and bottom of the wing from front to back. Because of the curvature in wing shape, the air flowing over the top of the wing will have to travel farther to traverse the wing surface than the air traveling across the bottom of the wing. The next key observation is that if the air travels farther over the top surface of the wing during the same amount of time, it will have to be traveling faster across the top surface of the wing than across the bottom. It is the differences in air speeds over the surfaces of the wing that create the forces that allow birds to fly.

Bernoulli's Law, named after mathematician Daniel Bernoulli (1700–1781) who rediscovered many of Leonardo's insights into fluid dynamics, helps us to understand the consequences of these differences in air speed over the surfaces of the wing. Bernoulli states that the sum of the *static* air pressure acting downward on a surface and the *dynamic* air pressure acting along a surface are constant. Thus, the faster the dynamic pressure, or air speed, the lower the static pressure, and vice versa. The Bernoulli effect can be observed by holding the edge of a small sheet of paper to your bottom lip; when you blow over the top of the sheet of paper, you will create an asymmetry in dynamic and static pressure between the two sides of the paper, and the paper will rise and begin to flap like a flag. Note that the paper is pushed upward toward the side with the higher dynamic pressure and, thus, lower static pressure.

Likewise, by establishing faster air flow over its curved upper surface, the asymmetrical shape of the bird wing creates *higher* dynamic pressure and *lower* static pressure on the top surface of the wing, and *lower* dynamic pressure and *higher* static pressure acting on the bottom of the wing. This difference in static pressure in between the upper and lower surfaces of the wing is the lift force that keeps a bird aloft in flight. The direction of this force is perpendicular to the surface of the wing.

In summary, the wing creates asymmetries in static air pressure on the two surfaces (top and bottom) of the wing to create net forces that propel the bird through the air. To stay aloft, a soaring bird, like a glider, needs to create enough lift to support its weight and counteract the loss of energy owed to drag, or friction. But what moves the bird forward during powered, flapping flight? How does the bird create forward thrust?

Leonardo envisioned human-powered flying technologies based on the flapping motion of birds. The most successful flying machines—airplanes—took a decidedly different route, however, by using wings to create lift and propellers (or jet engines) to create thrust. Since the invention of the airplane, bird flight has usually been incorrectly explained, using the airplane analogy. This rhetorical method is, in a perverse way, the opposite of Leonardo's intellectual method. Also, it is decidedly misleading because airplanes divide the jobs of creating lift and thrust forces between two different structures, whereas birds and other flying organisms use the same structures to create both lift and thrust. Indeed, in the preceding paragraph I also succumbed to the tempting airplane analogy by idealizing separate lift and thrust forces.

A propeller airplane flies on two sets of wings, both of which have the asymmetrical shape of a bird's wings. The main, static wings create lift. The whirring propeller is a second set of dynamic wings that create forward thrust. The asymmetrical shape of the propeller and its angle of attack as it rotates are functionally analogous to a bird's wings. This is a great engineering solution; however, it is not how organisms fly.

The key to understanding flapping flight is that birds *do not* create separate lift and thrust forces. Instead, they use their single pair of wings to create both forces simultaneously. How? Remember that lift is created perpendicular to the movement of air across the wing. So, birds rotate the angle of the wing forward during the powerful downstroke to change the direction of the lift force (fig. 35b). The angle of the wing to the moving air is called the *angle of attack*. By rotating the angle of attack forward or down, the lift force created perpendicular to the wing is now also rotated, or angled forward. Now, the wing has created a single force with a net forward thrust component as well as the traditional vertical component (fig. 35b). In this way, the flapping bird's wing works simultaneously like the wings *and* the propeller of a plane to create vertical and forward directing forces. Indeed, in this way, the bird is really more like a helicopter that suspends and propels itself with a single set of blades.

What about the upstroke? In general, the bird cannot maintain the same angle of attack on the upstroke as it uses on the downstroke, or it will create a backward rotated component of lift that will counteract forward thrust, and it will stall in midair. Although tiny hummingbirds hover in exactly this fashion, expending great amounts of energy, most birds are trying to fly forward and can't afford to stall in mid-flight. So, birds minimize the aerodynamic forces created by the wings on the upstroke by minimizing the angle of attack, or by changing the asymmetrical shape of the wing and producing almost no lift at all on the upstroke. While flight requires the asymmetry in wing shape to create

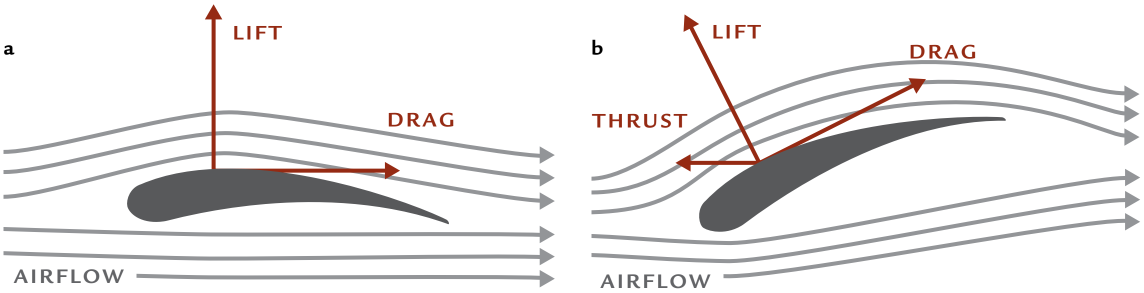

FIGURE 35 Airflow over the asymmetrical bird wing

[a] In gliding flight, the air flows faster over the top of the curved wing and creates the lift force

[b] In flapping flight, the bird rotates the wing forward, angling the lift vector forward, creating forward thrust

lift, powered flapping flight requires another asymmetry in the movement of the wing over the wingstroke to produce powered forward movement.[2]

At different speeds, birds fly with different *gaits,* which are generally analogous to the walk, trot, canter, and gallop of the horse. At slow speeds (imagine a pigeon bursting into flight from the ground), the asymmetry of the wingstroke is like the motion of a rower removing the oars from the water—highly asymmetrical. All the net forces are created on the downstroke, and the bird goes through complex maneuvers to create the minimum amount of lift on the upstroke. The upstroke is used to reset the system. In contrast, a duck or falcon in high-speed, level flight has much less asymmetrical wingstroke.

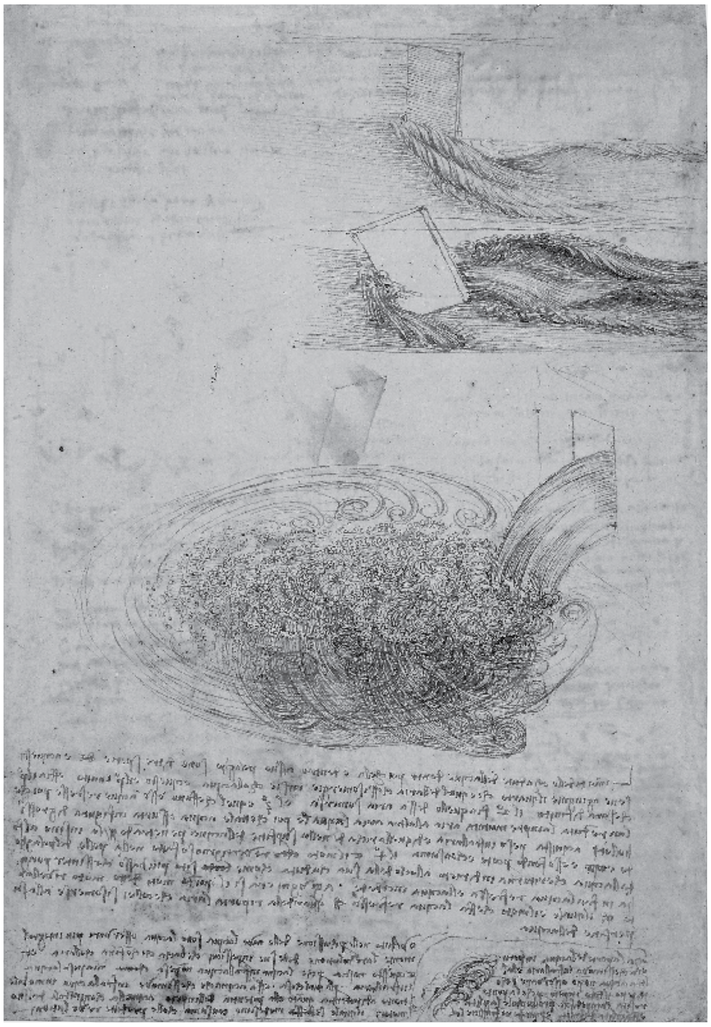

FIGURE 36 *Studies of Water Passing Obstacles and Falling into a Pool,* pen and brown ink over traces of black chalk on laid paper, Her Majesty Queen Elizabeth II, Royal Library, Windsor, RL 12660v

LEONARDO'S INSIGHTS INTO BIRD FLIGHT

The physics of the movement of water fascinated Leonardo throughout his life. Over several decades, he dedicated substantial intellectual energies to these investigations (fig. 36), thus initiating the science of *hydrodynamics,* and anticipated many fundamental scientific discoveries in this area by a few centuries. For example, Leonardo realized that liquid flowed faster through the narrower section of a tube than a wider section of a tube centuries before Bernoulli rediscovered the idea. In the context of flight, Leonardo discussed and clearly understood the commonality between the flow of water, which he had so acutely observed and so accurately described, and the flow of air, which is much more challenging to observe and comprehend. In this regard, Leonardo was absolutely pioneering. Today, the physics of flow in liquids and gases is considered a single, unified intellectual field of *fluid dynamics* in which the differences are described as variations in density, viscosity, and a few other constants.

In his exploration of flight, Leonardo made many accurate statements about the mechanics of physical processes. For example, he understood that the dynamics of air moving around a stationary bird and the movement of a bird through stationary air were identical. He wrote in the Codex Atlanticus, "As it is to move the object against the motionless air, so it is to move the air against the motionless object," and "The same force as is made by an object against the air, is made by the air against an object."[3] This now fundamentally obvious truth was by no means obvious in the early 1500s.

Thus, Leonardo appreciated that it was the *movement* of the air that was critical to bird flight, regardless of whether the bird moved through the air or the air moved over the bird. From his studies of water, Leonardo realized that air also has a tendency to swirl in complex patterns or vortices. Today, the cutting edge of animal flight science is focused on testing hypotheses about the nature of the vortices created by the movements of the wings (see Note below).

Likewise, in the Codex on the Flight of Birds, Leonardo lucidly describes the concept of inertia, or momentum. Of a turning bird, he writes, "every movement tends to maintain itself, or rather every body that is moved continues to move so long as the impression of the force of its mover is retained in it...."[4] It would be 180 years until Isaac Newton would articulate this same idea again, in his First Law of Motion.

Applying his graphical genius to the informal sketches of birds in flight that populate the margins of the Turin Codex, Leonardo became the first artist to use lines to depict the *invisible* movements of air around the bird and over the surfaces of the wings (fig. 37). While it is unlikely that he fully appreciated the intellectual power of this tool, Leonardo's use of lines to depict graphical forces presaged an entire field of mathematics based on *vectors*—quantities that express both magnitude and direction. We still use vector fields to describe and analyze the movement of air around the bird during flight, in a way that would have been instantly comprehended by Leonardo.

Leonardo was an excellent natural historian and observer of birds in the wild. Although he remained focused on the physical mechanisms of flight, he reported observations of various specific species, from the ubiquitous Black kite *(Milvus migrans)* to larks and the common European goldfinch *(Carduelis carduelis)*, bats, dragonflies, and butterflies. Leonardo appreciated well that different birds were flying in different ways at different times, and that variations in flight styles were related to the size and shape of the wings, and the size of the bird. In the Turin Codex he writes,

> The kite and other birds that beat their wings only a little, go in search of the current of the wind.... When there is no wind stirring in the air then the kite beats its wing more rapidly in its flight, in such a way that it rises to a height and acquires an impetus; with which impetus, dropping then very gradually, it can travel for a great distance without moving its wings.[5]

We now appreciate that many raptors use this method of flapping, thermal soaring, and gliding to accomplish annual intercontinental migrations—between Canada and Argentina, or Siberia and South Africa—exerting a minimum of energy.

Two of the four sections of the Codex are dedicated to explorations of flight under two different conditions: "The first [section] treats [bird] flight by the beating of their wings; the second of flight without the beating of the wings, and with the help of the wind."[6] In this fashion, Leonardo's lucid conception of the problem exactly parallels our introduction above; it is fundamentally easier to understand the motionless bird flying in moving air before conceptualizing the full complexity of flapping flight. Although Leonardo appears to address these in reverse order, we should remember that the Codex was a personal notebook in which, over many years, he explored various questions and issues that inspired him. It was not a formal presentation of an argument.

FIGURE 37 Cat. 12, folio 6 recto, Birds in flight using lines to depict airflow [DETAIL]

Leonardo explicitly describes the physical forces created by a bird's wings in the air. He comes very close to an accurate description of the variation in air pressure around the flying bird, but falls short of our modern conception of the mechanism producing these pressure differences. Leonardo reasons that the bird created its aerodynamic forces by lifting itself on the compressed air below the wing into the rarified air created above the wing by the same movement. He writes,

> When the bird desires to rise by beating its wings, it raises its shoulders and beats the tip of the wings towards itself, and comes to condense the air which is interposed between the points of the wings and the breast of the bird, and the pressure from this air raises it up a little.[7]

Elsewhere, Leonardo expresses a slightly but crucially different view that is much closer to our current understanding. In describing flapping bird flight, Leonardo writes in Paris Manuscript E,

> What quality of air surrounds the birds as they fly? The air surrounding birds is thinner above than the ordinary thinness of the other air, as it is accordingly thicker below. And it is as much thinner behind than above, accordingly as the movement of the bird is faster in the forward direction than in comparison to the direction of the wings toward the ground.[8]

If thinness and thickness are interpreted as variations in pressure, then Leonardo's description comes close to our modern understanding of differential pressure and dynamic vortices around the flying bird.[9] Although Leonardo did not conceive of the separate components of static and dynamic air pressures, he accurately perceived that pressure asymmetries were critical to producing aerodynamic forces, and that the flying bird would leave a wake, or vortex of movement, in the air behind it.

Leonardo correctly reasons that pressure differentials on the upper and lower surfaces of the wing are fundamental to creating lift, but his model conflicts with our current view on the source of this differential pressure. Leonardo expresses the thought in the quote above that the wing pushes down to compress the air below it, whereas we now understand that it is the differential speed of air over the convex and concave surfaces of the wing that produces the forces of lift and thrust.

Leonardo made other accurate observations about the mechanics of the flight stroke. In Paris Manuscript E he writes, "Birds raise their opened wings with greater facility than they lower them."[10] He clearly understands that the downstroke is the power stroke and requires more exertion than the upstroke. He also attributes the difference in exertion in part to the differences in flow over concave and convex surfaces of the wings,

> …because the wing is convex on top and concave below, so that the air can more conveniently escape from the percussion of the wings in their rising than in their lowering, where in the air included within the concavity tends to become more condensed than to escape.[11]

Here Leonardo thinks deeply about the aerodynamic consequences of the asymmetry in wing shape, where the genuine solution to the conundrum of avian flight is found. But Leonardo saw the differences in the energy required for the downstroke and the upstroke as constraints on the possible movements of the wing, rather than as functional properties that are the actual sources of the forces that make avian flight possible.

Given his pioneering exploration of hydrodynamics, which so closely anticipates Bernoulli, and his musing on the physical consequences of the asymmetry in wing profile shape, I feel certain that Leonardo da Vinci would have loved our elegant, modern explanation of bird flight, and that likely he would have cursed himself for not having figured it out himself!

Leonardo dedicates much of the Turin Codex to discussions of the maneuverability of birds in flight. In anticipation of the Wright brothers' single greatest contribution to achieving human flight, Leonardo realizes that maintaining control in flight would be as demanding as becoming airborne in the first place. He characteristically frames the question of aerodynamic control in terms that are still applicable today. For example, he identifies and differentiates between the "center of gravity" of the bird and the "center of resistance" (fig. 34). Leonardo realizes that each of the forces acting on the bird is localized at specific points, and that these loci are not necessarily coincident. Thus, the center of gravity, center of drag, center of lift, and center of thrust may be at different points depending on the shape and movement of the bird (fig. 34). Leonardo then accurately describes how a bird can turn in flight by manipulating its wings to alter the relationship between the center of gravity and the center of lift.

Leonardo conceived of the bird as flying "above the wind" or "below the wind," which we would now describe as the angle of attack, that is, the angle between the direction of air flow and the position of the wing (fig. 35b). Based on remarkably detailed observations of the flight of raptors, especially the Black kite, Leonardo describes many scenarios for the appropriate wing and tail movements to achieve stabilizing adjustments in response to various changes in wind conditions, angle of attack, and direction of flight.

LEONARDO AS BIOLOGIST

Many fields of endeavor can rightly claim Leonardo as a pioneer, or even as their founding member. These include Western painting, drawing, and sculpture, and human anatomy, physiology, physics, and engineering, among others. An explicitly biological analysis of the Turin Codex provides substantial evidence for adding yet another entire discipline to the list. But which discipline is this? Today Leonardo's research would be considered interdisciplinary, but it includes elements of what we now call *functional morphology* and, of course, *ornithology*. Leonardo was the first, or among the very first, to make testable scientific statements about bird biology and bird flight, indeed maybe all of avian biology, that are still considered to be scientific facts today.

A complete biomechanical analysis of Leonardo's notebooks on animal flight would explore many more topics than we can cover here. These would include detailed analyses of the numerous scenarios he outlined for rising, falling, and turning in various directions relative to the wind; of his comments on the properties and functions of feathers; and of his thoughts on the functions of the tail and its variations in shape.

Why haven't Leonardo's contributions to ornithology been better appreciated? Sadly, it is attributable to Leonardo's lamentable failings in another fundamental aspect of the mission of science—dissemination. Leonardo published none of his observations on flight or on any other scientific topic. Written in private notebooks in mirrored script, Leonardo made no effort to share his observations with others who might understand and follow up on them. This failure prevented him from creating any real intellectual impact on Renaissance concepts in biology. We *can* see that Leonardo did think about a future public audience. One section of the Codex is entitled "Arguments against the Skeptics." Here he seems to be mustering his arguments for some ultimate presentation, possibly in an attempt to gain funding for construction of his experimental flying devices.

Leonardo's brilliant, if private, contributions to biology constitute a remarkable example of a phenomenon that remains highly relevant to intellectual progress today. Although he had vibrant connections with many of the most important scholars of his day, Leonardo's lack of traditional, formal education facilitated his freewheeling intellectual style. Unconstrained by the highly inaccurate views of the classicists such as Aristotle, Leonardo broke free from a conservative, stultifying, and unproductive intellectual tradition. His achievements demonstrate that education can be a prison as well as a liberation—a dilemma facing all educators, especially those at the university level. Modern students must be familiar enough with the current intellectual world to make new contributions but also to be creative enough to imagine genuinely new paradigms, methods, and solutions to intellectual and practical problems.

NOTE: Five hundred years after Leonardo, the study of animal flight is still an extremely active field that is being revolutionized by new technologies, new data, and new paradigms. In the last five years, the world's top general science journals—including *Science, Nature,* and the *Proceedings of the U. S. National Academy of Sciences*—have published numerous articles on the physics, functional morphology, physiology, and evolution of animal flight.

For example, scientists are now able to "image" the complex vortices of air movement created by birds flying. For example, Douglas Warrick of Oregon State University, Bret Tobalske of University of Portland, and their colleagues are using digital particle imaging velocimetry (DPIV) with hummingbirds flying in wind tunnels. The DPIV technique uses focused sheets of laser light to analyze the movement of tiny particles floating in the air. These data provide new insights into the vortices birds create in flight and will introduce new precision to our models of flight mechanics and the variations in flight gaits used by various birds at different speeds.

Stephen Gatesy of Brown University, Ken Dial of the University of Montana, and their colleagues are using simultaneous, multi-camera, high-speed video and X-ray movies of birds in flight to resolve new details of the intricacy of avian flight stroke. Researchers have traditionally described flight movements by averaging over multiple flight strokes to minimize measurement errors. New 3D movie data by Gatesy and colleagues, however, reveal that avian flight is so dynamic, variable, and exquisitely controlled by the individual bird that each flight stroke is unique. For example, imagine trying to describe the movement and forces of a boxer or a ballet dancer by averaging over multiple movements. Mohammed Ali's bobbing, feinting, and punching movements would be so individually variable and specialized that the "average" would be nearly meaningless. Birds are in similarly close control of each flight stroke, and able to produce specifically appropriate variations in lift forces to accomplish their fluid flight. Much as nature inspired Leonardo to create engineering solutions, new biomimetic technologies are now at the forefront of technological research in endeavors such as the development of hovering robotic aircraft.

1 Most recently, see Domenico Laurenza, *Leonardo on Flight,* Baltimore: The Johns Hopkins University Press, 2004.

2 See also Frank B. Gill, *Ornithology,* New York: W. H. Freeman, 2007, and John J. Videler, *Avian Flight,* Oxford and New York: Oxford University Press, 2005.

3 Videler 2005, p. 7.

4 Edward MacCurdy, ed., *The Notebooks of Leonardo da Vinci,* New York: Reynal & Hitchcock, 1939, p. 413, 13[12]r. and v.

5 MacCurdy, 1939, p. 404, 6 [5] v.

6 MacCurdy, 1939, p. 403, 4 v.

7 MacCurdy, 1939, p. 404, 6 [5] r.

8 Videler 2005, p. 6.

9 John D. Anderson, *A History of Aerodynamics and Its Impact on Flying Machines,* Cambridge and New York: Cambridge University Press, 1997, pp. 21–27, and Videler 2005, pp. 6, 7.

10 Venerella 2002, p. 81, 39r.

11 Venerella 2002, p. 81, 39r.